Body mass and dive duration in alcids and penguins

Yutaka Watanuki and Alan E. Burger

Abstract: Interspecific allometric equations for dive duration were calculated for two groups of wing-propelled divers: penguins, which specializing in diving, and alcids, which balance demands for aerial flying with those of diving. The equations for maximum dive duration (min) were $1.433M^{0.702}$ and $3.612M^{0.735}$ (where M is body mass in kilograms) for penguins (10 species) and alcids (9 species), respectively, hence did not support a simple oxygen store/usage hypothesis based on the prediction that the mass exponent of aerobic dive limit is close to 0.25. Equations for feeding dives were $0.569M^{0.712}$ and $1.094M^{0.391}$ in penguins (9 species) and alcids (10 species), respectively. The allometric exponent for the duration of feeding dives for penguins did not match the predicted value of 0.25, but that for alcids did not differ significantly from this value. Alcids exhibited a maximum dive duration 2.5 times longer than that for penguins after mass effects were controlled for. The size of oxygen stores and metabolic rates based on laboratory studies of penguins and alcids failed to explain the longer dive duration in alcids than in penguins.

Résumé : Des équations allométriques interspécifiques de la durée des plongées ont été calculées pour deux groupes de plongeurs utilisant leurs ailes, les manchots, spécialisés dans la plongée, et les alcidés qui se servent de leurs ailes à la fois pour le vol aérien et pour la plongée. Les équations qui reflètent la durée maximale de plongée (min) chez les manchots (10 espèces) et les alcidés (9 espèces) sont $1{,}433M^{0{,}702}$ et $3{,}612M^{0{,}735}$ respectivement (où M est la masse corporelle en kilogrammes), ce qui ne supporte pas l'hypothèse de la réserve/utilisation d'oxygène basée sur la prédiction selon laquelle l'exposant de la masse à la limite d'une plongée aérobie a une valeur approximative de 0,25. Dans le cas des plongées de quête de nourriture chez les manchots (9 espèces), l'équation est $0{,}569M^{0{,}712}$ et celle des alcidés, $1{,}094M^{0{,}391}$. L'exposant allométrique pour la durée des plongées alimentaires chez les manchots ne correspond pas à la valeur prédite de 0,25, mais cette valeur n'est pas significativement différente de 0,25 dans le cas des plongées alimentaires des alcidés. Les alcidés font des plongées alimentaires de durée maximale 2,5 fois plus longue que les manchots lorsque l'effet de la masse est enlevé. L'ampleur des réserves d'oxygène et le taux de métabolisme, tels que mesurés en laboratoire chez les manchots et les alcidés, ne permettent pas d'expliquer la durée plus longue des plongées chez les alcidés.

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Introduction

Heavier animals are capable of making longer breath-hold dives (Kooyman 1989). Both oxygen-storage capacity and oxygen-consumption rate vary allometrically with body mass, the scaling exponents in birds being 0.91–1.19 and 0.748, respectively (Lasiewski and Calder 1971; Hudson and Jones 1986; Birt-Friesen et al. 1989). Consequently, according to the "oxygen store/usage hypothesis," the maximum duration of aerobic dives depends on body mass, with an expected exponent of ca. 0.25 (Hudson and Jones 1986; Wilson 1992; Kooyman and Kooyman 1995) in birds that appear to dive aerobically (Butler and Jones 1997).

Variable mass exponents of dive duration have been reported in seabirds. An interspecific comparison for cormorants and shags yielded an allometric exponent for dive duration of 0.66 ± 0.11 (mean ± SE) (Watanuki et al. 1996, based on data in Cooper 1986), though the mass exponent of maximum dive duration for 10 species of seabirds with various diving modes was 0.369 ± 0.065 (Boyd and Croxall 1996). This discrepancy seems to be due to the range of seabird groups included in the analyses and makes generalization difficult.

Recently, owing to the development of new technology, data on the diving behavior of many species in the wild have appeared in the literature. As a test of the simple oxygen store/usage hypothesis, we calculated the allometric mass exponent of the maximum dive duration for penguins (nonflying, wing-propelled divers) and alcids (flying, wing-propelled divers) separately, using the new data in addition to those from Boyd and Croxall (1996). We also reevaluate the general perception that alcids, which balance flying and diving abilities, are less efficient divers than penguins, which are more specialized for diving.

Methods

We calculated the allometric mass exponent of maximum dive durations for penguins and alcids. We used the maximum dive duration reported in each paper, as did Boyd and Croxall (1996), but

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excluded outlier values defined by each author. Maximum dive durations for 9 species of penguins and 4 species of alcids were obtained from studies of 1–65 individual birds that were either were fitted with time–depth recorders or monitored by radio-tracking; those for 1 species of penguin and 5 species of alcids were obtained by direct observation of an unknown number of individuals (Table 1).

Although the maximum dive durations reported in the studies mentioned may reflect the physiological limits of the species concerned, they may also be a function of the amount of data gathered in each case. To assess the central trend, we also used "normal" dive duration. For penguins, dives were often categorized as "feeding (deep)" or "travelling (shallow porpoising)", depending on the depth, duration, and frequency of dives and direction of travel, though criteria used to separate "feeding" and "travelling" dives sometimes varied among researchers and either modes or means were reported. In alcids, which travel by aerial flying, most of the dives were probably for feeding. Accordingly, we report the mean value of "normal dives" for species when available, and the mode when that was the only measure available for penguins (Table 1), following Boyd and Croxall (1996). In the case of alcids, the mean duration of all dives was used to assess "normal" diving performance (Table 1).

Sometimes within-species regional and seasonal variations in dive duration were found (Williams et al. 1992; Watanuki et al. 1997). Where different durations were reported for a species, the maximum value was used as the species representative for calculating the mass exponent of the maximum duration. The median value of "normal" dive durations was used as the species representative for calculating the mass exponent of "normal" dive duration.

Results

The maximum dive duration ($D_{\max}$, in minutes) and "normal" dive duration (D_{norm}, in minutes) depends on body mass (M, in kilograms) in both penguins and alcids (Fig. 1).

For penguins:

$$D_{\max} = 1.433M^{0.702} \ (\text{SE}_{\text{slope}} = 0.081,\ r^2 = 0.893,\ t = 8.70,\ P < 0.001,\ n = 10)$$

$$D_{\text{norm}} = 0.569M^{0.712} \ (\text{SE}_{\text{slope}} = 0.149,\ r^2 = 0.733,\ t = 4.79,\ P < 0.01,\ n = 9)$$

For alcids:

$$D_{\max} = 3.612M^{0.735} \ (\text{SE}_{\text{slope}} = 0.107,\ r^2 = 0.851,\ t = 6.84,\ P < 0.01,\ n = 9)$$

$$D_{\text{norm}} = 1.094M^{0.391} \ (\text{SE}_{\text{slope}} = 0.166,\ r^2 = 0.336,\ t = 2.36,\ P = 0.046,\ n = 10)$$

The mass exponents of maximum dive duration for penguins (0.702) and alcids (0.735) did not differ from each other (analysis of covariance; ANCOVA), and both were greater than the exponent predicted by the oxygen store/usage hypothesis (0.25; *t* test, $P < 0.05$). The mass exponents of "normal" dive duration for penguins (0.712) and alcids (0.391) did not differ (ANCOVA); however, that for penguins was greater than 0.25 (*t* test, $P < 0.05$) but that for alcids did not differ from 0.25 (*t* test, ns).

Alcids had longer maximum dive durations than penguins after mass effects were controlled for (ANCOVA, $P < 0.001$; Fig. 1). The maximum dive duration predicted for a hypothetical 1-kg alcid, 3.5 min, was more than double that for a 1-kg penguin, 1.4 min. Similarly a 1-kg alcid would have a longer "normal" dive (1.1 min) than a 1-kg penguin (0.6 min), although the difference was marginally significant (ANCOVA, $P = 0.07$; Fig. 1).

Discussion

The mass exponents of 0.702–0.735 for maximum dive duration in penguins and alcids were greater than the 0.25 predicted from the simple oxygen store/usage hypothesis. This suggests that aerobic dive limits based on metabolic studies of captive birds and tissue and lung oxygen stores may not accurately reflect the physiological limits of diving in penguins and alcids. A large within-species variation in "normal" dive duration (Table 1) and a small sample size make it difficult to determine the central trend in "normal" dive duration. However, the fact that three of the four regressions yielded mass exponents of 0.702–0.735 is interesting, and may indicate a dominant influence of metabolism (an expected *b* value of 0.75) on voluntary dive times.

Alcids dived for longer than penguins after the difference in body mass was controlled for, which is consistent with the discovery that, relative to body mass, maximum depths attained were greater for alcids than for penguins (Burger 1991). Both patterns are surprising, because alcids appear to be less specialized for diving than penguins and have to balance the demands of aerial flying with those of underwater diving (Spring 1971; Mill and Baldwin 1983; Lovvorn and Jones 1994).

The longer dive duration in alcids cannot be explained by the simple oxygen store/usage hypothesis. Since hemoglobin concentration, blood volume, and myoglobin concentration in the pectoral muscles were similar in penguins and alcids, estimated oxygen stores in alcids (45–47 mL/kg; Croll et al. 1992; M. Kuroki, A. Kato, Y. Watanuki, Y. Niizuma, A. Takahashi, and Y. Naito, unpublished data) were similar to those in penguins (45–63 mL/kg; Culik et al. 1991, 1994, 1996; Kooyman et al. 1992; Kooyman and Ponganis 1994; Bethge et al. 1997). The mass-specific metabolic rate during diving in captivity was similar for alcids (13.3–17.0 W/kg; Croll et al. 1992; Croll and McLaren 1993) and penguins (9.6–20.0 W/kg; Culik et al. 1991, 1994, 1996; Kooyman et al. 1992; Kooyman and Ponganis 1994; Bethge et al. 1997). The enzyme systems in the pectoral muscles indicate that both penguins (Baldwin et al. 1984) and alcids (Davis and Guderley 1987) rely extensively on aerobic metabolism during diving, and this is also suggested by Butler and Jones (1997), although adaptations for anaerobic metabolism are found in some penguin muscles (Baldwin 1988). These similarities suggest that the maximum duration of aerobic dives should be similar in alcids and penguins.

The effects of buoyancy should also be considered. The mass-specific volume of air in the plumage was greater for alcids than for penguins, indicating that alcids require more power to descend from the surface than penguins do (Lovvorn and Jones 1991, 1994; Wilson et al. 1992). Alcids, constrained by the conflicting demands of flying and diving (Lovvorn and Jones 1994), appear to have evolved adaptations for prolonged, deep diving but without a reduction in buoyancy. In penguins, which are unconstrained by the

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Table 1. Body masses and dive durations in penguins and alcids.

	Mass (kg)^a	"Normal" dive duration (min)	Dive type	Mean or mode^b	Max. dive duration (min)^c	Method^d	No. of birds	Source
Penguins								
Aptenodytes forsteri	28	3.4–5.0	Feeding	Mean	15.2–15.8	TDR	19	Kooyman and Kooyman 1995; Kirkwood and Robertson 1997
Aptenodytes patagonicus	13.4	4.5	Feeding	Mode	7.7	TDR	28	Kooyman et al. 1992
Pygoscelis papua	6.1	2.4–2.8	Feeding	Mean	4.5–6.2	TDR	9	Williams et al. 1992; Robinson and Hindell 1996
Pygoscelis adeliae	4.6	1.2–1.7	Feeding	Mean	2.7–4.5	TDR	65	Chappell et al. 1993; Watanuki et al. 1997
Pygoscelis antarctica	4.1	1.2	Feeding	Mean	3.0	TDR	4	Bengtson et al. 1993
Eudyptes chrysolophus	4.5	1.5	Day dive^e	Mean	3.0 (6.3)	TDR	2	Croxall et al. 1993
Eudyptes crysocome	2.8	—			3.0	TDR	1	Wilson et al. 1997
Spheniscus magellanicus	3.4	2.1	Long^f	Mode	3.9	TDR	9	Peters et al. 1998
Spheniscus demersus	3.2	1.8~2.4	Feeding	Mean	4.4	OB	—	Wilson 1985; Wilson and Wilson 1990
Eudyptula minor	1.2	0.4	All^g	Mean	1.5	TDR	8	Bethge et al. 1997
Alcids								
Uria lomvia	1.0	0.9–1.6	All	Mean	3.2–3.3 (3.7)	TDR	17	Croll et al. 1992; Y. Watanuki, F. Mehlum, A. Takahashi, unpublished data
Uria aalge	1.0	0.9–1.2	All	Mean	1.8–3.0 (3.4)	RT/OB	15	Wanless et al. 1988; Monaghan et al. 1994; A.E. Burger and G.K. Davoren, unpublished data
Alca torda	0.6	0.6	All	Mean	—	RT	1	Wanless et al. 1988
Cerorhinca monocerata	0.5	0.6–0.9	All	Mean	1.2–2.5	TDR/OB	8	A.E. Burger and G.K. Davoren, unpublished data; M. Kuroki, A. Kato, Y. Watanuki, Y. Niizuma, A. Takahashi, and Y. Naito, unpublished data; Burger et al. 1993
Fratercula arctica	0.4	0.5	All	Mean	1.9	RT	1	Wanless et al. 1988
Cepphus grylle	0.4	1.0–1.2	All	Mean	2.4	OB	—	Bradstreet and Brown 1985; Cairns 1992
Cepphus columba	0.5	1.0–1.5	All	Mean	1.8–2.4	OB	—	Ainley et al. 1990; Clowater and Burger 1994; A.E. Burger, J.S. Clowater, and G.K. Davoren, unpublished data
Brachyramphus marmoratus	0.22	0.7	All	Mean	1.0 (1.2)	OB	—	A.E. Burger and G.K. Davoren, unpublished data
Ptychoramphus aleuticus	0.17	0.7	All	Mean	1.2	OB	—	Ainley et al. 1990
Alle alle	0.16	0.4	All	Mean	0.7	OB	—	Bradstreet and Brown 1985

[a] Values were obtained during the chick rearing stage and are from Boyd and Croxall (1996), Williams (1995), and Gaston and Jones (1998).

[b] Mean or mode of duration of feeding dives and all dives is given for penguins and alcids, respectively.

[c] Numbers in parentheses are outlier values.

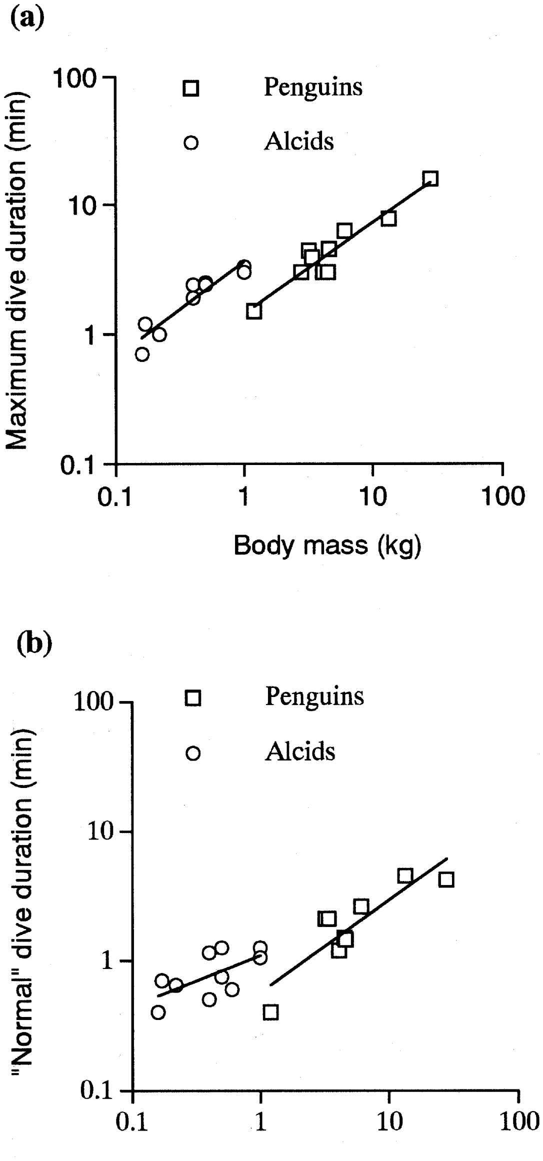
[d] TDR, time depth recorder; RT, radio-tracking; OB, direct observation from a boat.

[e] Dive deeper in the daytime.

[f] Where two modes were reported, the mode of longer duration is shown.

[g] The dive type was not specified.

Fig. 1. Allometric relationships ($\log_{10}$ scale) between maximum dive duration and body mass (*a*) and between duration of "normal" dives and body mass (*b*) for penguins (nonflying, wing-propelled divers) and alcids (flying, wing-propelled divers), based on data given in Table 1. We used the mean value for each species when it was available and the mode when that was the only measure available for penguins; we used the mean duration of all dives in alcids to analyze "normal" dive duration. Where different durations are reported for a species, the longest is used as the species representative for maximum duration and median values are used as the species representative for "normal" dive duration for the purposes of the regression analyses.



demands of flying, body density has increased, which allows both shallow and deep foraging without significant buoyancy costs. Because of hydrostatic compression of air with depth, however, deep-diving alcids and penguins may be able to enjoy neutral or negative buoyancy in most of their dive-depth range.

In conclusion, our knowledge of physiological parameters based on laboratory studies of captive birds cannot unambiguously explain both the greater mass exponent of maximum dive duration than that predicted by the oxygen store/usage hypothesis and the longer dives in alcids than in penguins. In particular, information on anaerobic metabolism and energy saving through regional hypothermia during natural dive bouts is lacking for alcids but is being reported for penguins (Culik et al. 1996; Handrich et al. 1997; Ponganis et al. 1997). Unravelling the nature of physiological adaptations for diving in penguins and alcids in the wild continues to promise fascinating research opportunities.

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