



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



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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

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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_{ave}) and dive depth (DE_{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 λ , 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 λ 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

Table 1
Raw data used in this study, including body mass, dive duration and depth in alcids. Also reported are oxygen stores and consumption rates in marine wing-propelled diving birds. Only dive behavior obtained by electronic loggers was included. Maximum values represent the average across individuals of the maximum value recorded for each individual studied. Where multiple papers report values from the same species and same colony, we averaged the maximum value by number of studies in DE_{\max} and DU_{\max} .

Species	Binary name	M	DMR (W)	[Mb]	DE_{\max}	DE_{ave}	DU_{\max}	DU_{ave}
Adelie penguin	<i>Pygoscelis adeliae</i>	4000	43.2	30				
Ancient murrelet	<i>Synthliboramphus antiquus</i>	197		10	36.8	9.4	69.5	25.5
Atlantic puffin	<i>Fratercula arctica</i>	400		13	36.3	8.7	123	42.5
Cassin's auklet	<i>Ptychoramphus aleuticus</i>	171		10.6	28.1	8.9	101.3	36
Chinstrap penguin	<i>Pygoscelis antarctica</i>	3800	33.8					
Common murre	<i>Uria aalge</i>	985		14	72.7	42.5	165.6	60.3
Empero penguin	<i>Aptenodytes forsteri</i>	23,300	153.1	64				
Gentoo penguin	<i>Pygoscelis papua</i>	5500	75.4	44				
Humboldt penguin	<i>Spheniscus humboldti</i>	4100	35.0					
King penguin	<i>Aptenodytes patagonicus</i>	11,500	96.6	43				
Little penguin	<i>Eudyptula minor</i>	1200	12.1	13.5				
Macaroni penguin	<i>Eudyptes chrysolophus</i>	3600	31.7					
Pigeon guillemot	<i>Cephus columba</i>	400		21.6				
Rhinoceros auklet	<i>Cerorhinca monocerata</i>	560		18	57	14	148	53
Thick-billed murre	<i>Uria lomvia</i>	1000	17.8	13.5	122.5	40.8	168.3	96.1
Razorbill	<i>Alca torda</i>	600			28.3	16	93	31
Dovekie	<i>Alle alle</i>	150			32.5	10	84.5	44.5
Black guillemot	<i>Cephus grylle</i>	430			29	20.5	110.5	74.5

Notes—M: body mass (g); DMR (W): dive metabolic rate; [Mb]: myoglobin concentration; DE_{\max} : maximum dive depth; DE_{ave} : average dive depth; DU_{\max} : maximum dive duration; DU_{ave} : average dive duration. Cells left blank represent missing values. Note DMR and [Mb] were collated from Elliott et al. (2010, 2013a,b) and Yamamoto et al. (2011).

auk and three ratites treated as outgroups to root the tree for the PGLS analyses) were assembled (see Table 3 for accession numbers and Shoji et al., 2015b for rationale). Coding sequences were aligned at the protein level and back-translated to DNA with translator using Muscle (Edgar, 2004). The best substitution model selected based on AIC as implemented in jModelTest (Posada and Crandall, 1998) was GTR + Γ (e.g., Aris-Brosou and Rodrigue, 2012). Phylogenetic trees were estimated by maximum likelihood with PhyML (Guindon et al., 2010) on the concatenated gene sequences. The three ratite species used to root the tree were discarded for the PGLS analyses. Because a PGLS analysis

depends on the actual phylogenetic tree (Felsenstein, 1985) and because some uncertainty in the phylogenetic reconstruction exists, we re-estimated each parameter by running the same PGLS analyses on a set of 1000 bootstrapped trees. Significance of the parameter estimates was assessed at the 1% level, unless otherwise stated.

3. Results

The phylogeny we estimated is generally well supported (Fig. 1), but the low support of some key internal nodes implies that the comparative

Table 2
Body mass and dive duration and depth in alcids. Only dive behavior obtained by electronic recorder during the breeding season was included. Maximum values represent the average of the maximum value recorded for each individual studied. Studies where data were separated by sex or time of day, and where no omnibus value was provided, were excluded from analyses.

Species	Mass (g)	Max duration (s)	Mean duration (s)	Max depth (m)	Mean depth (m)	Sample size**	Reference
Common guillemot <i>Uria aalge</i>	1000	212	64	152	30	9C	Hedd et al. (2009)
Common guillemot <i>Uria aalge</i>	908	–	–	–	–	71C	Thaxter et al. (2010)
Common guillemot <i>Uria aalge</i>	1000*	–	78	–	63	7C	Evans et al. (2013)
Common guillemot <i>Uria aalge</i>	960	–	–	67	29	1C	Watanuki et al. (2006)
Common guillemot <i>Uria aalge</i>	993	119	39	37	10	12C	Tremblay et al. (2003)
Brünnich's guillemot <i>Uria lomvia</i>	1000*	196	97	136	45	9C	Mehlum et al. (2001)
Brünnich's guillemot <i>Uria lomvia</i>	960*	–	105	–	–	3I, 3C	Benvenuti et al. (2002)
Brünnich's guillemot <i>Uria lomvia</i>	960*	187	98	–	–	17C	Jones et al. (2002)
Brünnich's guillemot <i>Uria lomvia</i>	970	–	–	120	48	5C	Watanuki et al. (2006)
Brünnich's guillemot <i>Uria lomvia</i>	960*	175	105	114	48	9C	Mori et al. (2002)
Brünnich's guillemot <i>Uria lomvia</i>	960	181	68	148	–	113C	Elliott et al. (2008c)
Brünnich's guillemot <i>Uria lomvia</i>	941	–	104	110	27	40C	Paredes et al. (2008)
Brünnich's guillemot <i>Uria lomvia</i>	1043	148	96	107	36	12C	Takahashi et al. (2008)
Brünnich's guillemot <i>Uria lomvia</i>	960*	123	–	–	–	14C	Falk et al. (2000)
Razorbill <i>Alca torda</i>	600	93	31	56	8	7C	Shoji et al. (2015a)
Razorbill <i>Alca torda</i>	583	–	23	–	7	20C	Thaxter et al. (2010)
Razorbill <i>Alca torda</i>	591	–	–	41	–	29C	Dall'Antonia et al. (2001)
Razorbill <i>Alca torda</i>	706	–	50	36	10	18C	Paredes et al. (2008)
Razorbill <i>Alca torda</i>	620	–	–	31	8	9C	Watanuki et al. (2006)
Rhinoceros auklet <i>Cerorhinca monocerata</i>	562	148	53	57	14	8C	Kuroki et al. (2003)
Atlantic puffin <i>Fratercula arctica</i>	420	123	36	48	12	7C	Shoji et al. (2015a)
Atlantic puffin <i>Fratercula arctica</i>	426	–	49	41	10	13C	Spencer (2012)
Atlantic puffin <i>Fratercula arctica</i>	398	–	–	20	4	10C	Harris and Wanless (2011)
Black guillemot <i>Cephus grylle</i>	359	131	95	43	32	2C	Masden et al. (2013)
Black guillemot <i>Cephus grylle</i>	386	90	54	15	9	4C	Shoji et al. (2015c)
Ancient murrelet <i>Synthliboramphus antiquus</i>	203	70	26	37	9	12I	Elliott et al. (2010)
Cassin's auklet <i>Ptychoramphus aleuticus</i>	184	101	36	28	9	8I, 4C	Elliott et al. (2010)
Dovekie <i>Alle alle</i>	164	90	52	27	10	4C	Harding et al. (2009)
Dovekie <i>Alle alle</i>	150	79	37	38	10	24C	Karnovsky et al. (2011)

* Body mass was not presented in the reference, and thus the typical value was entered.

** Tracked period is indicated either C = chick-rearing period or I = incubation period under the Sample size column: I/C (Sample sizes).

Table 3

Accession numbers used in this study for the *cox-1* and *cyt-B* mitochondrial genes. When full mitochondrial genomes were available, protein accessions are shown for reference although DNA sequences were used.

Binary	<i>cox-1</i>	<i>cyt-B</i>
<i>Ingroup species</i>		
<i>Pygoscelis adeliae</i>	DQ137183.1	AB776019.1
<i>Pygoscelis antarctica</i>	KF020634	KF020634
<i>Aptenodytes forsteri</i>	EU525299.1	DQ137225.1
<i>Pygoscelis papua</i>	EU525483.1	AB776018.1
<i>Spheniscus humboldti</i>	AY567888	AB776013
<i>Aptenodytes patagonicus</i>	EU525303.1	AY139623.1
<i>Eudyptula minor</i>	EU525354.1	KJ456273.1
<i>Eudyptes chrysolophus</i>	FJ582593	AF076052
<i>Uria aalge</i>	EF380335.1	DQ485892.1
<i>Uria lomvia</i>	EF380336.1	AJ242687.1
<i>Alca torda</i>	EF380318.1	AJ242683.1
<i>Alle alle</i>	EF380320.1	AJ242684.1
<i>Cephus grylle</i>	GU571326.1	AJ242688.1
<i>Cephus columba</i>	EF380325.1	EU372673.1
<i>Cerorhinca monocerata</i>	EF380326.1	U37295.1
<i>Synthliboramphus antiquus</i>	EF380331.1	U37303.1
<i>Fratercula arctica</i>	DQ385177.1	DQ385228.1
<i>Ptychoramphus aleuticus</i>	EF380330.1	U37302.1
<i>Outgroup species</i>		
<i>Rhea americana</i>	JN801969.1	L78808.1
<i>Struthio camelus</i>	U76062.1	U76055.1
<i>Dromaius novaehollandiae</i>	HQ910428.1	U76052.1

analyses need to account for phylogenetic uncertainty – which we do by running the PGLS analyses on bootstrapped trees. After accounting for phylogeny, DU_{ave} failed to show strong relationships with body mass in auks (Fig. 2; Table 4). Accounting for phylogenetic uncertainty, only DU_{max} showed partial (in about 50% of bootstrapped trees) significant allometric influenced by the shared phylogeny (Fig. 2). The 99% confidence interval (CI; ± 3 standard errors) of the mass exponent of DU_{max} (0.06–0.60) included the exponent predicted by the oxygen store/usage hypothesis (0.25), and our estimate was smaller than the

exponent for auks provided in a previous analysis (Watanuki and Burger, 1999). The 99% CI of the mass exponent of DU_{ave} (0.37) also included the value 0.39 provided in Watanuki and Burger (1999).

Similarly, after accounting for phylogeny, DMR (in W), DE_{ave} and [Mb] (but not DE_{max}) all significantly increased linearly with body mass, on a log scale (Table 4). Additional analysis revealed that DMR shows a virtually identical exponent (~ 0.87), with and without the auk value (Fig. S1), so that the enigma of high scaling exponent for dive duration is not driven by anomalous data. Repeated on 1000 bootstrap trees, the PGLS analyses proved to be robust to phylogenetic uncertainty both in terms of exponent estimates, of P -values and λ (Fig. 2) – which is consistent with the result that in no case the shared history mattered (see AIC values in Table 4).

4. Discussion

We updated the allometric relationship for the maximum dive duration on body mass in auks provided in Watanuki and Burger (1999), by adding new data obtained using electronic time-depth recorders. The 99% confidence interval for the mass exponent (0.06–0.60) for maximum dive duration in auks included both the value of 0.25 predicted from the traditional oxygen store/usage hypothesis and the value of 0.57 predicted from the 'updated' allometric relationships for oxygen use during diving (0.79) and muscle oxygen stores (1.36; [Mb]-mass exponent was 0.36, muscle mass exponent was assumed to be 1.00; $0.36 + 1.00 = 1.36$), but not the value of 0.735 previously reported (Watanuki and Burger, 1999). Based on the agreement between our estimate and its theoretical expectation, we suggest that the calculated exponent in Watanuki and Burger (1999) was over-estimated because some of the earlier data were unreliable. The potential for errors associated with earlier techniques is demonstrated by the observation that the maximum dive depth of 210 m recorded in thick-billed murrets (*Uria lomvia*) using a maximum depth gauge was later shown to be overestimated by roughly 33% (Elliott and Gaston, 2009).

Seabirds, including auks, consume very little oxygen during long dives (Bevan et al., 2002; Butler and King, 2004; Niizuma et al., 2007;

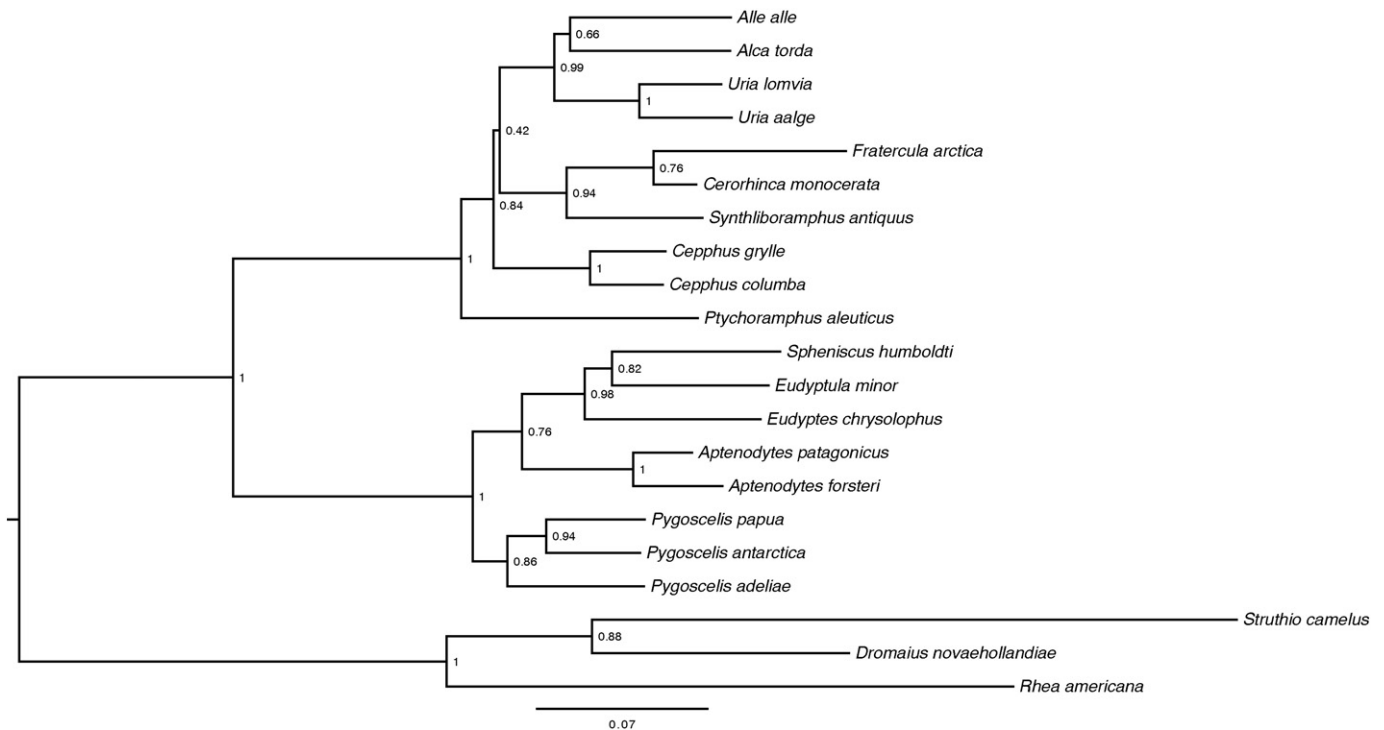


Fig. 1. Estimated maximum likelihood phylogenetic tree. The tree estimated from the concatenated data (*cox-1* + *cyt-B*) under the best fitting model. Node numbers show bootstrap support.

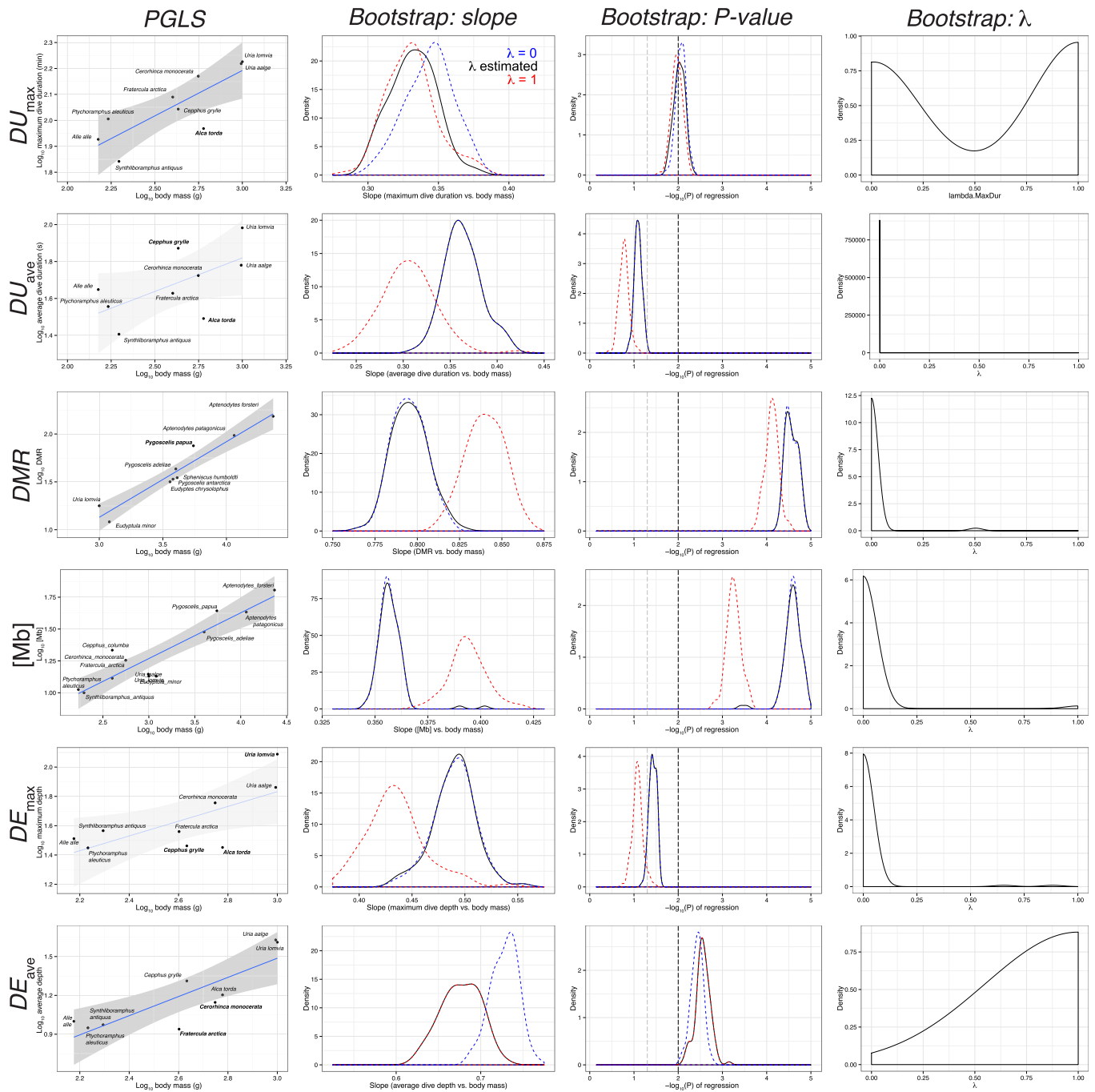


Fig. 2. Allometric relationship between each of the physiological variables examined in this study and body mass. The variables are listed in Table 1 and are displayed row by row. The first column shows the results of the PGLS regressions (on a log–log scale). The 95% confidence intervals are shown as shaded areas, that are darker when regressions are significant (as in Table 4). The next columns show results of the PGLS regressions over the 1000 bootstrapped trees for the estimated slopes (2nd column), their significance (3rd column) and the estimated λ values (last column). Results for three models are shown (2nd/3rd columns): $\lambda = 0$ (broken lines, in blue), $\lambda = 1$ (broken lines, in red) and λ estimated (solid lines, in black). The vertical broken line in the 3rd column indicates the significance at the 1% (black) and 5% (gray) levels.

Ponganis et al., 1997; Elliott et al., 2013) and it is the scaling of that minimal rather than average diving metabolic rate with body mass that is likely most relevant to maximum dive duration. Additional data on oxygen stores, especially blood volumes, and minimal diving metabolic rate of wild auks, are clearly needed to resolve any remaining discrepancy between the observed and expected allometric exponents for maximum dive duration.

Diving metabolic rate scaled with an exponent of about 0.79, with a confidence interval including the values of 0.67–0.75 typically found for avian basal metabolic rate (McKechnie and Wolf, 2004; McNab, 2009). Thus, our results support the traditional assumption that diving oxygen

consumption rate increases allometrically with an exponent of about 0.75 (e.g. Schreer and Kovacs, 1997; Watanuki and Burger, 1999). In contrast, myoglobin content increased more rapidly with body mass than expected, likely because the muscles of small auks have very high densities of mitochondria and associated enzymes due to their high mass-specific metabolic rates, leaving little space for myoglobin (Elliott et al., 2010; Mirceta et al., 2013). The allometric increase in myoglobin content, ignored by some earlier formulations of the oxygen use-oxygen tradeoff hypothesis (e.g. Schreer and Kovacs, 1997; Watanuki and Burger, 1999), illustrates the importance of considering the scaling of physiological constraints alongside maximum dive duration when

Table 4

Results of the PGLS regressions for the data shown in Table 2. Each regression was performed on a log–log scale, so that the inferred slope is the exponent of the allometric relationship tested; the standard error (SE) of the slope estimates as well as the multiple r^2 of each model fit are shown. Each PGLS regression fitted a model where λ was estimated as a free parameter; this estimate is denoted $\hat{\lambda}$ is the parameter. Δ AIC is the difference in AIC between this model and a model where λ is set to 0 (no phylogenetic effect).

	Exponent	SE _{exponent}	r^2	P-value	$\hat{\lambda}$	Δ AIC
<i>DU</i> _{max}	0.33	0.09	0.63	0.0107	1.00	-0.60
<i>DU</i> _{ave}	0.37	0.18	0.37	0.0818	0.00	-0.00
DMR (W)	0.79	0.08	0.92	3.50E-05	0.00	-0.00
<i>DE</i> _{max}	0.47	0.19	0.46	0.0453	0.00	-0.00
<i>DE</i>_{ave}	0.68	0.15	0.74	0.0028	1.00	-1.78
[Mb]	0.36	0.05	0.84	2.60E-05	0.00	-0.00

Notes—Boldface indicates significant relationships at the $\alpha = 1\%$ level (in black) or at the 5% level (gray).

attempting to understand how maximum dive duration varies among taxa. The lack of importance of phylogeny is unsurprising given that auks and penguins have a very similar body plan and similar diving mode (wing-propelled diving). Given that our sample of species is fewer than the 20 typically required to see a phylogenetic signal (Blomberg et al., 2003) – after all there are only ~24 species in the entire extant auk clade – we argue that it is important to consider the exponent both with (λ estimated in Fig. 2) and without ($\lambda = 0$ in Fig. 2) a phylogenetic signal. This might indeed be critical as we found that phylogenetic effects for both *DMR* and [Mb] may lead to increased allometric exponents. Those data were almost entirely derived from data on penguins, although the inclusion of the only available data point from auks (*U. lomvia*) fell within the 95% confidence intervals for the log–log regression for penguins. Although we clearly need more data on auks, our results support the idea that the relationship between body mass and *DMR* in a group of wing-propelled diving birds separate from the auks is not very different than that previously assumed.

Average, but not maximum, dive depth scaled with body mass (at the conservative 1% level: Table 4 and Fig. 2). The exponent for the scaling relationship for average dive depth (0.68) was substantially higher than the scaling exponent for either average or maximum dive duration (0.33–0.37). Thus, larger auks were using their lengthier dive duration primarily to achieve deeper average depths rather than extend dive duration to spend more time at the bottom of each dive. Some of the larger auks, such as guillemots and murrelets, are partial benthic foragers. Whereas very little of the coastal environment's benthos would be available to small auks foraging only to 10 m in depth, the deep-diving murrelets, by investing heavily in lengthy transit times, can access depths to 180 m meaning that they can access the benthic environment of much of the continental shelf, presumably increasing food availability.

Two species fall outside of the 95% confidence intervals for the regression of dive duration (*DU*_{max}) against body mass: ancient murrelet and razorbill. Indeed, without those two outliers, the relationship between *DU*_{max} and body mass becomes much more statistically significant ($P = 0.0006$, $r^2 = 0.92$, exponent = 0.34, $SE = 0.04$). Whereas data for the other species were obtained during the chick-rearing period, the data for ancient murrelets is from the incubation period because ancient murrelets do not rear their chicks at the colony. As dive depth and duration is generally deeper and longer during chick rearing than during incubation (Benvenuti et al., 2002; Elliott et al., 2008b; Ito et al., 2010), the stage difference may explain why murrelets fall outside of the confidence intervals. The data for razorbills, however, is from the chick-rearing period, and cannot be explained by difference in breeding period. Thaxter et al. (2010) suggested that razorbills dive for shorter periods (and fly more) than murrelets because they have a lower wing-loading, a specialization for flying rather than diving. However, razorbills make shorter dives for their body mass than all other auks studied

to date, even though the smaller auks have a lower wing-loading (wing-loading is proportional to body mass). For instance, puffins dive longer than razorbills at the same study site despite being smaller and with a lower wing-loading (Shoji et al., 2015a). We argue that while razorbills may be able to dive longer, there must be some aspect of razorbill ecology, aside from wing-loading, that leads to shallow diving, as wing-loading does not appear to be associated broadly with dive patterns in auks. In particular, average dive duration for razorbills is predicted by allometry, and consequently it is only the lack of very long dives – a less right-skewed distribution of durations – that leads to the anomalously low maximum dive duration for razorbills.

In contrast to maximum dive duration, average dive duration (and to some extent, maximum dive depth: Fig. 2) was clearly independent of body mass. There is large variation in dive duration among colonies (Sala et al., 2014), stage (Benvenuti et al., 2002; Elliott et al., 2008b; Ito et al., 2010) and individuals (Woo et al., 2008), and variation in average dive duration and depth apparently reflects ecological variation in local bathymetry, light levels, breeding stage and prey availability rather than physiological constraints.

In conclusion, our results suggest that the higher exponent in maximum dive duration reported in Watanuki and Burger (1999), 0.74, is likely to be due to inaccuracies in the earlier sampling methods and hence the maximum dive duration is largely explained by physiological limitations. To understand how some behavioral processes scale with body mass, it is important to measure how physiological constraints scale with body mass. Although many ecological, behavioral and physiological phenomena scale with body mass, the scaling exponent varies widely and we encourage the simultaneous examination of physiological alongside behavioral data to reveal the potential cause(s) of such variation.

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