



# Physiological constraints and dive behavior scale in tandem with body mass in auks: A comparative analysis



A. Shoji <sup>a,\*</sup>, S. Aris-Brosou <sup>b</sup>, K.H. Elliott <sup>c</sup>

<sup>a</sup> Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

<sup>b</sup> Departments of Biology, Mathematics & Statistics, University of Ottawa, Ottawa, ON K1N 6N5, Canada

<sup>c</sup> Department of Natural Resource Sciences, McGill University, Ste Anne de Bellevue, QC H9X 3V9, Canada

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## ABSTRACT

Many behavioral processes scale with body mass ( $M$ ) because underlying physiological constraints, such as metabolism, scale with  $M$ . A classic example is the maximum duration of dives by breath-hold divers, which scales with  $M^{0.25}$ , as predicted from the ratio of oxygen stores ( $M^{1.0}$ ) to diving oxygen consumption rate ( $M^{0.75}$ ) – assuming classic scaling relationships for those physiological processes. However, maximum dive duration in some groups of birds does not have a 0.25 scaling exponent. We re-examined the allometric scaling of maximum dive duration in auks to test whether the discrepancy was due to poor data (earlier analyses included data from many different sources possibly leading to bias), phylogeny (earlier analyses did not account for phylogenetic inertia) or physiology (earlier analyses did not analyze physiological parameters alongside behavioral parameters). When we included only data derived from electronic recorders and after accounting for phylogeny, the equation for maximum dive duration was proportional to  $M^{0.33}$ . At the same time, myoglobin concentration in small breath-hold divers was proportional to  $M^{0.36}$ , implying that muscle oxygen stores were proportional to  $M^{1.36}$ , but diving oxygen consumption rate in wing-propelled divers was only proportional to  $M^{0.79}$ . Thus, the 99% confidence interval included the exponent of 0.57 predicted from the observed relationships between oxygen stores and consumption rates. In conclusion, auks are not exceptions to the hypothesis that a trade-off between oxygen stores and oxygen utilization drives variation in maximum dive duration. Rather, the scaling exponent for maximum dive duration is higher than expected due to the higher than expected scaling of muscle oxygen stores to body mass.

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## 1. Introduction

In diving animals, oxygen stores are generally believed to increase isometrically with body mass ( $M^{1.00}$ ) while oxygen consumption rate is believed to be proportional to basal metabolic rate, which scales to roughly  $M^{0.75}$  (Birt-Friesen et al., 1989; Halsey et al., 2006; Hudson and Jones, 1986; Kooyman, 1989; Lasiewski and Calder, 1971). Therefore, body mass determines much of the capacity to make long breath-hold dives both within and across species (Butler, 1989; Kooyman and Kooyman, 1995) and dive duration across species scales to body mass with an exponent of about 0.25, as would be expected from the ratio of  $M^{1.0}$  to  $M^{0.75}$  (Halsey et al., 2006). Nonetheless, body mass alone does not always explain much of the variance in dive duration across species (Mirceta et al., 2013) and some animals dive longer than expected for their body size (Boyd and Croxall, 1996; Elliott et al., 2008a; Watanuki et al., 1996). Such relationships are apparently particularly weak in seabirds. Three reasons have been put forward to explain the weak relationship in seabirds: (1) dive duration scales to

wing surface area due to conduction of heat to water (Boyd and Croxall, 1996); (2) diving, flying birds, such as cormorants, are among the few exceptions to allometric relationships, likely because of the contrasting constraints of diving and flying (Schreer and Kovacs, 1997); (3) *Procellariiformes* showed a negative relationship between body mass and dive duration because of the contrasting body plans within that order (albatrosses have long wings specialized for soaring flight and make only shallow dives whereas diving petrels with small wings forage primarily by wing-propelled diving and make relatively deep dives; Halsey et al., 2006; Dunphy et al., 2015).

In the context of the allometric relationship between body mass and dive duration, auks represent an oddity among seabirds; being among the smallest marine breath-hold divers, they would be expected to be particularly limited by constraints on oxygen stores and use. Furthermore, auks have a relatively uniform body plan and all auks forage primarily by wing-propelled diving in the marine environment. Therefore, variation in body plan, which explains why dive duration in some other seabirds (i.e. *Procellariiformes*) does not scale positively with body mass, is less likely to play a role in auks. Nonetheless, the scaling exponent in maximum dive duration for auks is higher than the expected 0.25 (~0.7; Watanuki and Burger, 1999). This result is particularly surprising

\* Corresponding author.

E-mail address: [akikosho@gmail.com](mailto:akikosho@gmail.com) (A. Shoji).

because, along with seals, auks have the longest dive duration for a given body mass of any animal (Halsey et al., 2006) and would therefore be expected to be (i) operating near their physiological maximum and (ii) particularly constrained by allometry. Furthermore, a high proportion of dives in auks exceeds their theoretical aerobic dive limit (Elliott et al., 2008b, 2010), which is the time when oxygen stores are theoretically depleted from the body and individuals must switch to costly anaerobic respiration – implying that auks are often working near their physiological maximum. This unexpected result might be due to inaccurate data used in those studies, as they included estimates derived from direct observations of birds under unusual circumstances (such as from shore, where dive duration would likely be short) or radio tracking, which can overestimate dive duration if the signal is faint and therefore missed. There is therefore a need to obtain more information using more accurate electronic time–depth records from the various auk clades.

Instead of being caused by inaccurate data/measurements, the unexpected large scaling exponent might be caused by our poor understanding of the physiological constraints – oxygen consumption and stores – governing these allometric relationships. Indeed, the hypothesis that dive duration should scale to body mass with a 0.25 exponent depends completely on the relationship between body mass and diving oxygen consumption rate and oxygen stores. Those assumptions have seldom been tested, especially within relatively small groups. For instance, it is known that foot-propelled diving seabirds (some ducks, cormorants) have higher oxygen consumption rates during diving than wing-propelled diving seabirds (auks, penguins), and that those rates increase more rapidly with body mass in foot-propelled than wing-propelled divers (Elliott et al., 2013a). At the same time, an analysis of over 30 diving animal species showed that muscle oxygen stores, especially muscle myoglobin content, increase more rapidly with body mass than expected (Fig. 5c in Elliott et al., 2010). Small animals have insufficient space available for high myoglobin content because of the high concentrations of mitochondrial enzymes in the muscle cells needed to power higher mass-specific metabolic rates (Elliott et al., 2010). Thus, one way to explain why dive duration increases more rapidly with body mass than expected in auks (a 0.7 instead of 0.25 exponent) would be if (i) oxygen consumption rate increases with body mass less rapidly than expected and (ii) oxygen stores increase more rapidly than expected. In this case, the steep relationship between dive duration and body mass would not be due to inaccurate measurements but rather represent variation in underlying physiological constraints. Previous attempts to examine the relationship between dive duration and body mass in diving animals either included potentially inaccurate data (e.g. Boyd and Croxall, 1996; Schreer and Kovacs, 1997; Watanuki and Burger, 1999), did not account for phylogeny despite using small, phylogenetically unbalanced sample sizes (e.g. Boyd and Croxall, 1996; Watanuki and Burger, 1999), or did not analyze oxygen stores or consumption rate to test to the underlying assumptions (e.g. Boyd and Croxall, 1996; Schreer and Kovacs, 1997; Watanuki and Burger, 1999; Halsey et al., 2006).

Here, to test whether the high allometric mass exponent of maximum dive duration and dive depth in auks is due to inaccurate data, phylogeny or physiology, we examined the relationship between maximum and average dive duration and body mass (i) within a comparative analysis framework, accounting for phylogeny, (ii) using only data collected from electronic recorders to avoid some of the potential biases present in the earlier work and (iii) alongside allometric relationships for oxygen stores and consumption rates. We thus determined whether those relationships were different from conventional assumptions, potentially explaining the discrepancy in the allometric exponent for dive duration. We focused on myoglobin content as a measure of oxygen stores because a recent analysis showed in mammals showed that myoglobin net charge (closely tied to myoglobin content because to prevent precipitation dense concentrations of myoglobin must have high charge) predicted ~80% of the variation in dive duration (Mirceta et al., 2013). Furthermore, whereas myoglobin content varies over almost two orders of magnitude, hemoglobin content varies relatively

little among species. We were particularly interested in maximum dive duration because average dive duration could likely be influenced by many other factors, such as prey abundance, distribution and bathymetry (Butler and King, 2004). We predicted that oxygen stores would increase with body mass, diving metabolic rate would increase with an exponent of 0.75 and dive duration would increase with an exponent of 0.25.

## 2. Materials and methods

We obtained body mass (kg), dive depth (m) and dive duration (min) measured using electrical recorders (average and maximum) for 9 auk species from the literature (Tables 1, 2) and used both maximum and mean values of dive duration within each species. We defined maximum duration as the ave

rage maximum value in duration across all individuals measured within a species. We also collated information on muscle oxygen stores in marine birds ( $N = 12$  species available, including 7 auks and 5 penguins) and diving metabolic rate in wing-propelled diving birds ( $N = 9$  species available 1 auk and 8 penguins) to determine whether allometric relationships may be different for those parameters. For oxygen stores, we focused on muscle oxygen stores (roughly 33% to total stores in penguins: Kooyman, 1989) because blood volume and respiratory stores have only been measured for very few species. For diving metabolic rate, we only included wing-propelled divers including eight penguin species to supplement the sample size, because auks are wing-propelled divers and, across 19 species, foot-propelled divers have a higher diving metabolic rate than wing-propelled divers (Elliott et al., 2013a). Data for diving metabolic rates and myoglobin concentrations were taken from Elliott et al. (2010, 2013a,b) and Yamamoto et al. (2011). We assumed that variation in muscle oxygen stores was primarily associated with myoglobin content rather than total muscle mass because the proportion of total body mass that consists of the pectoralis muscle (the largest muscle in birds), itself does not vary with total body mass for flying birds (Kaiser, 2007).

We calculated the allometric mass exponent of maximum dive duration ( $DU_{\max}$ ) and dive depth ( $DE_{\max}$ ) as the estimated slope of the  $\log_{10}$ – $\log_{10}$  (henceforth denoted log) linear regressions. We were interested in relationships with dive depth because most of the dive costs in auks are associated with descending to depth (Elliott et al., 2008b; Lovvorn et al., 1999, 2004), so that dive depth may be more constrained by oxygen store–oxygen utilization trade-offs than dive duration. We used  $DU_{\max}$  and  $DE_{\max}$  to examine the physiological limits, as well as average dive duration ( $DU_{\text{ave}}$ ) and dive depth ( $DE_{\text{ave}}$ ) to examine general trends. Although anaerobic respiration may play a role in extending dive duration for an individual species, the extension in duration is relatively minor and unlikely to drive allometry in dive duration over scales that cover almost an order of magnitude difference in body mass. To address how oxygen stores are related to the dive duration in auks, we examined myoglobin concentration ([Mb], in  $\text{g} \cdot 100 \text{g}^{-1}$ ;  $N = 12$ ) and dive metabolic rate ( $DMR$ , in  $W$ ;  $N = 9$ ). As we combined values from one auk and several penguins, which could lead to an anomalous slope, we also analyzed the  $DMR$  data without the auk data. These data (Table 1) were analyzed using phylogenetically informed analysis (phylogenetic generalized linear models or PGLS; Freckleton et al., 2002). PGLS analyses were conducted in R (R Development Core Team, 2014) with the *caper* library (Orme et al., 2013). The influence of the shared history on the process governing trait evolution is quantified by a parameter  $\lambda$ , which can either imply complete independence ( $\lambda = 0$ ) or complete dependence ( $\lambda = 1$ ) on the phylogeny. We therefore further tested the impact of the phylogeny on trait evolution by running the PGLS in three different ways: (i) setting  $\lambda = 0$ , (ii)  $\lambda = 1$  and (iii) estimating  $\lambda$  from the data by maximum likelihood; we then compared the three models using the Akaike Information Criterion (AIC; Burnham and Anderson, 2002). For this PGLS analysis, data on 18 species (the 14 species, plus an additional

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