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Author(s): Philip A. Stephens, Chris Carbone, Ian L. Boyd, John M. McNamara, Karin C. Harding, and Alasdair I. Houston

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The Scaling of Diving Time Budgets: Insights from an Optimality Approach

Philip A. Stephens,^{1,*} Chris Carbone,^{2,†} Ian L. Boyd,^{3,‡} John M. McNamara,^{1,§} Karin C. Harding,^{4,||} and Alasdair I. Houston^{5,#}

1. Department of Mathematics, University of Bristol, University Walk, Bristol BS8 1TW, United Kingdom;

2. Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, United Kingdom;

3. Sea Mammal Research Unit, Gatty Marine Laboratory, University of St. Andrews, St. Andrews, Fife KY16 8LB, United Kingdom;

4. Department of Marine Ecology, Göteborg University, Box 461, 405 30 Göteborg, Sweden;

5. School of Biological Science, University of Bristol, Woodland Road, Bristol BS8 1UG, United Kingdom

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ABSTRACT: Simple scaling arguments suggest that, among air-breathing divers, dive duration should scale approximately with mass to the one-third power. Recent phylogenetic analyses appear to confirm this. The same analyses showed that duration of time spent at the surface between dives has scaling very similar to that of dive duration, with the result that the ratio of dive duration to surface pause duration is approximately mass invariant. This finding runs counter to other arguments found in the diving literature that suggest that surface pause duration should scale more positively with mass, leading to a negative scaling of the dive-pause ratio. We use a published model of optimal time allocation in the dive cycle to show that optimal decisions can predict approximate mass invariance in the dive-pause ratio, especially if metabolism scales approximately with mass to the two-thirds power (as indicated by some recent analyses) and oxygen uptake is assumed to have evolved to supply

the body tissues at the required rate. However, emergent scaling rules are sensitive to input parameters, especially to the relationship between the scaling of metabolism and oxygen uptake rate at the surface. Our results illustrate the utility of an optimality approach for developing predictions and identifying key areas for empirical research on the allometry of diving behavior.

Keywords: allometry, diving physiology, marginal value theorem, metabolic scaling, optimal foraging, symmorphosis.

Species that forage underwater but are constrained to breathe at the surface exhibit a range of striking behavioral and physiological adaptations to their way of life (Boyd 1997; Kooyman and Ponganis 1997). In spite of the variety of adaptations that exists, the constraints imposed by foraging underwater are powerful selective forces, leading to a high degree of convergence in aspects of physiological performance (Halsey et al. 2006a). Understanding the limits imposed by this environment is crucial for applications as diverse as explaining breeding strategies (Houston et al. 2007), determining the energetic viability of species in changing marine environments (Winship et al. 2002), and understanding the evolution of brain size among marine mammals (Marino et al. 2006). One approach to determining the constraints imposed on breath-hold divers by their lifestyle is to examine cross-taxa relationships between diving performance and body size.

A recent phylogenetically informed analysis of dive parameters in birds and mammals used data on 195 species, with masses spanning six orders of magnitude, to show that dive depth, dive duration, and surface duration all scaled positively to the one-third power of body mass; furthermore, these relationships were consistent across most taxonomic groups of diving birds and mammals (Halsey et al. 2006b). The scaling of dive duration is consistent with the oxygen store/usage hypothesis (Butler and Jones 1982). This is because, at least in some studies, metabolic rate scales to the two-thirds power of mass (Bennett and Harvey 1987; White and Seymour 2003; McKechnie and Wolf 2004), but the ability to store oxygen is generally believed to increase in proportion to mass (Lasiewski and

* Corresponding author. Present address: School of Biological and Biomedical Sciences, Durham University, South Road, Durham DH1 3LE, United Kingdom; e-mail: philip.stephens@durham.ac.uk.

† E-mail: chris.carbone@ioz.ac.uk.

‡ E-mail: ilb@st-andrews.ac.uk.

§ E-mail: john.mcnamara@bristol.ac.uk.

|| E-mail: karin.harding@swipnet.se.

E-mail: a.i.houston@bristol.ac.uk.

Calder 1971). Therefore, dive duration should increase with mass to the one-third power (assuming, implicitly, that the fraction of potential oxygen stores used during typical dives is constant across species).

Halsey et al. (2006*b*) also found that duration of time spent at the surface between dives scaled with mass to the one-third power, such that the ratio of time spent underwater to that spent at the surface (the dive-pause ratio; Dewar 1924) appeared approximately mass invariant. This result is less readily explained. Indeed, Halsey et al. (2006*b*) summarized arguments prevalent in the diving literature, suggesting that surface duration would increase with body mass more rapidly than dive duration, leading to a negative relationship between dive-pause ratio and body mass. Although these arguments are superficially compelling, they are based on simplistic assumptions regarding the scaling of oxygen uptake with mass (see further below). By contrast, past theoretical and experimental research on diving behavior implies that, in addition to the importance of oxygen stores and average metabolic rate, diving time budgets are affected by rates of oxygen uptake and specific rates of oxygen use at different stages in the dive cycle (Houston and Carbone 1992; Carbone and Houston 1994). One outcome of those findings is that diving time budgets are unlikely to be easily explained on the basis of simple arguments.

In this article, we develop an analysis to explore how diving time budgets are related to body mass. Our analysis is based on an optimal diving model (Houston and Carbone 1992) and observed diving depths (Halsey et al. 2006*a*, 2006*b*). We use this approach to assess variation in diving time budgets and, in particular, the relationship between the dive-pause ratio and the body mass of air-breathing divers. The model is a simple representation of the allocation of time during the dive cycle, based on the assumption that oxygen consumption over the whole cycle is balanced by oxygen intake while at the surface. This generally assumes aerobic diving, an assumption that is well supported for the majority of dives (Kooyman 1966; Kooyman et al. 1983; Butler 2006; Green et al. 2007; but see, e.g., Carbone and Houston 1996; Mori 1999 for consideration of divers performing anaerobically). It is assumed that a diver will maximize its fitness by maximizing the proportion of its time during the dive cycle that is spent foraging. By considering plausible allometric relationships for the model's main parameters, we are able to assess the implications of optimal diving behavior for the dive-pause ratio.

Methods

We begin by outlining the basic structure of the model, before going on to describe plausible scaling relationships

for its underlying parameters. For further details of the model, see Houston and Carbone (1992).

Model Outline

Dives are assumed to be of the "square" type, composed of descent, a relatively horizontal foraging phase, and ascent; square dives account for the vast majority of observed dives in a wide range of taxa (Schreer et al. 2001). The complete dive cycle is divided into three components: τ is the time spent traveling between the surface and the foraging stratum and back again, t is the time spent foraging, and s is the time spent at the surface. It is assumed that the oxygen used during these three periods depends on the different rates (per unit time) of metabolic oxygen consumption, m_1 , m_2 , and m_3 , respectively.

During time at the surface, it is assumed that oxygen concentration in the tissues increases but that it does so at a rate that is proportional to the difference in oxygen partial pressures between the air and the oxygen storage tissues (Wilson and Quintana 2004). As a result, the rate of replenishment of oxygen stores diminishes with time (Kramer 1988; Parkes et al. 2002; Halsey et al. 2003). From this, it follows that a plausible ordinary differential equation for rate of oxygen store replenishment after time s at the surface is

$$\frac{dx(s)}{ds} = \alpha[K - x(s)].$$

When $x(0) = 0$, this gives the following function to describe the replenishment of oxygen stores (Houston and Carbone 1992):

$$x(s) = K(1 - e^{-\alpha s}), \quad (1)$$

where $x(s)$ is oxygen stores accumulated by a diver that spends time s at the surface (net of the oxygen used while at the surface, m_3s), K is the upper limit to the oxygen that can be stored (i.e., total oxygen storage capacity), and α is the initial rate of oxygen replenishment (as a proportion of K). Over a series of dives, the total oxygen stores gained during surface periods are assumed to balance oxygen use during the dive (Wilson and Quintana 2004), so

$$x(s) = m_1\tau + m_2t$$

and

$$t = \frac{x(s) - m_1\tau}{m_2}. \quad (2)$$

It is assumed that the diver will maximize the proportion of time spent foraging, $t/(t + \tau + s)$, which is equivalent to maximizing

$$\pi = \frac{t}{(s + \tau)}.$$

Using equation (2), we have

$$\pi(s) = \frac{x(s) - m_1\tau}{m_2(s + \tau)}. \tag{3}$$

From the optimality condition, $\pi' = 0$, so

$$x(s) - m_1\tau = x'(s)(s + \tau). \tag{4}$$

Using equation (1), we have an equation for the optimal value of s , termed s^* :

$$K(1 - e^{-\alpha s^*}) - m_1\tau - \alpha K e^{-\alpha s^*}(s^* + \tau) = 0. \tag{5}$$

This equation can be solved numerically to yield s^* , the optimal surface duration, as a function of the equation's other parameters (τ , m_1 , K , and α). Given an estimate for m_2 , values of s^* can be substituted in equation (2), in order to yield estimates of t^* (the period of the dive that is spent foraging). Thus, given certain assumptions about the scaling of the other parameters of equation (5), s^* and t^* can be derived for any diver body mass. Together with an empirical estimate of the scaling of τ (Halsey et al. 2006b), therefore, it is possible to use the optimality model to determine expected allometric relationships for surface duration, total dive duration, and dive-pause ratio.

Allometry of Model Parameters

We are interested in the allometric relationships (for surface duration, dive duration, and dive-pause ratio) that emerge from the model, given assumed relationships about the allometries of underlying parameters. In all our discussions of allometric relationships, we use the notation $p = b_p M^{\beta_p}$, where p is the parameter subject to allometric prediction, b_p is a coefficient, and β_p is the allometric exponent. To determine how s^* and t^* are likely to scale with body mass, we need to know the scaling of other components of equation (5), including τ , m_1 , K , and α , as well as the scaling of m_2 . The principal relationships that we use are summarized in table 1, but, where necessary, we discuss the derivation of those relationships in greater detail.

Scaling of Travel Duration (τ)

No theory currently exists to suggest how travel duration during the dive would be expected to scale with body mass. However, an indication of plausible empirical values and scaling of τ can be inferred from the work of Halsey et al. (2006b). They showed that dive depth among diving birds and mammals varied as $10.5M^{0.389}$ and $3.8M^{0.389}$, respectively. Because we are interested primarily in the scaling of these relationships (rather than the absolute magnitudes), and because we draw on metabolic rate data for marine mammals (see below), we used the empirical relationship for mammals. To convert depths into "commuting" times (sensu Ropert-Coudert et al. 2002) it is necessary to know vertical travel speeds during square dives. Although swim speed scales positively with body mass in many vertebrates (Bainbridge 1958; Brett 1965; Domenici 2001), empirical support for such a relationship among diving birds and mammals is lacking (Williams and Worthy 2002; Sato et al. 2007). Indeed, detailed data

Table 1: Allometry of parameters used to solve equation (5)

Parameter	Description (units)	Relationship with mass	Comments and references
τ	Round-trip travel duration between surface and foraging stratum; excludes time spent foraging (s)	$7.6M^{.39}$	Schreer et al. 2001; Halsey et al. 2006b
m_1, m_2	Metabolic rate while traveling or foraging underwater (W)	$.00065M^{.75}$	Kleiber 1975; Boyd 2002
K	Total oxygen storage capacity (L)	$.00037M^{.87}$	Lavigne et al. 1986
α	Initial proportional rate of oxygen replenishment (s^{-1})	$.00080M^{.68}$	Frappell et al. 2001; White and Seymour 2003
		$.03M$	See text
		$zM^{-.33}$	z was a variable used to yield plausible dive durations for divers of intermediate mass (ca. 150 kg) for any given parameter set
		$zM^{\beta_m - 1.0}$	β_m = metabolic rate exponent; see text

Note: See text for further details.

on species of disparate sizes suggest that, although speeds and dive angles may differ somewhat between species (Watanuki et al. 2006), speeds of descent and ascent are unaffected by size (Butler and Jones 1997; Ropert-Coudert et al. 2002; Beck et al. 2003; Davis et al. 2003), and we assumed an average vertical speed of 1 m s^{-1} (Schreer et al. 2001, p. 146).

Scaling of Metabolic Rates (m_1 , m_2)

The allometry of metabolic rates is very hard to determine with conviction (Glazier 2005), and a wide range of exponents (here termed β_m) is obtained when studies using different methodologies are included (Boyd 2002). Boyd (2002) notes that for predictions of basal metabolic rate (BMR in W), the Kleiber (1975) equation remains useful and is given as $\text{BMR} = 3.39M^{0.75}$. However, data have suggested relationships with very different allometric exponents, varying from $\beta_m = 0.68$ for birds and mammals (Frappell et al. 2001; White and Seymour 2003) to $\beta_m = 0.87$ for phocid seals (Lavigne et al. 1986). Consequently, we examined cases using all three of these possible relationships. Data from 26 studies of field metabolic rates in marine mammals show mean and median energy expenditures in the region of 3.6 and 3.4 times predicted BMR, respectively (Boyd 2002). These probably underestimate metabolic rate during active diving, although to what extent is unclear and depends on the methods by which diving metabolic rate was measured (de Leeuw 1996). As an approximate, baseline estimate of metabolism during a dive, we multiplied all relevant constants by a factor of 3.75 (representing $3.75 \times$ predicted BMR), but we examined model sensitivity to this factor (see below). To obtain the relationships shown in table 1, we converted metabolic rates from watts into liters of O_2 per second, assuming an energy yield from metabolism of $19,670 \text{ J L}^{-1} \text{ O}_2$ (Boyd 2002). In the absence of more detailed information, we assume the same scaling relationships for m_1 and m_2 .

Scaling of Oxygen Storage Capacity (K)

Total oxygen storage capacity is generally believed to scale approximately with mass, and, although some species appear to have exceptionally high oxygen storage capacities (e.g., Weddell seals, *Leptonychotes weddellii*; Ponganis et al. 1993), median values for mass-specific oxygen stores appear to be closer to 40 mL kg^{-1} (Gentry et al. 1986; Butler 2001; McIntyre et al. 2002; Richmond et al. 2006). Oxygen is always required for the central nervous system and heart (Butler 2006). Consequently, the dive lactate threshold (the dive duration at which postdive blood lactate concentration increases, potentially invalidating our assumption of

oxygen balance over the dive cycle) will be reached before oxygen stores are completely exhausted (Butler and Jones 1997). Because little is known about the proportion of oxygen stores that can be used before equation (1) is invalidated, we assumed a value of 75% (see, e.g., Hudson and Jones 1986), suggesting a figure of 30 mL kg^{-1} for oxygen stores available during diving.

Scaling of the Initial Rate of Oxygen Uptake (α)

The initial rate of oxygen replenishment, α (expressed as a proportion of total available stores, K), depends on the speed of oxygen uptake. Empirical data with which to assess plausible scaling patterns for this parameter are limited (see further in "Discussion"). However, theory suggests two possible scaling relationships for the initial rate of oxygen replenishment. First, ignoring that α is relative to K , oxygen uptake might be expected to be limited by the surface area available for gaseous exchange (implying a scaling exponent of approximately two-thirds). Alternatively, the principle of symmorphosis (Weibel et al. 1998) has been used to argue that each component of the oxygen supply chain must have evolved to supply oxygen at the rate required by the muscles (Taylor and Weibel 1981); consequently, we might expect oxygen uptake to scale with the same exponent as metabolism (see above). As α is a rate proportional to K (which scales with $M^{1.0}$), α itself is likely to scale with an allometric exponent in the region of $\beta_\alpha = -0.33$ if the surface area argument holds or $\beta_\alpha = \beta_m - 1$ if symmorphosis holds.

Results

The allometric relationships shown in table 1 yielded six possible parameter sets: the three metabolic rate relationships with $\alpha \propto M^{-0.33}$ and the three metabolic rate relationships with $\alpha \propto M^{\beta_m - 1}$ (where β_m is the exponent for the scaling of metabolism). For each set of relationships and for body masses ranging from 10 to over 1,250 kg, we determined surface durations that would maximize time available for foraging during the dive cycle. The consequences of these calculations for the allometry of dive parameters are summarized in table 2.

All of the parameter sets summarized in table 2 suggest negative scaling of the dive-pause ratio with mass. However, there was considerable variation among sets, with lower values of β_m typically leading to mass exponents of the dive-pause ratio that were closer to 0. Unsurprisingly, given the similarity of input parameters, sets 3 and 6 gave very similar results. Both suggested that dive duration and surface duration could scale with mass to exponents in the region of one-third and, consequently, dive-pause ratios that varied with mass to a very low exponent (-0.03

Table 2: Allometry of input and emergent dive parameters in the optimal diving model

Parameter set	Underlying allometries		Emergent allometries		
	m_1, m_2	α	Dive duration ($t + \tau$)	Surface duration (s)	Dive-pause ratio ($(t + \tau)/s$)
1	$.00065M^{-.75}$	$.090M^{-.33}$	$32.94M^{.28}$	$13.38M^{.40}$	$2.46M^{-.12}$
2	$.00037M^{.87}$	$.080M^{-.33}$	$52.09M^{.18}$	$11.49M^{.45}$	$4.53M^{-.28}$
3	$.00080M^{.68}$	$.075M^{-.33}$	$27.04M^{.34}$	$16.82M^{.37}$	$1.61M^{-.03}$
4	$.00065M^{-.75}$	$.060M^{-.25}$	$31.72M^{.28}$	$18.34M^{.34}$	$1.73M^{-.05}$
5	$.00037M^{.87}$	$.040M^{-.13}$	$49.95M^{.19}$	$20.31M^{.29}$	$2.45M^{-.10}$
6	$.00080M^{.68}$	$.075M^{-.32}$	$27.07M^{.34}$	$16.84M^{.36}$	$1.61M^{-.02}$
Relationships from table 2 of Halsey et al. 2006b			$21.20M^{.37}$	$18.80M^{.33}$	$1.80M^{.04}$

and -0.02 , respectively). Because the outcomes of these parameter sets matched empirical observation most closely, and because the two sets were highly similar, we used parameter set 6 for further illustration. For dive duration and surface duration, the relationships emerging from parameter set 6 are illustrated in figure 1.

In addition to the allometric exponents explaining variation in metabolism and α with body size, it is important to examine model sensitivity to a number of other parameters. Using parameter set 6, we varied each remaining parameter independently, observing the consequences for the three emergent allometric exponents (fig. 2). As expected, none of the coefficients had a strong effect on emergent allometries within the ranges examined. The only substantially nonlinear effects of varying a coefficient resulted when the coefficient of oxygen stores, b_K , was reduced to a low level. However, as stated above, such low levels of usable oxygen are not well supported by empirical data. The effects of varying allometric exponents were more pronounced (fig. 2E, 2F). Scaling of the component of dive duration that is spent traveling (τ) is difficult to determine, and here we have based our estimates on the scaling of dive depth. Given the sensitivity of outcomes to this (fig. 2E), further work might usefully examine the scaling of transit times more accurately. Outcomes were especially sensitive to β_K , the exponent determining how oxygen stores scale with mass (fig. 2F). Although oxygen stores are generally believed to scale proportionally with mass, there is some evidence for diving animals having exponents greater than unity (i.e., $\beta_K > 1.0$; Hudson and Jones 1986). A relatively small increase (ca. 5%) in β_K could lead to emergent exponents using parameter set 6 that match much more closely those found by Halsey et al. (2006b).

Discussion

In this article, we have shown that an optimal foraging model can be used to refine predictions, identifying de-

ficiencies in our understanding of diving behavior and the scaling of diving time budgets. Optimality models have previously been used to provide insights into the scaling of diving behavior. In particular, Mori (2002) incorporated both aerobic and anaerobic processes and considered optimal depth in one of his models; however, a systematic exploration of the allometric relationships that are generated by optimal diving was not conducted. We suggest that combining optimality models with available empirical data, as we have done, represents a potentially productive means to understand the allometry of many other behav-

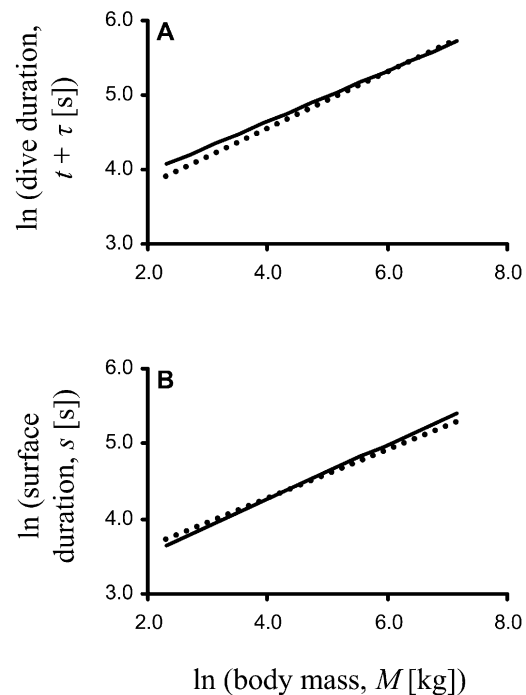


Figure 1: Allometry of dive parameters emerging from model 6 (see table 2; solid lines) and determined by Halsey et al. (2006b; dotted lines): (A) dive duration and (B) surface duration, both as a function of body mass.

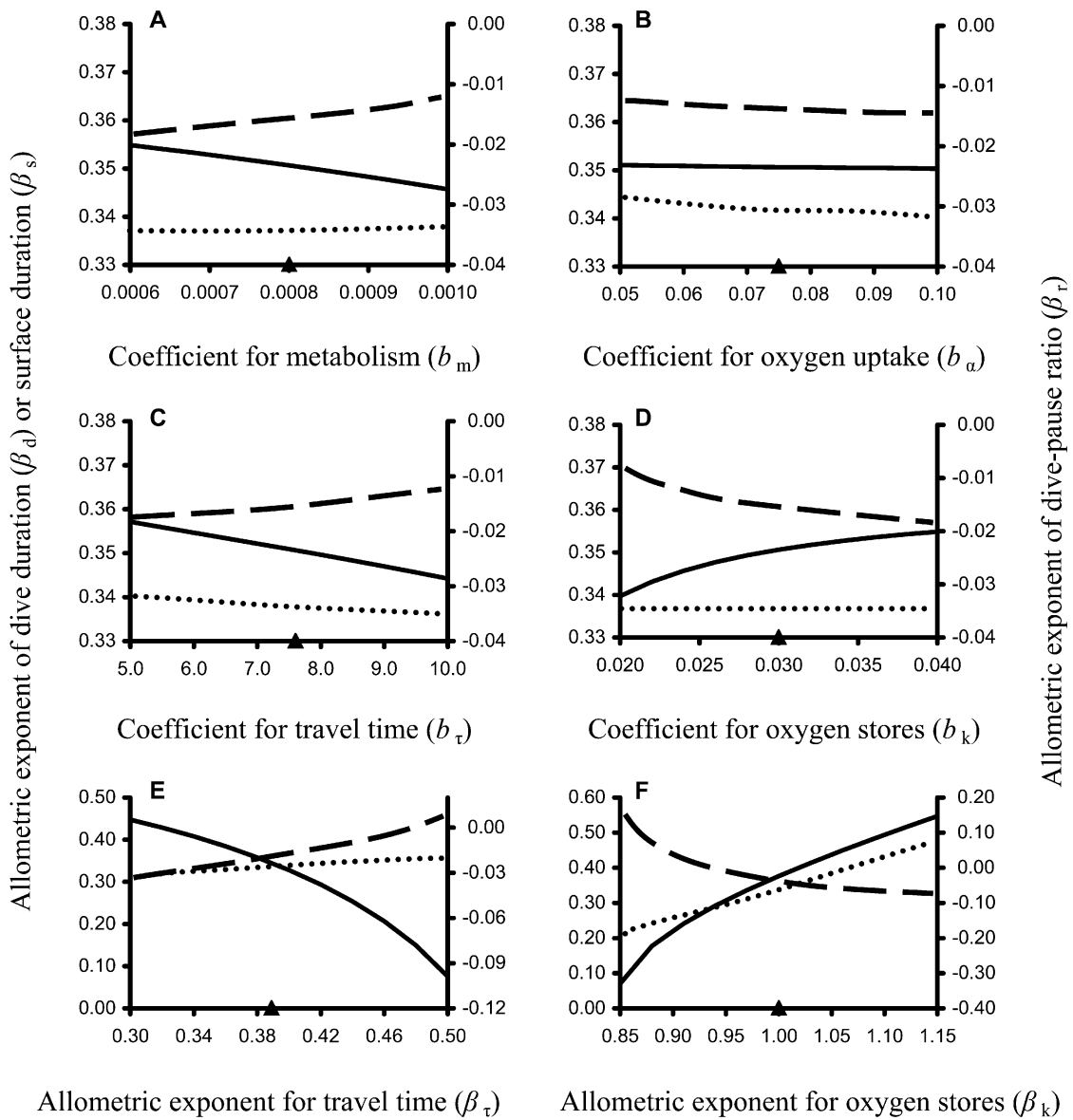


Figure 2: Sensitivity of parameter set 6 to variation in individual parameters. All panels show emergent allometric exponents of dive duration (dotted lines, left-hand Y-axes), surface duration (dashed lines, left-hand Y-axes), and dive-pause ratio (solid lines, right-hand Y-axes). Each of the key parameters in equation (5) is predicted by a relationship of the form $p = b_p M^{\beta_p}$, where p is the parameter, b_p is a coefficient, and β_p is the allometric exponent. Results of specific scenarios for the allometric exponents of metabolism (β_m) and oxygen uptake (β_a) are shown in table 2. Here we focus on sensitivity to (A) coefficient of metabolism (b_m), (B) coefficient of oxygen uptake (b_a), (C) coefficient of travel time (b_τ), (D) coefficient of oxygen stores (b_k), (E) allometric exponent of travel time (β_τ), and (F) allometric exponent of oxygen stores (β_k). All other parameters are estimated as indicated for parameter set 6 in table 2. In each panel, these standard parameter values are indicated by the triangle. Note that in A, the range of b_m illustrated is equivalent to in-water metabolism varying from $1 \times \text{BMR}$ to $2 \times \text{BMR}$. In E, the range of β_τ illustrated is approximately equivalent to 1 SE either side of the mean value reported by Halsey et al. (2006b).

ioral traits. Using allometric relationships (with empirical and theoretic support) for dive depth and physiological parameters, we have shown that it is possible to explain the approximate mass invariance of dive-pause ratios among breath-hold divers. Our results are sensitive to the

allometric exponents of all input parameters, however, suggesting that those exponents would need to be determined with conviction before the insights gained can be treated with complete confidence.

Our results are broadly consistent with the oxygen store/

usage hypothesis (Butler and Jones 1982), but departures from the expectations of that hypothesis (that dive duration should scale with an exponent of $1 - \beta_m$) become more marked when metabolism scales more steeply (i.e., β_m increases). The allometric exponent for the dive-pause ratio, β_r , was also closer to mass invariance for lower values of β_m , particularly where the initial rate of oxygen uptake was modeled as scaling with mass to the power $\beta_m - 1$ (which might be expected on the basis of symmorphosis). For the six parameter sets examined, β_r did not approach the low positive value determined by Halsey et al. (2006b). This discrepancy could be attributed to uncertainty in the input parameters (see fig. 2F in particular). In reality, however, even a highly approximate match between theory and empirical data is surprising, given the variation inherent in the empirical data set. For example, the data set must include divers with dive patterns other than the square dives of Schreer et al. (2001), as well as single-prey loaders (Thompson and Fedak 2001), lunge feeders (Goldbogen et al. 2006), species with an additional component of aerial travel after surfacing (Falk et al. 2002), and, potentially, data recorded during periods of anaerobic activity. This type of inherent variation suggests that pursuing an exact match between theory and data with a model based on a single diving strategy (constant-rate, pelagic foragers diving aerobically) is unlikely to yield success.

As we noted at the outset, Halsey et al. (2006b) developed simple arguments to suggest that dive-pause ratios would be expected to decrease with increasing mass. It is worth considering their argument in greater detail. Specifically, Halsey et al. reasoned that dive duration would scale positively with mass because K scales with $\beta_k = 1.0$, while metabolism scales with $\beta_m < 1.0$. Thus, potential dive duration scales with $\beta_k - \beta_m > 0$. They further suggested that longer dive durations among larger-bodied divers would lead to greater absolute oxygen use and, owing to diminishing returns in restoring depleted oxygen reserves (Kramer 1988; Houston and Carbone 1992), exponentially longer surface durations. Although it is likely that Halsey et al.'s (2006b) argument holds when considering longer dives among animals of equal body mass, it is not clear why it should apply to longer dives among animals of greater body mass. In particular, it assumes that oxygen uptake ability does not scale with mass, so that the time taken to restore some absolute volume of oxygen reserves is the same in two divers of different size.

In contrast to Halsey et al. (2006b), we have shown that the scaling of surface duration (and consequent scaling of the dive-pause ratio) is critically dependent on the scaling of α , the initial proportional rate of oxygen replenishment. Consider, for example, the case where all divers use some fixed proportion (θ) of their oxygen reserves during a dive. In this case, we can rewrite equation (1) as

$$\theta K = K(1 - e^{-\alpha s}),$$

so

$$s = \frac{-\ln(1 - \theta)}{\alpha},$$

suggesting that surface duration should scale with $-\beta_\alpha$ (the allometric exponent for the initial rate of oxygen replenishment). This suggests that where maximum oxygen uptake is sufficient to meet the demands of metabolism (i.e., α scales with $\beta_\alpha = \beta_m - 1$; see "Methods"), surface duration should scale with $1 - \beta_m$. Given that this is the same as the scaling of dive duration (see above), then this simple argument, based on the use of a constant proportion of oxygen stores regardless of body mass, does predict a mass-invariant dive-pause ratio. As we showed (table 2), the optimal dive model does not always predict the same outcomes as these simple arguments. In particular, the proportional use of oxygen reserves, θ (and consequent surface duration), is sensitive to the metabolic rate mass exponent (β_m), suggesting that approximate mass invariance of dive-pause ratios will be observed only when β_m is toward the low end of its suggested range (i.e., around 0.6–0.7; fig. 3). This illustrates two important points. First, it appears that a mass-invariant dive-pause ratio depends on approximate mass invariance in θ , the proportion of oxygen storage potential that is used in a dive. Second, although there is no a priori reason to assume that θ should be mass invariant, for metabolic exponents in the region of 0.6–0.7, the optimality model does suggest that this would be approximately the case.

The findings of our model depend critically on input parameters, and, consequently, data limitations are important. Among the input parameters, perhaps the most weakly supported are those that model the scaling of α , the initial rate of oxygen uptake (net of oxygen use at the surface). There have been relatively few attempts to measure this rate (but see Parkes et al. 2002; Halsey et al. 2003), and, certainly, too few data exist to determine the broad-scale allometric relationships necessary for our purposes here. Assessing data from individual studies carries the risk of focusing on the idiosyncrasies of a small number of species, rather than appreciating the broad, cross-taxa patterns necessary for allometric prediction. Moreover, it would be difficult to determine oxygen uptake and storage parameters applicable to the model from studies that use variable dive durations, as implied parameters depend on the degree to which oxygen stores have been depleted by the preceding dive (see Halsey et al. 2003, fig. 4).

Our work suggests some important avenues for further research. In particular, we have developed a framework for pelagic, constant-rate foragers. It should be possible

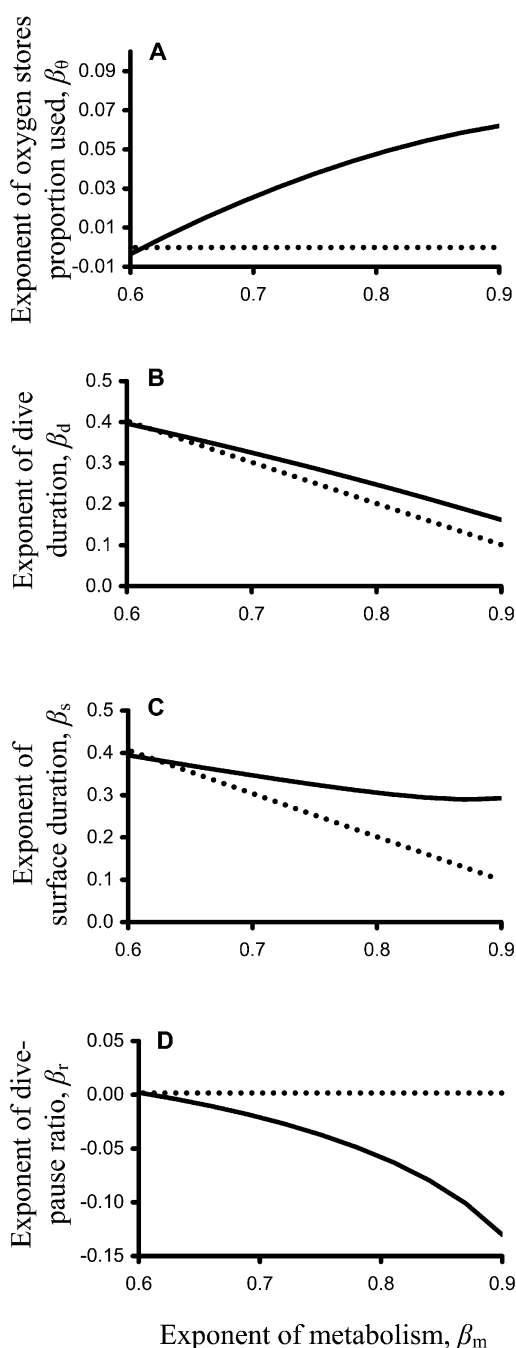


Figure 3: Comparison between predictions of simple scaling arguments (*dotted lines*) and emergent predictions of the optimal diving model (*solid lines*). The simple scaling arguments are based on the assumption that (A) proportional use of oxygen stores does not vary with body mass, and they predict that both (B) dive duration and (C) surface duration will scale with $1 - \beta_m$, while (D) dive-pause ratio remains mass invariant. By contrast, the optimality model suggests that proportional use of oxygen stores will be sensitive to the scaling of metabolic rate, so that the dive-pause ratio will be close to mass invariance only when the metabolic mass exponent is low (in the region of $0.6 \leq \beta_m \leq 0.7$).

to modify this type of framework for benthic feeders, as well as single-prey loaders or lunge feeders, in order to determine whether those activities give rise to similar emergent allometries. More intriguingly, we have been constrained to using empirical data on travel distance in our model. Clearly, dive depth (and hence travel time) among benthic foragers is dictated by the water depth. However, for pelagic species, it remains unclear why larger species often dive so deeply. Mori (1998, 2002) showed that where food is normally distributed with depth, larger divers are expected to dive closer to the depth of maximal food availability. Moreover, when food is abundant in relatively shallow waters, the efficiency of smaller divers may be greater than that of larger divers; this will select for smaller size in areas where food is exploited in shallow waters (Mori 2002). Nevertheless, many large divers dive to such depths that they must pass through some of the most productive parts of the ocean. It is possible that theoretical models could yet shed additional light on the scaling of dive depth with size. For example, simple geometric models of the scaling of day range in terrestrial mammals (Garland 1983; Carbone et al. 2005) illustrate the importance of the scaling of food items taken in relation to consumer mass and the density of those items. Future research could fruitfully consider whether these parameters are also associated with the scaling of dive depth among breath-hold divers. Finally, agreement between empirical estimates of the scaling of the dive-pause ratio and those emerging from the model appears to depend on mass invariance in the proportion of potential oxygen stores used during typical dives. Whether this requirement is supported by empirical data will have important implications for our understanding of diving behavior.

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Literature Cited

- Bainbridge, R. 1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *Journal of Experimental Biology* 35:109–133.
- Beck, C. A., W. D. Bowen, J. I. McMillan, and S. J. Iverson. 2003. Sex differences in the diving behaviour of a size-dimorphic capital breeder: the grey seal. *Animal Behaviour* 66:777–789.
- Bennett, P. M., and P. H. Harvey. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. *Journal of Zoology (London)* 213:327–363.
- Boyd, I. L. 1997. The behavioural and physiological ecology of diving. *Trends in Ecology & Evolution* 12:213–217.

- . 2002. Energetics: consequences for fitness. Pages 247–277 in A. R. Hoelzel, ed. *Marine mammal biology*. Blackwell Science, Oxford.
- Brett, J. R. 1965. Relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* 22:1491–1501.
- Butler, P. J. 2001. Diving beyond the limits. *News in Physiological Sciences* 16:222–227.
- . 2006. Aerobic dive limit: what is it and is it always used appropriately? *Comparative Biochemistry and Physiology A* 145: 1–6.
- Butler, P. J., and D. R. Jones. 1982. The comparative physiology of diving in vertebrates. *Advances in Comparative Physiology and Biochemistry* 8:179–364.
- . 1997. Physiology of diving of birds and mammals. *Physiological Reviews* 77:837–899.
- Carbone, C., and A. I. Houston. 1994. Patterns in the diving behavior of the pochard, *Aythya farina*: a test of an optimality model. *Animal Behaviour* 48:457–465.
- . 1996. The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Animal Behaviour* 51:1247–1255.
- Carbone, C., G. Cowlshaw, N. J. B. Isaac, and J. M. Rowcliffe. 2005. How far do animals go? determinants of day range in mammals. *American Naturalist* 165:290–297.
- Davis, R. W., L. A. Fuiman, T. M. Williams, M. Horning, and W. Hagey. 2003. Classification of Weddell seal dives based on 3-dimensional movements and video-recorded observations. *Marine Ecology Progress Series* 264:109–122.
- de Leeuw, J. J. 1996. Diving costs as a component of daily energy budgets of aquatic birds and mammals: generalizing the inclusion of dive-recovery costs demonstrated in tufted ducks. *Canadian Journal of Zoology* 74:2131–2142.
- Dewar, J. M. 1924. *The bird as a diver*. Witherby, London.
- Domenici, P. 2001. The scaling of locomotor performance in predator-prey encounters: from fish to killer whales. *Comparative Biochemistry and Physiology A* 131:169–182.
- Falk, K., S. Benvenuti, L. Dall'Antonia, G. Gilchrist, and K. Kampp. 2002. Foraging behaviour of thick-billed murres breeding in different sectors of the North Water polynya: an inter-colony comparison. *Marine Ecology Progress Series* 231:293–302.
- Frappell, P. B., D. S. Hinds, and D. F. Boggs. 2001. Scaling of respiratory variables and the breathing pattern in birds: an allometric and phylogenetic approach. *Physiological and Biochemical Zoology* 74:75–89.
- Garland, T., Jr. 1983. Scaling the ecological cost of transport to body mass in terrestrial mammals. *American Naturalist* 121:571–587.
- Gentry, R. L., D. P. Costa, J. P. Croxall, J. H. M. David, R. W. Davis, G. L. Kooyman, P. Majluf, et al. 1986. Synthesis and conclusions. Pages 220–264 in R. L. Gentry and G. L. Kooyman, eds. *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton, NJ.
- Glazier, D. S. 2005. Beyond the “3/4-power law”: variation in the intra- and interspecific scaling of metabolic rate in animals. *Biological Reviews* 80:611–662.
- Goldbogen, J. A., J. Calambokidis, R. E. Shadwick, E. M. Oleson, M. A. McDonald, and J. A. Hildebrand. 2006. Kinematics of foraging dives and lunge-feeding in fin whales. *Journal of Experimental Biology* 209:1231–1244.
- Green, J. A., L. G. Halsey, P. J. Butler, and R. L. Holder. 2007. Estimating the rate of oxygen consumption during submersion from the heart rate of diving animals. *American Journal of Physiology* 292:R2028–R2038.
- Halsey, L., A. Woakes, and P. Butler. 2003. Testing optimal foraging models for air-breathing divers. *Animal Behaviour* 65:641–653.
- Halsey, L. G., T. M. Blackburn, and P. J. Butler. 2006a. A comparative analysis of the diving behaviour of birds and mammals. *Functional Ecology* 20:889–899.
- Halsey, L. G., P. J. Butler, and T. M. Blackburn. 2006b. A phylogenetic analysis of the allometry of diving. *American Naturalist* 167:276–287.
- Houston, A. I., and C. Carbone. 1992. The optimal allocation of time during the diving cycle. *Behavioral Ecology* 3:255–265.
- Houston, A. I., P. A. Stephens, I. L. Boyd, K. C. Harding, and J. M. McNamara. 2007. Capital or income breeding? a theoretical model of female reproductive strategies. *Behavioral Ecology* 18:241–250.
- Hudson, D. M., and D. R. Jones. 1986. The influence of body-mass on the endurance to restrained submergence in the Pekin duck. *Journal of Experimental Biology* 120:351–367.
- Kleiber, M. 1975. *The fire of life: an introduction to animal energetics*. Krieger, Huntington, NY.
- Kooyman, G. L. 1966. Maximum diving capacities of Weddell seal *Leptonychotes weddelli*. *Science* 151:1553–1564.
- Kooyman, G. L., and P. J. Ponganis. 1997. The challenges of diving to depth. *American Scientist* 85:530–539.
- Kooyman, G. L., M. A. Castellini, R. W. Davis, and R. A. Maué. 1983. Aerobic diving limits of immature Weddell seals. *Journal of Comparative Physiology* 151:171–174.
- Kramer, D. L. 1988. The behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology* 66:89–94.
- Lasiewski, R. C., and W. A. Calder. 1971. Preliminary allometric analysis of respiratory variables in resting birds. *Respiration Physiology* 11:152–166.
- Lavigne, D. M., S. Innes, G. A. J. Worthy, K. M. Kovacs, O. J. Schmitz, and J. P. Hickie. 1986. Metabolic rates of seals and whales. *Canadian Journal of Zoology* 64:279–284.
- Marino, L., D. Sol, K. Toren, and L. Lefebvre. 2006. Does diving limit brain size in cetaceans? *Marine Mammal Science* 22:413–425.
- McIntyre, I. W., K. L. Campbell, and R. A. MacArthur. 2002. Body oxygen stores, aerobic dive limits and diving behaviour of the star-nosed mole (*Condylura cristata*) and comparisons with non-aquatic talpids. *Journal of Experimental Biology* 205:45–54.
- McKechnie, A. E., and B. O. Wolf. 2004. The allometry of avian basal metabolic rate: good predictions need good data. *Physiological and Biochemical Zoology* 77:502–521.
- Mori, Y. 1998. Optimal choice of foraging depth in divers. *Journal of Zoology (London)* 245:279–283.
- . 1999. The optimal allocation of time and respiratory metabolism over the dive cycle. *Behavioral Ecology* 10:155–160.
- . 2002. Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology* 15:269–276.
- Parkes, R., L. G. Halsey, A. J. Woakes, R. L. Holder, and P. J. Butler. 2002. Oxygen uptake during post dive recovery in a diving bird *Aythya fuligula*: implications for optimal foraging models. *Journal of Experimental Biology* 205:3945–3954.
- Ponganis, P. J., G. L. Kooyman, and M. A. Castellini. 1993. Determinants of the aerobic dive limit of Weddell seals: analysis of diving

- metabolic rates, postdive end-tidal Po_2 's, and blood and muscle oxygen stores. *Physiological Zoology* 66:732–749.
- Richmond, J. P., J. M. Burns, and L. D. Rea. 2006. Ontogeny of total body oxygen stores and aerobic dive potential in Steller sea lions (*Eumetopias jubatus*). *Journal of Comparative Physiology B* 176: 535–545.
- Ropert-Coudert, Y., A. Kato, K. Sato, Y. Naito, J. Baudat, C. A. Bost, and Y. Le Maho. 2002. Swim speed of free-ranging Adélie penguins *Pygoscelis adeliae* and its relation to the maximum depth of dives. *Journal of Avian Biology* 33:94–99.
- Sato, K., Y. Watanuki, A. Takahashi, P. J. O. Miller, H. Tanaka, R. Kawabe, P. J. Ponganis, et al. 2007. Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proceedings of the Royal Society B: Biological Sciences* 274:471–477.
- Schreer, J. F., K. M. Kovacs, and R. J. O. Hines. 2001. Comparative diving patterns of pinnipeds and seabirds. *Ecological Monographs* 71:137–162.
- Taylor, C. R., and E. R. Weibel. 1981. Design of the mammalian respiratory system. 1. Problem and strategy. *Respiration Physiology* 44:1–10.
- Thompson, D., and M. A. Fedak. 2001. How long should a dive last? a simple model of foraging decisions by breath-hold divers in a patchy environment. *Animal Behaviour* 61:287–296.
- Watanuki, Y., S. Wanless, M. Harris, J. R. Lovvorn, M. Miyazaki, H. Tanaka, and K. Sato. 2006. Swim speeds and stroke patterns in wing-propelled divers: a comparison among alcids and a penguin. *Journal of Experimental Biology* 209:1217–1230.
- Weibel, E. R., R. C. Taylor, and L. Bolis. 1998. *Principles of animal design*. Cambridge University Press, Cambridge.
- White, C. R., and R. S. Seymour. 2003. Mammalian basal metabolic rate is proportional to body mass^{2/3}. *Proceedings of the National Academy of Sciences of the USA* 100:4046–4049.
- Williams, T. M., and G. A. J. Worthy. 2002. Anatomy and physiology: the challenge of aquatic living. Pages 73–97 in A. R. Hoelzel, ed. *Marine mammal biology*. Blackwell Science, Oxford.
- Wilson, R. P., and F. Quintana. 2004. Surface pauses in relation to dive duration in imperial cormorants: how much time for a breather? *Journal of Experimental Biology* 207:1789–1796.
- Winship, A. J., A. W. Trites, and D. A. S. Rosen. 2002. A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. *Marine Ecology Progress Series* 229:291–312.

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