**Title**: Phylogenetic allometric scaling of basal breathing frequency in terrestrial, semi-aquatic, and aquatic mammals

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**NEW FINDINGS**

**What is the central question of this study?** This study examines the relationship between breathing frequency and body mass in mammals from different habitats (aquatic, semi-aquatic, and terrestrial) under basal conditions. Restricting data to inactive, non-pregnant/non-lactating, adult mammals in their thermoneutral environment following an overnight fast helps clarify this relationship by reducing any influence of factors that may alter respiratory rate.

**What is the main finding and its importance?**

Similar to past studies, the results suggest that the basal respiratory frequency scales differently in aquatic/semi-aquatic mammals as compared with terrestrial mammals. However, only including data with a more restrictive definition of basal, the mass-exponent (slope) for aquatic/semi-aquatic mammals is less steep as compared with past studies. This highlights the importance of careful data screening for comparative studies.

***Abstract***

We collected breathing frequency following an overnight fast in adult, non-pregnant/non-lactating, inactive, mammals ranging in body mass from 15-5520 kg. The data included results from 347 indivdual animals from 36 species that were divided into terrestrial, semi-aquatic and aquatic mammals based on their life history. Following attempts to limit collection of breathing frequency using a basal definition, our results suggest that there are differences in the allometric mass-exponent between terrestrial and aquatic/semi-aquatic mammals. An allometric regression model, where both body mass (*Mb*) and breathing frequency were transformed using the common logarithm (log10), suggested that the allometric mass-exponent for terrestrial mammals (-0.303±0.061) was different from both aquatic (-0.124±0.045) amd semi-aquatic mammals (-0.091±0.051). For semi-aquatic mammals, the breathing frequency was lower in water, but we detected no association of the breathing frequency and the temperature of the medium (water/air). We propose that allometric studies of cardiorespiratory function should, if possible, adhere to the basal defintion during data collection, similar that used for metabolic rate. Such data will provide valuable information for comparative medicine of large, exotic species where controlled baseline data may be difficult to obtain.

***1) Introduction***

The term allometric scaling was coined by Julian Huxley and Georges Tessier in 1936 (Huxley & Teissier, 1936), but the study of the relationship between body size and morphology, or physiology, dates back to the late 17th century when Otto Snell (Snell, 1892) outlined the relationship between brain weight and body size. The relationship between body size and basal metabolic rate (BMR), also often refered to as the *Kleiber law*, was published by Max Kleiber (Kleiber, 1932), where it was shown that energy requirements correlate non-linearly with body mass (Mb) to the power of 0.75, commonly called the allometric scaling factor. There have been numerous publications that debate the value of the allometric scaling factor, but it remains frequently discussed and it has been shown to vary with conditions such as diet and habitat/environment (Darveau *et al.*, 2002; White *et al.*, 2007; McNab, 2008, 2009; White, 2010; He *et al.*, 2023).

A number of variables are known to alter metabolic rate, including digestion (called heat increment of feeding or specific dynamic action) and thermoregulation in an environment with a temperature outside the thermoneutral zone (Secor, 2009; Metze, 2016). The definition of “basal” metabolic rate restricts measurements to adult, non-pregnant and not lactating, post-prandial, animals that are inactive/resting, but not sleeping, and in their thermoneutral range (Kleiber, 1932). Comparing metabolic rates between indviduals or species that are not measured using the basal definition, therefore, increases variation, and in severe cases, can result in erroneous conclusions.

Aerobic metabolism depends on two convective steps to supply the cell with O2: ventilation (breathing frequency and tidal volume), and cardiac output (heart rate and stroke volume). Therefore, not surprisingly, similar scaling relationships have been shown for both ventilation and perfusion (Stahl, 1967; Seymour & Blaylock, 2000; He *et al.*, 2023). However, unlike BMR, cardiorespiratory variables like tidal volume, breathing frequency, heart rate, or stroke volume are seldom standardized, and some studies include anesthetized or restrained animals, or average daily values where the animals have varying activity (Stahl, 1967; Seymour & Blaylock, 2000; Mortola & Limoges, 2006; He *et al.*, 2023). In smaller cetaceans, where digestive processes can increase metabolic rate as much as 40% above BMR following a standard meal (Yeates & Houser, 2008; Fahlman *et al.*, 2024), it was shown that the avergae heart rate in fed bottlenose dolphins increased by between 9-14% as compared with after an overnight fast, after correcting for breathing frequency (Blawas *et al.*, 2021).

In recent studies, it has been shown that the allometric scaling factor for breathing frequency is different in terrestrial and aqautic species (Mortola & Limoges, 2006; He *et al.*, 2023). As the data in these studies were not measured under basal conditions, it therefore difficult to evaluate the potential variation around each data point and the conclusions from these studies. To better understand how breathing frecuency varies with metabolic demands (Fahlman *et al.*, 2016; Roos *et al.*, 2016; Videsen *et al.*, 2023), the cardiorespiratory coupling (Mortola, 2015; Fahlman, 2024), and also as a tool to diagnose respiratory health (Butterworth *et al.*, 2004), it is of interest to define how how breathing frequency scales between species, and varies for species that inhabit different habitats, e.g. terrestrial vs. aquatic environment (Agostoni *et al.*, 1959). Therefore, in this study the aim was to collect data on respiratory frequency in awake, un-restrained, adult, fasted mammals. We specifically wanted to assess 1) whether data collection under more controlled conditions limits variation in results, and also to 2) define the allometric relationship among terrestrial, semi-aquatic, and aquatic mammals.

***2. Material and Methods***

2.1 Data collection and ethical approval

The data collection in the current study was done by focal observations that did not impact the animals or their behavior (e.g. habitat alteration, offering food or nesting material choices, calling, or baiting), and each participating facility approved the data collection. In addition, focal observations to collect breathing frequency were part of the daily husbandry routine in all participating institutions.

A request was sent out to different facilities that house mammals in professional care to collect breathing frequency from focal observations in awake, non-restrained, adult, post-prandial (after an overnight fast), non-pregnant mammals at rest. As opportunistic focal observations could not guarantee that all animals were at rest, the observer was asked to score the activity in 3 levels: 1) rest/inactive, 2) minimal activity, and 3) active.

Data were received from a total of 23 zoological institutions from a total of 1214 measurements in 332 individual animals, from 34 species (and one sub-species of bottlenose dolphin) ranging in body mass from 15 kg to 5270 kg (Table 1). Data included common name (and taxonomic order, family, genus and species), animal ID, sex, body mass, year of birth (for wild caught individuals the age was estimated), activity level during focal observation, number of breaths and duration of measurement, whether measured in water or on land (for semi-aquatic species), temperature of environment where measured (water and/or air), institution, and date of measurement.

2.2 Statistical Analysis

We used a linear mixed model in R (*glmmTMB*), using breathing frequency (*f*R) as a dependent variable, and habitat (Aquatic, Semi-aquatic or Terrestrial), environmental temperature where the individual was measured (air or water; for some semi-aquatic measurements were done both in air and water and the temperature where the individual was measured was used), activity level (rest, some activity, active) and body mass (*M*b) as independent variables. Both *f*R and *M*b were transformed using the common logarithm (log10). We used a hierarchical model, including a random effect of individual ID and nested random effects of order, family, genus and species. We used a Type II ANOVA to test for associations between breath frequency and independent variables (function Anova from the car package in R, Fox & Weisberg, 2019)), and a post-hoc test to asses variation in slopes between habitats (function emtrends in the package *emmeans* in R, Lenth, 2022). All values are reported as means (± s.e.) unless otherwise specified.

***3. Results***

The results from the statistical analysis are presented in Table 2, and the post-hoc testing for differences in slopes between habitat and body mass in Table 3.

The results indicate that there is an allometric relationship between body mass and breathing frequency (Table 2). The full model passed assessment, including checks for linearity as well as normality, independence, and constant variance of residuals. Supplementary material including R code and access to all data: are available at: https://stacyderuiter.github.io/mammal-breath-rate/allometry-of-breathing-frequency.html.

The results indicate that there were differences in the slope of the breath rate – mass relationship between aquatic/semi-aquatic and terrestrial mammals, but not between aquatic and semi-aquatic mammals (Tables 2 and 3). Breathing frequency increased with increasing activity level, but was not affected by the temperature of the environment (water or air) where the individual was measured.

Figure 1 shows breathing frequency against body mass, separated by habitat (with lines showing expected breath rates at rest, that is, an activity level of 1). In this figure are also plotted values from two previously published studies that investigated the relationship with breathing frequency and body mass in terrestrial and aquatic mammals (Mortola & Limoges, 2006; He *et al.*, 2023).

***4. Discussion***

In the current study, we collected breathing frequency from 332 unrestrained individual terrestrial, semi-aqautic and aqautic mammals following an overnight fast. Although focal collection of breathing frequency included measurements of both resting and active individuals at different environmental temperatures, the analysis enabled us to estimate breathing frequency for in active mammals (activity level 1). We therefore believe that these data provide near basal estimates of breathing frequency in mammals.

Allometric scaling is often used to compare energetic needs across species of different body sizes (White *et al.*, 2007; McNab, 2008, 2009; White, 2010; He *et al.*, 2023). Such studies commonly use data from the published literature that have measured basal metabolic rate (BMR), which helps reduce variation due to confoudning factors which is helpful in comparative studies. The allometric mass component, the slope of the relationship between body mass and metabolic rate, ranges between 0.66-0.75 (White, 2010). As increased aerobic metabolism results in elevated convective demand for O2, similar relationships have been shown for to exist for ventilation and perfusion, and both minute ventilation (breating frequency x tidal volume) and cardiac output (heart rate x stroke volume) scale with a similar mass-exponent to that for BMR (Stahl, 1967; Seymour & Blaylock, 2000; He *et al.*, 2023). Despite differences in the breathing strategy between aquatic and terrestrial mammals, where terrestrial mammals generally have a higher breathing frequency and lower tidal volume as compared with aquatic mammals (Mortola, 2015; Fahlman *et al.*, 2017; He *et al.*, 2023), the minute volume has been shown to scale with metabolic rate in both groups, i.e. with an allometric mass-exponent around 0.66-0.75. However, as few comparative studies on cardiorespiratory physiology have attempted to control for variables that may alter metabolic rate, the potential confounding effect of digestion, age, and activity is not known. For example, it was shown that dolphins that had fasted overnight had lower heart rate than those that had been recently fed (Blawas *et al.*, 2021). Thus, studies that have not controlled for potential confounding effects could suffer from increased varaibility, potentially resulting in erroneous conclusions.

The main objective with this study was to determine the allometric relationship between breathing frequency and body mass for mammals that reside in different habitats by restricting the data to basal measurements, i.e. post-prandial, adult individuals, at rest and in their thermoneutral environment. While basal metabolic rate is a well defined unit that allows comparison between species of different sizes, and that resides in different habitat, a similar definition is not commonly done for physiological varaibles that are known to vary with metabolic rate, like breathing frequency. Focal observations, as those presented here, allow the breathing frequency to be measured with minimal interference to the individual animal. However, during such observations it is not always possible to provide measurements of animals at a specific activity level. One option would be to reduce the data set to only include animals at rest. We chose to include all observations and recorded the observed activity level (a separate analysis of the restricted data set provided equivalent results), but then displayed model predictions for only animals at rest (Fig. 1). Although we attempted to measure all animals while post-prandial, true BMR may not be possible for species like ruminants that may require up to 7 days to be post-prandial (Baxter, 1967; National Research Council Subcommittee on Environmental, 1981; McNab, 1997), or certain species of carnivores that consume a large meal and then fast for several days. For all species, we therefore made the measurements before they were fed in the morning following an overnight fast. While this may not be a suffuiciently long fasting period for some species, this was the longest period that was justified to prioritize animal welfare. In addition, the breathing frequency for the ruminants in the current study did not differ noticeably from other groups (Fig. 1). However, unlike past studies, we found the allometric scaling factor for aquatic and semi-aquatic species to be considerably lower than previously reported.

In two past studies it was shown that the allometric scaling factor for breathing frequency for aquatic species had a steeper negative slope (-0.34 to -0.42) as compared with terrestrial mammals (-0.24 to -0.25) (Mortola, 2015; He *et al.*, 2023). In the current study, the allometric mass-exponent for breathing frequency was not different for aqautic and semi-aquatic mammals, but the mass-exponent for aquatic and semi-aquatic was lower as compared with terrestrial mammals (Table 2 and 3). There are several potential reasons for these differences. In past studies, data collection was not controlled for fasting state and came from a wide range of sources such as animals in human care, laboratory studies and results from wild animals where neither fasting state, body mass, age/maturity, or pregnancy status were known (Mortola & Limoges, 2006; He *et al.*, 2023). Another potential reason could be how the species were separated into different habitats. For example, in this study we did not consider capybara to be an aquatic species, and the data set in the current study did not include any otter species or the polar bear (Figure 1). As these species had higher breathing frequencies than expected from the results in the current study (see Fig. 1 semiaquatic), their inclusion may have increased the slope of the relationship in the past studies. When overlaying the results from the past studies on the regression line obtained in the current study, it can be observed that most data points used in the earlier studies fall above the regression lines, espeically for the semi-aquatic mammals (Fig. 1).

The results in the current study highlight the importance of carefully selecting the data depending on the research question. For example, the allometric scaling of BMR is used in comparative veterinary medicine to estimate drug dosage in species for which there is little or no information. However, during general anesthesia, the mode of ventilation and anesthetic dose may also depend on the individual species’ mode of breathing (Le-Bert *et al.*, 2024). For example, adapting the manual ventilation mode for the bottlenose dolphin helped improve ventilation and gas exchange during anesthesia (Le-Bert *et al.*, 2024), since this species has a lower breathing frequency, higher tidal volume as compared with terrestrial mammals, breaths that begin with exhalation followed by inhalation, and long inter-breathing intervals (Fahlman *et al.*, 2015; Fahlman *et al.*, 2017; Piscitelli-Doshkov *et al.*, 2024).

The results presented here highlight how comparative respiratory physiology may provide useful for comparative medicine and wildlife conservation. Breathing frequency is relatively easy to measure and is a potentially useful index for respiratory health and overall stress (Divers, 2008). However, this requires measurements that define baseline values, which may be logistically challenging when dealing with larger, exotic, and difficult-to-study species (He et al., 2023). In the current study, collaboration with several institutions that house terrestrial, semi-aquatic, and aquatic mammals permitted non-invasive data collection which provided baseline respiratory information that could be used to identify respiratory health in wild species. For example, respiratory disease is one of the most common causes for morbidity and mortality in cetaceans in both wild animals and those housed in managed care (Sharp et al., 2014; Sweeney and Ridgway, 1975; Venn-Watson et al., 2012). Respiratory disease is often masked and symptoms often occur when the disease has progressed to an advanced stage. Thus, breathing frequency may be a simple and useful method to evaluate respiratory health and stress. In poorly studied species, allometric extrapolation from related wild species may complement wildlife health assessments, including habitat quality monitoring, climate change and human activities impact, and early management of potential disease outbreaks.

From a clinical point-of-view, empirical extrapolation of medical protocols or drug delivery is already common practice, but may result in problems when extrapolating between species (Freitas and Carregaro, 2013; Mahmood, 2007). Clinicians often use allometric scaling of BMR to estimate drug dose or other clinical assessments, while species-specific physiological details, such as respiratory rate, are often ignored (Freitas and Carregaro, 2013; Mahmood, 2007). The allometric relationship presented here, using data collected on animals with a basal definition, provides a complementary method to evaluate baseline respiratory physiology, which reduces the risk of medical extrapolation, improving safety and efficacy. Moreover, understanding how breathing frequency scales with size between species permits an initial evaluation of respiratory and systematic health. This may be particularly valuable in a field setting approach, where rapid triage and prioritization is required before a more detailed comprehensive diagnostis of respiratory or other underlying disorders are possible.

***5. Conclusion***

In the current study, we collected breathing frequency the morning after an overnight fast in adult, inactive mammals species over a body mass range of 2.5 orders of magnitude. We divided the mammals into terrestrial, semi-aquatic, and aquatic based on their life style. The results suggest that there are differences in the allometric relationship between breathing frequency and body mass, with a different slope (allometric constant) between aquatic/semi-aquatic mammals and terrestrial mammals, but not between aquatic and semi-aquatic mammals. The results in aquatic/semi-aquatic mammals differ substantially from previous studies, which may reflect differences in studies on fed and fasted mammals. These data may provide useful baseline values for estimating respiratroy frequency in exotic, and large species where controlled studies are difficult, and could help with conservation management of threatened species.

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**Tables**

**Table 1.** Summary of all orders, genus and species of terrestrial, semi-aquatic and aquatic mammals with range of body mass (*M*b) and breathing frequency (*f*R). Superscripted numbers in parentheses represent number of terrestrial, semi-aquatic, and aquatic species for each order.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Order** | **Family** | **Genus** | **Species** | ***M*b (kg)** | ***f*R (breaths • min-1)** |
| Artiodactyla | 6 | 14 | 15(7,0,8) | 35.5-3690 | 0.2-45.2 |
| Carnivora | 4 | 10 | 13(4,10,0) | 15-939 | 0.6-42.6 |
| Perissodactyla | 2 | 2 | 2(2,0,0) | 184-2200 | 4.4-22.5 |
| Proboscidea | 1 | 1 | 1(1,0,0) | 3340-5570 | 1.8-9.7 |
| Rodentia | 1 | 1 | 1(1,0,0) | 43-55 | 22.8-44.3 |
| Sirenia | 1 | 1 | 2(0,0,2) | 200-2000 | 0.2-1.6 |
| All | 15 | 29 | 34(15,8,8) | 15-5570 | 0.2-45.2 |

**Table 2.** Parameter estimate (± SE), Z-value (and corresponding P-value), c2 for Type II Wald statistics (and corresponding P-value) from the linear mixed model with log10-transformed breathing frequency (breaths · min-1, log10*f*R) as the dependent variable, and log10-transformed body mass (kg, log10*M*b), and temperature (°C) as independent continuous variables, and habitat (terrestrial, semi-aqautic and aquatic), activity level (1-rest, 2- limited/minimal activity, 3-active), location (whether the individual was measured on *land* or in *water*), and an interaction between log10*M*b and habitat to test for differences in slopes.

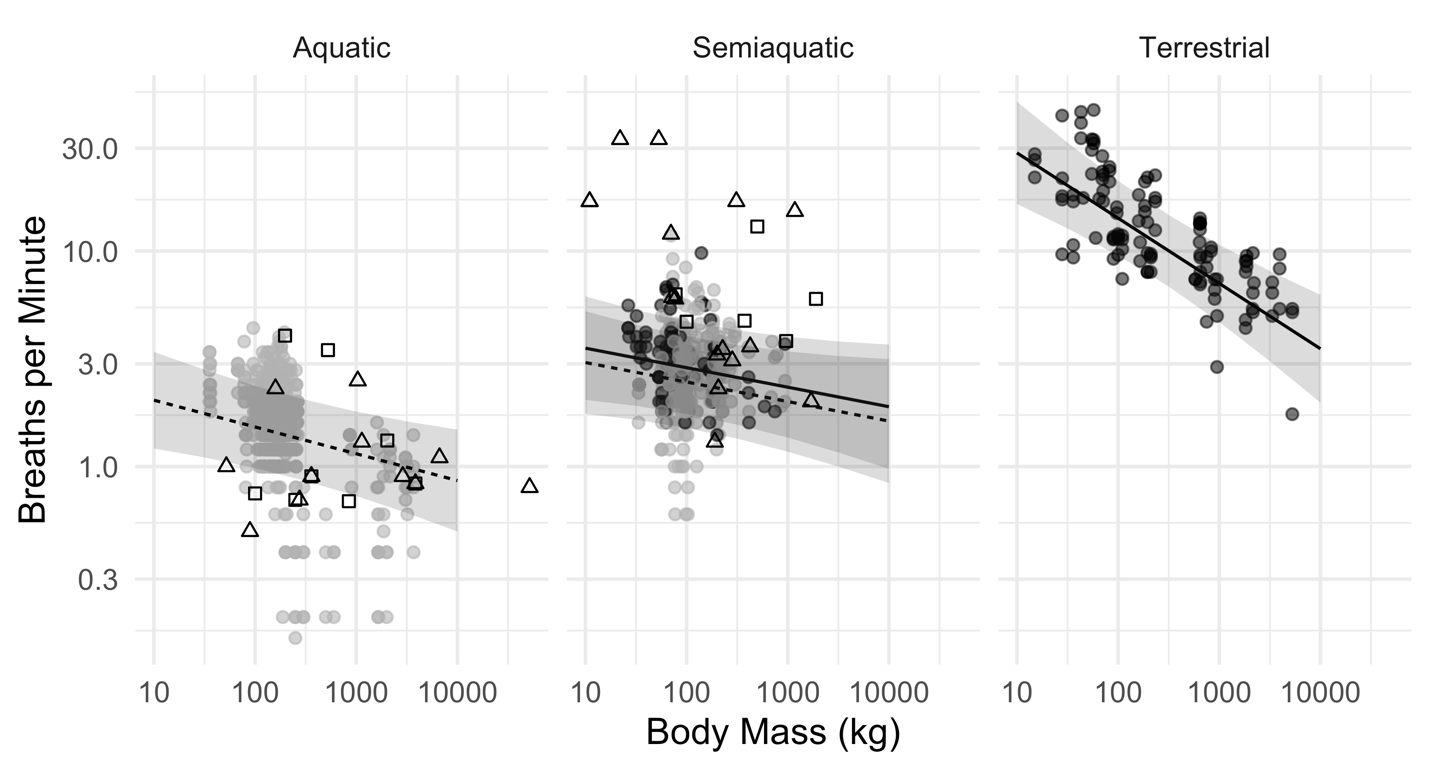
|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Parameter |  | Parameter estimate ± SE | Z-value (P-value) | c2 (P-value) |
| Intercept |  | 0.505 ± 0.150 | 3.366 (0.00076) |  |
| log10*M*b |  | -0.124 ± 0.045 | -2.758 (0.0058) | 27.6 (< 0.0001) |
| Habitat | Semi-Aquatic | 0.141 ± 0.177 | 0.798 (0.425) | 199.4 (< 0.0001) |
| Terrestrial | 1.260 ± 0.191 | 6.615 (<0.0001) |
| Activity level | 2 | 0.081 ± 0.010 | 7.996 (< 0.0001) | 116.5 (< 0.0001) |
| 3 | 0.172±0.017 | 9.851 (< 0.0001) |  |
| Locationwater |  | -0.067 ± 0.024 | -2.770 (0.0056) | 7.7 (0.0056) |
| Temperature |  | -0.00028 ± 0.0011 | -0.243 (0.775) | 0.06 (0.808) |
| log10*M*b x habitat | Semi-aquatic | 0.034 ± 0.068 | 0.496 (0.620) | 8.0 (0.0182) |
| Terrestrial | -0.179 ± 0.076 | -2.366 (0.018) |

**Table 3.** Allometric mass-exponent (± s.e.) for each habitat and post-hoc testing (t-ratio and P-value) for differences in slopes between log10-transformed body mass (log10*M*b) and habitat (terrestrial, semi-aquatic and aquatic).

|  |  |  |  |
| --- | --- | --- | --- |
| Habitat | Parameter estimate ± SE | t-ratio (P-value) comparing Habitats | |
| Terrestrial | Semi-aquatic |
| Terrestrial | -0.303 ± 0.061 |  |  |
| Semi-aquatic | -0.091 ± 0.051 | 2.677 (0.021) |  |
| Aquatic | -0.124 ± 0.045 | 2.366 (0.048) | -0.496 (0.873) |

**Figures**

**Figure 1.** Common logarithm (log10) transformed breathing frequency (breaths · min-1) against body mass (kg) for aquatic (left), semi-aquatic (middle), and terrestrial mammals (right) for 340 individual animals from 6 orders and 34 species of mammals. Grey dots show measurements taken in water, and black on land. Dashed lines indicate model predictions for mammals in water (activity level 1), and solid lines in air, with grey bands showing 95% confidence intervals. On the plot are also data from He et al., (2023) in open squares and from Mortola and Limoges (2006) in open triangles. Note: and interactive version of this figure is available in the online supplementary materials, which allows users to identify data points by order and species.



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