Allometry of diving capacities: ectothermy vs. endothermy

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Abstract

Body mass positively influences diving capacities in air-breathing vertebrates and has been identified as a key determinant for the evolution of diving. Our review on the relationship between body mass and dive duration (a major parameter of dive performances) encompassed for the first time a wide diversity of air-breathing vertebrates. We included a substantial number of nonavian and nonmammalian diving species belonging to various independent lineages (sea snakes, iguana, turtles and crocodiles). Our analyses suggest that the widely accepted size dependency of dive duration applies with significantly less force in ectotherms compared with endotherms; notably we failed to detect any effect of body mass in ectotherms. We hypothesize that the absence of tight physiological links between body mass and respiratory demands documented in ectotherms blurred our ability to detect the expected correlation. Further exploration of the evolution of diving physiology may well necessitate adopting novel perspectives to encompass both ectothermic and endothermic modes.

Introduction

Phylogenetic transitions in habitat use provide exceptionally powerful opportunities to understand the selective pressures operating on morphology, physiology and behaviour. For example, in air-breathing vertebrates, aquatic life exerts major influences on attributes such as the ability to move efficiently through water, to hold the breath to remain underwater for long time periods, and to dive to considerable depths (Kooyman, 1989). Some of the most clear-cut examples of adaptation to marine life have been documented in marine endothermic vertebrates: whales, dolphins, seals, penguins, etc. These organisms exhibit deep morpho-functional adaptations that considerably increase their diving performance, notably their capacity to remain underwater without breathing, when compared with their terrestrial relatives (Boyd, 1997; Butler & Jones, 1997). However, despite the effectiveness of these adaptations, air-breathing endotherms are highly constrained in dive duration and depth (Butler & Jones, 1997).

Using a large data set, recent reviews (Schreer & Kovacs, 1997; Halsey *et al.*, 2006a, b) have identified a

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strong and consistent correlation between dive duration and body mass. In endotherms adapted to aquatic life, body size is inversely correlated with relative metabolic rate and positively associated with relative oxygen stores. Large animals can therefore hold their breath and dive for longer absolute time periods compared with small species. As expected, they can also reach greater depths and can access peculiar foraging sites. Although highly oriented towards endothermic vertebrates (because these organisms have been intensively studied), a previous review (Schreer & Kovacs, 1997) incorporated some air-breathing diving ectotherms (several sea turtles). The main trend identified in endotherms remained identical: body mass-corrected dive durations of turtles were within the range of those observed in mammals and birds. Consequently, the strong and tight relationship between body size and dive duration was proposed as a general rule for air-breathing marine vertebrates (Schreer & Kovacs, 1997; Halsey *et al.*, 2006a, b).

However, such a general rule is not expected to apply equally in all air-breathing vertebrates. Constraints on dive duration should apply with much less force to ectotherms than to endotherms. Notably, the low metabolic rate of ectotherms, relative to endotherms, reduces considerably their oxygen demands (Pough, 1980). Similarly, the marked flexibility of ectothermic vertebrates

for almost all of their physiological parameters (body temperature, anoxia, acidosis, glycaemia; Belkin, 1963; Shelton & Boutilier, 1982) suggests that the influence of body mass *per se* on dive duration should be relaxed compared with endotherms. Consequently, for a given body mass, we may expect that, on average, ectothermic air-breathing vertebrates should be able to remain underwater without breathing for longer time periods compared with endothermic species. In the current review, we incorporated a substantial sample of air-breathing ectothermic vertebrates, both in terms of body size and taxonomic diversity, to examine the relationship between body mass and dive duration. Our analyses show that diving ectothermic vertebrates diverge markedly from the classical trends exhibited by the more intensively studied marine endotherms, and challenge the widely accepted notion that body size is the main predictor of dive duration in air-breathing aquatic vertebrates.

Methods

Data collection

Data on body mass and maximum diving duration were collected from the literature. As a basis, we used one of the most complete reviews on diving performances of aquatic air-breathing vertebrates (Schreer & Kovacs, 1997). From this starting point, we added as many as possible information. Because of an accelerating development of bio-logging techniques, the rate of acquisition of novel results has also increased rapidly over the last 10 years (Ropert-Coudert & Wilson, 2005). We therefore updated previous data sets using recent studies in mammals and birds available in a comprehensive database on air-breathing divers (Ropert-Coudert *et al.*, 2006; online appendix).

The taxonomic diversity of ectothermic vertebrates is poorly reflected by the confusing terminology associated with the words amphibians, reptiles, birds and mammals (see Tree of Life, http://www.tolweb.org). Although crocodiles are more closely related to birds than to lizards for instance (Hedges & Poling, 1999), the term 'reptiles' is still often employed as if it had an unquestionable taxonomic value. Any attempt to explore the morpho-functional implications imposed by marine habitat on air-breathing vertebrate should embrace a wide taxonomic diversity to take into account the phylogeny of vertebrates. Owing to a deficit of data, and to a scientific lack of interest for ectotherms (Bonnet *et al.*, 2002), such effort has not been previously undertaken. Bringing new results on ectothermic air-breathing diving vertebrates was the most innovative contribution of the present study; we now present data for freshwater turtles, marine iguanas, saltwater crocodiles, freshwater crocodiles and sea snakes (Hobson, 1965; Heatwole, 1975; Grigg *et al.*, 1985; Rubinoff *et al.*, 1986; Van Dam & Diez, 1996;

Schreer & Kovacs, 1997; Gordos & Franklin, 2002; Hays *et al.*, 2004; Hochscheid *et al.*, 2005; Seebacher *et al.*, 2005; Sale *et al.*, 2006; McMahon *et al.*, 2007). Finally, we included our own unpublished data on a species of sea kraits (*Laticauda saintgironsi*; F. Brischoux, X. Bonnet, T. R. Cook & R. Shine, unpublished data).

Selection of the data

The method employed by the researchers to measure diving performances was an important criterion for the selection of the data. For both ectotherms and endotherms, we used only studies where animals dived voluntarily. Cases where animals were forced to remain underwater (sometimes leading to death) were not kept for the analyses. The rationale for such selection against forced submergence studies is explained by ethical considerations, and also by the strong biases associated with this technique (Kooyman, 1985). We also excluded studies on ectotherms where the animals where monitored while resting or hibernating (e.g. freshwater turtles; Ultsch, 2006) and we restricted our analyses to swimming animals because our goal was limited to explore diving performances.

Among different criteria, we selected maximum dive duration as an indicator of diving performances because this parameter directly traduces the upper limit associated with diving physiology. Unfortunately, exact maximum dive durations are rarely recorded, intensive studies are generally needed to characterize the actual maximal duration tolerated by animals while diving (e.g. less than 0.01% of all the recorded dives in emperor penguins reached the 22-min maximum dive duration). Because few studies examined diving performances in air-breathing ectotherms, the data available probably provide underestimated diving performances. As endotherms have been more intensively studied, such sampling bias rendered our analyses and main conclusions conservative (see *Results*).

Eventually, we gathered data on 75 species of mammals, eight species of turtles, 62 species of birds, two species of crocodiles, one species of iguana and 11 species of snakes, which represents 25 families belonging to contrasted taxonomic lineages (online appendix).

Analyses

The main goal of the study was to compare the relationships between body size and dive duration for the two metabolic modes and thus to compare the strength of the relationships between ectotherms and endotherms. We analysed the difference in the correlation coefficients of ectotherms vs. endotherms. To appreciate the reliability of such comparison, we performed bootstrap analysis (sampling with replacement) to generate a set of 1000 Spearman correlations (coefficients of correlation are thus given ±SD).

We did not frame our analysis in a phylogenetic context for several reasons. Current phylogenies are very incomplete for many nonmammalian and nonavian taxons (see Tree of Life, http://www.tolweb.org). Several major connective branches are lacking, or the distances are poorly reliable. Setting the length of the multitude of branches involved (see http://www.tolweb.org) to one by default would have been both a necessity and a poorly rigorous method to integrate phylogeny in the analyses. More importantly, our results (see below) clearly show that the metabolic mode enabled to separate completely, without overlapping, the data sets gathered, respectively, in ectotherms vs. endotherms. Superposing various phylogenic trees would add no information in our assessment. For instance, crocodiles remained clearly within the ectothermic group in terms of dive duration/body mass relationship despite their relatedness to birds.

Results

Pooling all the data, we found a significant correlation between body mass and dive duration (Spearman correlation, $r_s = 0.53$, $P < 0.001$), suggesting that body mass influences dive duration capacities in air-breathing vertebrates. However, when the analyses were performed separately in endotherms vs. ectotherms, the conclusion above was challenged (Fig. 1). A graphical inspection of the data revealed a clear-cut segregation between the ectotherms and the endotherms (Fig. 1). All the dive durations measured in ectotherms were above the range of those recorded in endotherms. Therefore, we further
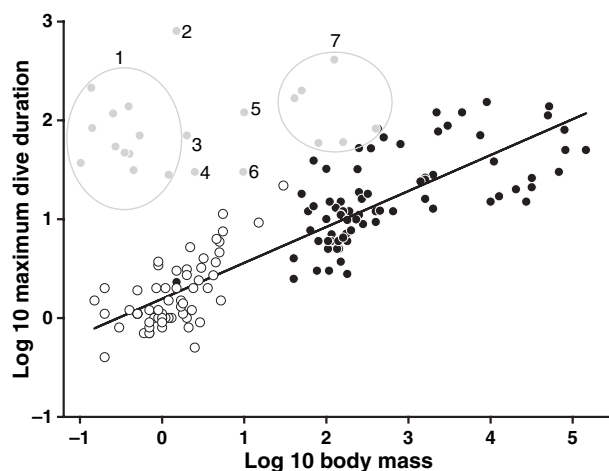

Fig. 1 The relationship between maximum dive duration and body mass, in air-breathing diving vertebrates for the main phylogenetic groups. White and black circles are for birds and mammals respectively (regression line for endotherms; $y = 2.91x + 0.2$). Grey circles are for snakes (1), freshwater turtles (2 and 3), marine iguana (4), freshwater crocodile (5), saltwater crocodile (6) and marine turtles (7).

examined the relationship between body mass and dive duration within each metabolic mode separately.

Considering the endotherms solely, the addition of studies (and families) did not modify the pattern presented in previous reviews: a strong positive correlation between dive duration and body mass was observed (Spearman correlation, $r_s = 0.88 \pm 0.02$, $P < 0.0001$; Fig. 1). In ectotherms, no relationship between body mass and maximum dive duration was detected (Spearman correlation, $r_s = 0.13 \pm 0.21$, $P = 0.44 \pm 0.30$). The distribution of the data did not overlap between endotherms and ectotherms (Fig. 1), and their respective range of Spearman rank correlations generated through bootstraps remained clearly different.

Discussion

Incorporating a substantial number of studies carried out in ectothermic species challenged the paradigm that diving capacities are mainly constrained by body mass in air-breathing vertebrates (Schreer & Kovacs, 1997; Halsey *et al.*, 2006a, b). The two major recent reviews published, respectively, in 1997 and 2006a,b provided a baseline to understand how such a paradigm was progressively established. The analyses presented by Schreer & Kovacs (1997) provided a convincing general picture where air-breathing diving vertebrates ($N > 120$ species) spread along a general correlation between body mass and diving performances. However, closer analyses, focused on the different taxonomic groups, failed to demonstrate that the constraints imposed by body mass were always a key determinant (e.g. within otariid seals). This led to a discrepancy between micro-evolutionary and macro-evolutionary processes: if the body mass limitation for diving performances did not apply within a family, it was hard to understand how such a putative influence could also apply among families. In a second step, Halsey *et al.* (2006a, b) successfully handled the complications intrinsic to the analysis of phenotypic data gathered on disparate entities (e.g. small seabirds vs. giant mammals). Notably, they increased the data set ($N = 195$ species) and framed the analysis within a phylogenetic context. When the diving performances were controlled for phylogenetic independence, not only were all the above discrepancies resolved, but also most of the diving variables became statistically undistinguishable between birds and mammals. The authors concluded that more than the evolutionary pathways followed by different lineages of divers, body mass was the main determinant of diving performances, and thus was likely a general feature of diving evolution (Halsey *et al.*, 2006a, b).

Our analyses with a much diverse data set partly support the validity of the conclusions drawn by previous reviews (Schreer & Kovacs, 1997; Halsey *et al.*, 2006a, b). Nevertheless, we emphasize that size dependency of dive duration applies with significantly less force in

ectothermic air-breathing vertebrates compared with endothermic species. One could argue that such results could be related to the limited number of studies carried out in ectothermic air-breathing diving vertebrates. However, the differences of sample size between ecto-therms and endotherms cannot explain the lack of overlap in the distribution of the data (Fig. 1). The metabolic mode (endothermy or ectothermy) appears to be a major element for interpreting the range of diving performances in air-breathing vertebrates. Consequently, further comparisons of various diving traits (e.g. respiratory capacities and energy budget) should be framed within such a contrast.

Marine endotherms have been intensively studied, and remarkable characters clearly associated with increasing diving abilities have been documented (see Butler & Jones, 1997 for a review). The physiological adaptations of diving endotherms are tightly linked to respiration and metabolism (e.g. increased oxygen stores, reduced global oxygen demands while diving; Boyd, 1997; Butler & Jones, 1997). As a consequence, the physiological traits involved in the respiratory metabolism are characteristic of diving endotherms compared with their terrestrial relatives.

Unfortunately, equivalent deep investigations are lacking for air-breathing diving ectotherms. The available information is nonetheless rich enough to better understand how ectothermic vertebrates cope with the constraints imposed by diving habits (Heatwole & Seymour, 1975; Lutz & Bentley, 1985). The most salient element that emerges from the comparison between diving vs. terrestrial ectothermic vertebrates is the absence of unique, or specific, physiological attributes associated with respiration and metabolism (Heatwole & Seymour, 1975). Major traits linked to lung volume, heart rates, haematological characteristics or metabolic rates are influenced more by the life style of the species (active vs. sit-and-wait foragers) rather than by diving habits (Thomson & Withers, 1997). Most of the studies failed to observe an over-development of the respiratory capacities in marine reptiles (Heatwole & Seymour, 1975; Lutz & Bentley, 1985; but see Lutcavage *et al.*, 1992 for Leatherback turtles). Apparently, most ectothermic air-breathing vertebrates circumvented the respiratory challenges posed by marine life by exploiting several characteristics already well developed in terrestrial species. Notably, ectothermic vertebrates exhibit an extraordinary flexibility with regard to their respiratory physiology: prolonged apnoea, marked bradychardia or resistance to anoxia (all essential attributes for long dives, Bartholomew & Lasiewski, 1965; Lutcavage *et al.*, 1992; Southwood *et al.*, 1999; Seebacher *et al.*, 2005) are documented in nondiving species (Belkin, 1963; McDonald, 1974; Heatwole & Seymour, 1975). The failure to observe an exaggeration of the respiratory capacities in many marine ectotherms compared with their terrestrial relatives generated the notion that the primary

adaptations for diving would be morphological and behavioural rather than physiological (Heatwole & Seymour, 1975; Dawson *et al.*, 1977). The tolerance of ectothermic vertebrates with regard to their respiratory demands is a well-established fact (Pough, 1980). Altogether, these results enable to better appreciate why these organisms outperform endotherms in dive durations (Fig. 1).

However, it is clearly insufficient to understand why body mass was such a poor determinant of diving performances, and it would be a mistake to conclude that diving ectothermic vertebrates are not adapted to aquatic life. As body size influences virtually all aspects of the physiology of animals (Peters, 1983; Calder, 1984), alternative perspectives should be considered. Clearly, marine ectothermic air-breathing vertebrates present sets of morpho-functional adaptations for aquatic life (e.g. nostril valves, skin permeability, salt glands and paddle-shaped limbs). Importantly, if endotherms are well isolated from the environment, the reverse is observed in ectotherms. Important consequences for diving can be stressed. Skin permeability of ectotherms, especially in small-sized species (i.e. sea snakes), means that part of the respiratory constraints are relaxed (transcutaneous underwater oxygen absorption and CO_2 elimination; Graham, 1974; Heatwole & Seymour, 1975). On the other hand, such permeability means that the hydro-mineral balance is highly subject to deviations; most notably important quantities of salt penetrate through the body walls and thus pose a permanent challenge in small species. All marine ectotherms show specializations for salt excretion and water conservation (Peaker & Linzell, 1975). It would be of interest to consider interspecific differences in the relationship between body mass/skin surface ratios and diving performances. Perhaps that this factor, along with skin thickness, skin permeability and vascularization, or foraging mode, is determinant. The effect of body mass *per se* on dive duration could be blurred in an interspecific comparison. If so, the strong putative influence of body mass on diving capacities would be more easily revealed through intraspecific studies. As most ectothermic vertebrate species display extensive variations of body size within populations, such a hypothesis is testable.

Endothermy evolved from ectothermic taxon independently in birds and mammals. The evolution towards endothermy entailed a marked canalization of most of the morphological and physiological traits; the respective anatomies and physiologies of birds and mammals resemble each other more than what could be expected by chance (Farmer, 2000). Therefore, it is not surprising to observe that these two phylums exhibit the same size dependency of dive duration (Schreer & Kovacs, 1997; Halsey *et al.*, 2006a, b). By strong contrast, ectothermy does not lock up life-history traits within a narrow range of variations (Pough, 1980). The exploration of the

evolution of diving physiology may well necessitate adopting novel perspectives to encompass both ectothermic and endothermic modes.

Acknowledgments

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 List of the families used in this study

Appendix S2 List of the studies used to gather maximum dive durations

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/ 10.1111/j.1420-9101.2007.01438.x

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