**The aquatic breathing strategy sustains elevated basal metabolic rates in aquatic mammals**

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**Abstract:** The literature is still unclear about whether BMR differs systematically between terrestrial and aquatic taxa, and, if so, how the cardiorespiratory system functions to support these differences. To address this, we performed a comparative analysis of BMR across 722 mammalian species showing that aquatic mammals have elevated BMRs compared to terrestrial mammals. We then hypothesized that, to provide elevated tissue oxygen (O2) to support their higher BMRs, aquatic mammals would have a higher delivery of O2 through the cardiorespiratory system. Although the minute ventilation and cardiac output of aquatic mammals was not elevated relative to terrestrial mammals, we calculated that the breathing strategy exhibited by the former, characterised by a lower breathing frequency and higher tidal volume, results in elevated alveolar ventilation – a more accurate measure of effective gas exchange. Moreover, aquatic mammals have higher blood hemoglobin concentrations giving them a higher O2 loading capacity, which may be an alternative mechanism to a higher cardiac output for supporting their increased BMR. The physiological phenotypes of aquatic species provide valuable models to better understand how different groups of mammals across a wide range of sizes and from diverse environments maintain metabolic homeostasis.

**Introduction**

Basal metabolic rate (BMR) is a fundamental metric in comparative physiology that describes a standardized unit of energy flow which can be used to compare the baseline energetic requirements of organisms and understand how changes in an organism’s environment affect its metabolism (Kleiber, 1961). It is well known that BMR scales with body mass (*M*) as *BMR = cMn* , where *n* is the allometric mass-exponent, and *c* a constant. There continues to be considerable controversy over the value of the allometric mass-exponent (Benedict and Ritzman, 1935; Darveau et al., 2002; Kleiber, 1947; Rubner, 1865; West et al., 2002; White, 2010), but values between 0.67 to 0.75 have been the most commonly cited, and a number of theoretical models have been developed to justify their existence (Darveau et al., 2002; West et al., 1997; West et al., 2002; White and Seymour, 2003). However, there are also studies that argue there is no single universal mass-exponent that encompasses all species (Darveau et al., 2002; Kolokotrones et al., 2010; White, 2010), or that diet, ambient temperature and phylogeny may alter the relationship between body mass and BMR, thereby increasing variability of measured mass-exponents (McNab, 1988, 2008; Naya et al., 2018; Upham et al., 2019).

A number of studies have measured BMR in marine mammals and concluded that these semi- and fully aquatic species have higher metabolic requirements than terrestrial mammals (Hart et al., 1959; Irving and Hart, 1957; Irving et al., 1941; Irving et al., 1935; Kanwisher and Sundness, 1965; Kanwisher and Ridgway, 1983; Scholander, 1940; Scholander et al., 1942; Scholander et al., 1950; Sergeant, 1973; Snyder, 1983; South et al., 1976; Williams et al., 2001). However, several studies have opposed this view and presented data that suggest the BMR of marine mammals is not elevated (Gallivan and Ronald, 1979; Lavigne et al., 1986; Pedersen et al., 2020; Rosen and Trites, 2013; Schmitz and Lavigne, 1984; Worthy et al., 2013). There are a number of potential reasons for this discrepancy. First, BMR is a standardized unit defined under strict conditions to allow for accurate comparisons between species. For example, BMR should be measured in an organism’s thermoneutral zone (TNZ), but a TNZ has not been determined for many marine species (Rosen and Trites, 2014), and it is therefore unclear which studies provide true estimates of BMR. In one study which adhered to the strict conditions for BMR, the authors could not reject the hypothesis that BMR is the same for terrestrial and marine mammals (Lavigne et al., 1986).

Second, heteroscedasticity, or non-constant variance of regression residuals, could influence analyses of the scaling of BMR. Heteroscedasticity, can be seen in the ‘mouse to elephant’ scatter plot/regression in a number of studies investigating metabolic scaling. For example, Figure 5 in White et al. (White, 2010) and Figure 1a in Kolokotrones et al. (2010) demonstrates that the best fit regression line underestimates measured BMR for body mass of 10 kg. Given that all marine mammals are larger than 10 kg, BMR may appear elevated. A past study tried to account for this anomaly by using a quadratic equation to estimate the allometric relationship in terrestrial mammals (Kolokotrones et al., 2010). However, the quadratic model becomes isometric for body masses above approximately 700 kg, which suggests that the BMR of a blue whale (190 tonne) would be 388% higher than that estimated from the equation by Kleiber.

We address this issue with a robust analysis of one of the largest datasets assembled on BMR in mammals that includes phylogenetic information to account for species relatedness. We hypothesized that if BMR differs between terrestrial and marine (or aquatic) mammals, the delivery of O2 should scale similarly for minute ventilation and cardiac output, the products of *V*T x *f*R, and *f*H x SV, respectively. Thus, if BMR is greater in aquatic mammals, both the effective ventilation and the volume of O2 pumped out by the heart should also be greater (Fig. 1), providing further evidence of elevated BMR. Specifically, we hypothesize that: 1) BMR is higher in aquatic mammals than terrestrial mammals (Fig. 1), and in addition, this higher BMR is supported by 2) an elevated delivery of O2 through the cardiorespiratory system (Fig. 1).

In the field of comparative energetics, there remains a controversy as to whether aquatic mammals have higher basal metabolic rates (BMR) than terrestrial mammals. One reason that we might expect aquatic mammals to have elevated BMRs is based on a prediction arising from the heat dissipation limit (HDL) theory. In 2010, Speakman and Król introduced the HDL theory, which proposes that endotherms are often not limited by their ability to access food and convert it into energy as is typically assumed, but rather that metabolic rate is limited by an endotherm’s capacity to remove heat (Speakman and Król, 2010). Because water has a higher thermal capacity than air, aquatic mammals can potentially dissipate heat more effectively than terrestrial mammals. This would result in a lower maximal metabolic rate in terrestrial species and may explain the elevated field metabolic rates of aquatic species (Figure 5 in Speakman et al., 2004)). In turn, terrestrial mammals may have evolved lower BMRs in response to having relatively low maximal metabolic rates, in order to maintain a suitably large aerobic scope, and/or aquatic species may have higher BMRs because of the greater physical and physiological machinery needed to support their high field metabolic rates (Killen et al., 2016) Indeed, some studies have reported higher BMRs in aquatic mammals (Hart et al., 1959; Irving and Hart, 1957; Irving et al., 1941; Irving et al., 1935; Kanwisher and Sundness, 1965; Kanwisher and Ridgway, 1983; Scholander, 1940; Scholander et al., 1942; Scholander et al., 1950; Sergeant, 1973; Snyder, 1983; South et al., 1976; Williams et al., 2001), although others have not (Gallivan and Ronald, 1979; Lavigne et al., 1986; Pedersen et al., 2020; Rosen and Trites, 2013; Schmitz and Lavigne, 1984; Worthy et al., 2013).

All previous studies on the topic can be criticized regarding limitations to the data used and/or analyses employed, which could either generate false differences or mask true differences.

First, while BMR is a standardized measurement that must be recorded while the mammal is within their thermoneutral zone, a putative thermoneutral zone has not been determined for many aquatic species (Rosen and Trites, 2014), and thus many supposed measures of BMR in aquatic mammals may be spurious overestimates. Therefore, in the case of aquatic mammals there may only be a limited number of studies that provide a true BMR estimate, and the resting metabolic rate could be an alternative measure to use. Second, no previous studies have accounted for phylogeny, thus violating a key assumption of regression analyses that the data points are independent. Third, there appears to be variation in the relationship for mammals of larger size (McNab, 2008) resulting in heteroscedasticity (see Fig. 1 in Kolokotrones et al., 2010).

We address this issue with a robust analysis of one of the largest datasets assembled on BMR in mammals that includes phylogenetic information to account for species relatedness. Moreover, we further interrogate the literature on cardiorespiratory parameters to investigate the physiological means by which aquatic mammals service a high field metabolic rate and a putatively high BMR. Specifically, we hypothesize that: 1) BMR is higher in aquatic mammals than terrestrial mammals (Fig. 1), and in addition, this higher BMR is supported by 2) an elevated delivery of O2 through the cardiorespiratory system (Fig. 1).

**Materials and Methods**

As the objective was to compare aquatic and terrestrial mammals, all data obtained were from species with a body mass of 10 kg, representing the body mass of the smallest aquatic mammal, and less than

*Basal metabolic rate*

Basal metabolic rate from 43 terrestrial and 20 aquatic mammal species were compiled from previously published datasets (Genoud et al., 2018; McNab, 2008; White and Seymour, 2003; White and Seymour, 2005), and previous publications (Table 1). For species that were included in more than one database or publication the reported body mass and BMR were averaged. The criteria for measuring BMR included mammals that were inactive adults in a postabsorptive and nonreproductive state, measured under thermoneutral conditions (Kleiber, 1961), and mammals living in aquatic environments had measurements taken in the water. We aimed to only include data for which all criteria for BMR were followed, but for some species this could not be assured, .e.g. the thermoneutral zone is only known for a few number of aquatic species (see Table 2). We therefore include the reported criteria in the supplementary material based on the primary source. Mammals were categorized as terrestrial or marine/aquatic. We hereafter use the term aquatic rather than marine mammal, as not all species included in the definition are defined as marine mammals (cetaceans, pinnipeds, sirenians, marine fissipeds), such as the beaver and muskrat. We restricted mammals over a similar body mass range from 10 kg (smallest aquatic mammal) to 5318 kg (largest aquatic mammal). We therefore exclude a large number of smaller terrestrial mammals which have been used in previous studies.

*Cardiorespiratory variables*

We collected previously published data for heart rate (*f*H), stroke volume (SV), tidal volume (*V*T)and breathing frequency (*f*R)measured on inactive, awake, adult mammals (Table 1). The number of species included in each group and the average body mass of each of those species are summarized in Table 1. We regressed each of these cardiorespiratory variables against body mass for mammals from 11 kg up to 6,650 kg. Data for juvenile animals and those larger than 6,650 kg were included in the dataset but not in the statistical analyses.

*Statistical analysis*

The allometric relationships between dependent variables (BMR, *f*H, *f*R, *V*T, and VT) and the independent variables body mass and habitat [aquatic/terrestrial] were analyzed using a general linear mixed-effects (GLM) model with nested random effects of family and order. Models were fitted in R statistical computing software (R Core Team, 2021; RStudio Team, 2021) using the nlme package (Pinheiro et al., 2021); all code and data files are included in the [supplementary materials](https://stacyderuiter.github.io/mammal-allometry/). For all analyses, BMR (kcal day-1), *f*H (beats • min-1), *f*R (breaths • min-1), *V*T (mL) and body mass (kg) were transformed using the base 10 logarithm (log10). Models included an interaction between habitat and body mass, to determine whether there were differences in slopes or intercepts. For each model, following several standard model assessment checks, a type II ANOVA was performed to estimate the contributions of each predictor.

*Estimating cardiac output and minute ventilation*

We used the results from the regression equations of *V*T, *f*R, *f*H and SV and a parametric bootstrap to obtain predictions with uncertainty estimates of cardiac output (CO = SV  *f*H) and respiratory minute ventilation (MV = *V*T  *f*R) for aquatic and terrestrial mammals (and the difference between aquatic and terrestrial species) for the body mass range of the data. Briefly, we used function predict.glmmTMB from the glmmTMB R package (Brooks et al., 2017), and function bootMer from the lme4 R package (Bates et al., 2015) to predict 100 parametric bootstrap predictions of *V*T, *f*R, *f*H and SV for each species in the datasets, incorporating uncertainty in model parameter estimates and random effects of order, genus and species; the parametric bootstrap samples were multiplied to estimate cardiac output (CO = SV  *f*H) and minute ventilation (MV = *V*T  *f*R) and the results used to obtain estimated predicted values with percentile-based 95% confidence intervals (see SECTIONS 6.1 AND 6.2 IN SUPPLEMENTARY MATERIAL for code details). We followed a similar procedure to obtain estimates and confidence intervals for the expected *difference* in cardiac output and minute ventilation for hypothetical species of varying masses differing only in habitat (aquatic vs. terrestrial). Population-level predictions were used for these differences (neglecting all random effects; see SECTIONS 7.1 AND 7.2 IN SUPPLEMENTARY MATERIAL for code details).

**Results**

The GLM approach was used, which included phylogenetic information and provided taxon-specific predictions. Predictions from the fitted GLM compared favorably with the observed data (see sections 1-5 in SUPPLEMENTARY SUPPLIES). For all models, we only considered measurements performed on in-active, adult, and awake animals (Table 2).

*Basal metabolic rate*

There were significant differences in the both the intercepts (terrestrial = 1.49; aquatic = 2.04) and the slopes (terrestrial = 0.83; aquatic = 0.66) between terrestrial and aquatic mammals (Table 2, see Appendix section 1.2 and Fig. 1.6). A model assessment showed that the full model did not show any evidence of problems with residual normality, residual independence, constant residual variance and linearity (see Appendix section 1.2.1), and predictions from the model showed good relation between observed and predicted BMR (see Appendix section 1.2.2). Using the full model showed that BMR that was 140% higher in aquatic mammals at 10 kg but 17% lower at 5000kg.

*Heart rate and stroke volume*

There were no significant differences between terrestrial and aquatic mammals in the scaling of heart rate (*f*H) (Table 2, see Appendix section 2.2 and Fig. 2.6). After accounting for phylogeny, there was a slight indication that the model overestimated *f*R for smaller mammals (see Appendix Figs. 2.7).

Similar to *f*H, there were no differences in intercepts or slopes between aquatic and terrestrial mammals for stroke volume (SV) (Table 2, see Appendix section 4.2 and Fig. 4.6), and there were no departures from normality, evidence of heteroscedasticity, and the predicted showed good agreement with observed data (see Appendix sections 4.2.1, 4.2.2, and Fig. 4.7).

*Breathing frequency and tidal volume*

The intercept for breathing frequency(*f*R) was higher (terrestrial: 1.51; aquatic: 1.41), while the slope for tidal volume (*V*T) was lower (terrestrial: 0.89; aquatic: 1.10) terrestrial mammals as compared with aquatic mammals (Table 2, Appendix sections 2.2, 5.2, and Figs. 2.6 and 5.6). The model tended to overestimate *f*R for smaller mammals (Fig. 2.7 in Appendix), while for *V*T the models showed no departures from normality of did not indicate heteroscedasticity (see Appendix Fig. 5.7). At 10 kg and 5000 kg, respectively, this resulted in a *f*R that was 61% and 81% lower in aquatic as compared with terrestrial mammals (Table 2, Appendix Fig. 2.6). Tidal volume, on the other hand, was 90% and 602% higher in a 10 kg and 5000 kg aquatic mammal as compared with a terrestrial mammal (Table 2, Appendix Fig. 5.6).

*Estimating minute ventilation, alveolar ventilation, cardiac output, and cardiac O2 output*

A parametric bootstrap (see Appendix section 6.1 and 6.2) was used to estimate cardiac output (CO, Fig. 6.2) and minute ventilation (MV, Fig. 6.4) based on the random-effects models (Table 2), where CO is the product of *f*H and SV, and MV the product of *f*R and *V*T. The differences in the resulting CO and MV between aquatic and terrestrial mammals were computed using a parametric bootstrap (see Appendix section 7.1 and 7.2). For both the estimated CO (Appendix Figs. 7.2 and 7.4) and MV (Appendix Figs. 7.6 and 7.8), confidence limits overlapped and there were no indication of significant differences.

**Discussion**

DISUCSSION-MAY EXPLAIN PAST RESULTS THAT SUGGEST THAT BMR IS HIGHER AS MOST WORK HAS BEEN DONE IN SMALL MARINE MAMMALS. JUSTIFIED TO RESTRICT BODY MASS RANGE AS THERE APPEARS TO BE HETERSTEDASTITY WHEN USING ALL AVAILABLE DATA AND THOSE FROM SMALL MAMMALS. MAYBE BMR IS NOT CHANGING EQUALLY WITH SIZE

Our analyses indicate that the BMR for small aquatic mammals is higher as compared with terrestrial mammals, but the varying slopes and intercepts results in BMR that is the same for body masses > 100 kg. This may explain previous contradictory results that report both equal or higher BMR in aquatic mammals as compared with terrestrial mammals (Allen et al., 2022; Gallivan and Ronald, 1979; Hart et al., 1959; Irving and Hart, 1957; Kanwisher and Sundness, 1965; Lavigne et al., 1986; Pedersen et al., 2020; Worthy et al., 2013). We initially hypothesized that differences in BMR in aquatic and terrestrial mammals was hypothesized to be associated with elevated delivery of O2 through the cardiorespiratory system, i.e. increased minute ventilation and cardiac output. Our analysis suggested that for *f*H, *V*T, and CO there were no differences between habitat. For respiration, *f*R was lower and *V*T was higher in aquatic mammals as compared with terrestrial mammals, but the estimated MV did not differ. We propose that smaller aquatic mammals may be thermally challenged and therefore exhibit a higher BMR as compared with similar sized terrestrial mammals, and both breathing strategy and higher blood O2 capacity helps to increase O2 delivery to support the higher BMR.

**Limitations of the current study**

Numerous studies have attempted to define the allometric relationship between BMR and body mass, resulting in contradictory results and a number of hypotheses relating to the varying allometric mass-exponents (Darveau et al., 2002; Genoud et al., 2018; McNab, 1988, 2008; Rubner, 1865; West et al., 1997; West et al., 2002; White and Seymour, 2003; White and Seymour, 2005). It has been shown that a number of factors may influence the relationship, such food habits, habitat, and climate (McNab, 2008), and data selection has been shown to highly influence results (Genoud et al., 2018). A previous study showed that the allometric mass-exponent changed from 0.60 for mammals of small size (< 300 g) to 0.75 for larger mammals (> 300 g, McNab, 1988), resulting in heteroscedasticity when not accounted for (see Fig. 1 in Kolokotrones et al., 2010). As we were specifically interested in comparing the metabolic requirements for aquatic and terrestrial mammals, we restricted the analysis of BMR in the current study to data where the aquatic and terrestrial mammals had a similar weight range. We carefully restricted the selected data for metabolism to assure that most or all requirements for complying with BMR measurements were fulfilled (see appendix XXX). However, information about the thermoneutral zone is not available for most species, and we therefore included measurements that were within the temperature range where a certain species is found. Furthermore, for measurements of cardiorespiratory variables no standardized criteria exist, but only data for inactive, adult, and awake (not sedated) mammals were included. Thus, given these restrictions the results presented here are based on limited data.

**Higher BMR in aquatic mammals**

One of the early hypotheses to explain the observed allometric relationship between BMR and body mass was based on geometric principles, where body volume and surface area changes disproportionally, and smaller animals therefore have higher mass-specific metabolic rate to offset the higher heat loss (Rubner, 1865; White and Seymour, 2003). With the higher heat capacity of water, small mammals have a greater heat loss as compared with large mammals. Although many aquatic species have a number of anatomical adaptations to reduce heat loss, such as large adipose stores, and countercurrent heat exchangers in peripheral tissues, these may not be sufficient for small aquatic mammals to remain thermally stable, and may therefore rely on higher metabolic set points to deal with the increased heat loss when in water. In larger aquatic mammals, the reduced volume to surface area ratio may reduce heat loss and these species may be able to permit a lower basal metabolic rate.

**What supports elevated BMR in aquatic mammals?**

Our analyses suggest that the heart rate (*f*H ) and stroke volume (SV) for awake, inactive adult mammals were the same in terrestrial as compared with aquatic mammals (Table 2, Figs. 2B-C). Thus, the estimated cardiac output (CO) was therefore the same between habitats. In the current study, the allometric mass exponent for *f*H was slightly lower, but within the confidence limits, and SV similar to that previously published for mammals (Stahl, 1967). Another study, which included data from sedated (anesthetized) mammals with some measurements performed on animals over a full day, reported similar allometric mass exponents of -0.23 for *f*H and 1.03 for SV (Seymour and Blaylock, 2000). Thus, despite our conservative approach of not including only inactive and awake adult mammals, our results are similar to previous estimates (Seymour and Blaylock, 2000; Stahl, 1967).

The breathing frequency (*f*R) of aquatic mammals was lower than that of terrestrial mammals (Fig. 2.6 in appendix), and the lower *f*R has been proposed to help regulate buoyancy rather than having a respiratory function (Mortola, 2015). The results in the current study agree with a previous study that proposed that the allometric mass-exponent is lower in aquatic mammals (-0.34) as compared with that for terrestrial mammals (-0.25, Mortola and Limoges, 2006). Thus, *f*R decreases faster with mass in aquatic mammals as compared with terrestrial mammals, where the aquatic breathing strategy resembles apneustic breathing with brief breaths followed by prolonged inter-breath intervals (Fahlman et al., 2017).

Tidal volume (*V*T), on the other hand, was higher in aquatic species (Table 2), in agreement with previous reports (Fahlman et al., 2017; Piscitelli et al., 2013), but with varying slopes (aquatic: 1.10, terrestrial: 0.89) rather than differences in intercepts (Table 2, Fig. 5.6 in appendix). The allometric mass-exponent previously reported for mammals (1.04, Stahl, 1967), was in between the values reported in the current study. Thus, large aquatic mammals take relatively larger breaths as compared with similar sized terrestrial mammals. Although it is clear that *V*T differs between these two groups of mammals, the limited sample size and non-overlapping body masses warrants additional measurements for small aquatic and large terrestrial mammals (Fig. 5.6 in appendix).

Despite these differences in breathing strategy, the estimated minute ventilation, which is often used as a measure of ventilatory capacity, that, similarly to CO (Figs. 7.2 and 7.4), was the same between habitat (Figs. 7.6 and 7.8 in appendix). The allometric equation presented for mammals reported mass-exponents of 0.80 for MV and 0.81 for CO (Stahl, 1967), which compares well with our estimates of 0.73 (Fig. 7.6 in appendix) and 0.89 (Fig. 7.2 in appendix), respectively. Thus, there does not appear to be any evidence of increased O2 delivery to support the higher BMR in small aquatic mammals either through elevated cardiac output, or minute ventilation (Fig. 1).

What other aspects of the cardio-respiratory system, then, could enhance the oxygen cascade in aquatic mammals? (Fig. 1). Alveolar ventilation () accounts for dead space ventilation and consequently is a more accurate reflection of effective ventilation than is minute ventilation. The breathing strategy of aquatic mammals, characterised by a high *V*Tand low *f*R, could therefore result in higher for the same minute ventilation. To explore this, we used the allometric equations for *V*T and *f*R (Table 2) to calculate alveolar minute ventilation () for a range of body masses from 10 to 10,000 kg as:

= (*V*T - *V*D) • *f*R-1 Eq. 1

assuming that the respiratory dead space volume (*V*D) is 7 and 3% of total lung capacity for aquatic and terrestrial mammals, respectively (Kooyman, 1973). Based on these calculations, alveolar ventilation scaled non-linearly, and the equation for an aquatic mammal was:

(L • min-1) = 1.07 • body mass0.52 Eq. 2

while for a terrestrial mammal the equation was

(L • min-1) = 0.21 • body mass0.73 Eq. 3

We know that aquatic mammals have greater blood O2 loading capacity as an adaptation to increase their blood O2 stores during diving (Beechler et al., 2009; Choy et al., 2019; Vestweber et al., 1991). Thus, the same volume of blood ejected from the heart would contain more O2 in an aquatic than a terrestrial mammal. We calculated cardiac O2 output (, L O2 • min-1) as:

(L O2 • min-1) = *f*H • SV • Hb • 1.34 • 0.01 Eq. 4

where *f*H and SV was calculated using the prediction equations in Table 2, and Hb was either the published hemoglobin concentration for a beluga (23 g • dl-1,(Choy et al., 2019) or the average hemoglobin concentration (12.6 g • dl-1) for a horse (15.5 g g • dl-1) (Plotka et al., 1988) and cow (9.6 g • dl-1) (Rusoff et al., 1951); 1.34 is the O2 loading capacity (ml O2 per g) of hemoglobin. Based on these calculations, the estimated and for a 200 kg aquatic mammal are 49 and 64% higher, respectively, than for a terrestrial mammal.

Combining our analyses with information in the literature suggests that the aquatic breathing strategy and higher blood O2 loading capacity of aquatic mammals provide the means for increased O2 delivery to support their higher BMR.

In addition to greater alveolar ventilation, cyclic changes in *f*H over the breathing cycle, commonly-called respiratory sinus arrhythmia (RSA) may be another mechanism that improves gas exchange in aquatic mammals. RSA has been proposed to improve perfusion ventilation matching and reduce cardiac work (Ben-Tal et al., 2012; Hayano et al., 1996), and is present in both terrestrial and aquatic mammals (Blawas et al., 2021b; Cauture et al., 2019; Fahlman et al., 2020b). The aquatic breathing strategy, with long respiratory pauses and elevated *V*T, results in an RSA that is higher in aquatic than terrestrial mammals (Blawas et al., 2021a; Blawas et al., 2021b; Cauture et al., 2019; Fahlman et al., 2020b; Fahlman et al., 2019). We propose, therefore, that the aquatic breathing strategy not only enhances alveolar ventilation but also elevates RSA, both which help improve ventilation, ventilation-perfusion matching, and gas exchange (Ben-Tal et al., 2012; West, 2012).

Our analysis shows that aquatic mammals demonstrate an elevated BMR in comparison to terrestrial mammals. The elevated BMR requires increased O2 delivery to the cells, which we argue is supported by the aquatic breathing strategy, which elevates alveolar ventilation, matching with higher blood haemoglobin concentration. These findings show how comparative physiology provides valuable insights that help us understand how metabolic homeostasis is maintained in different environments.

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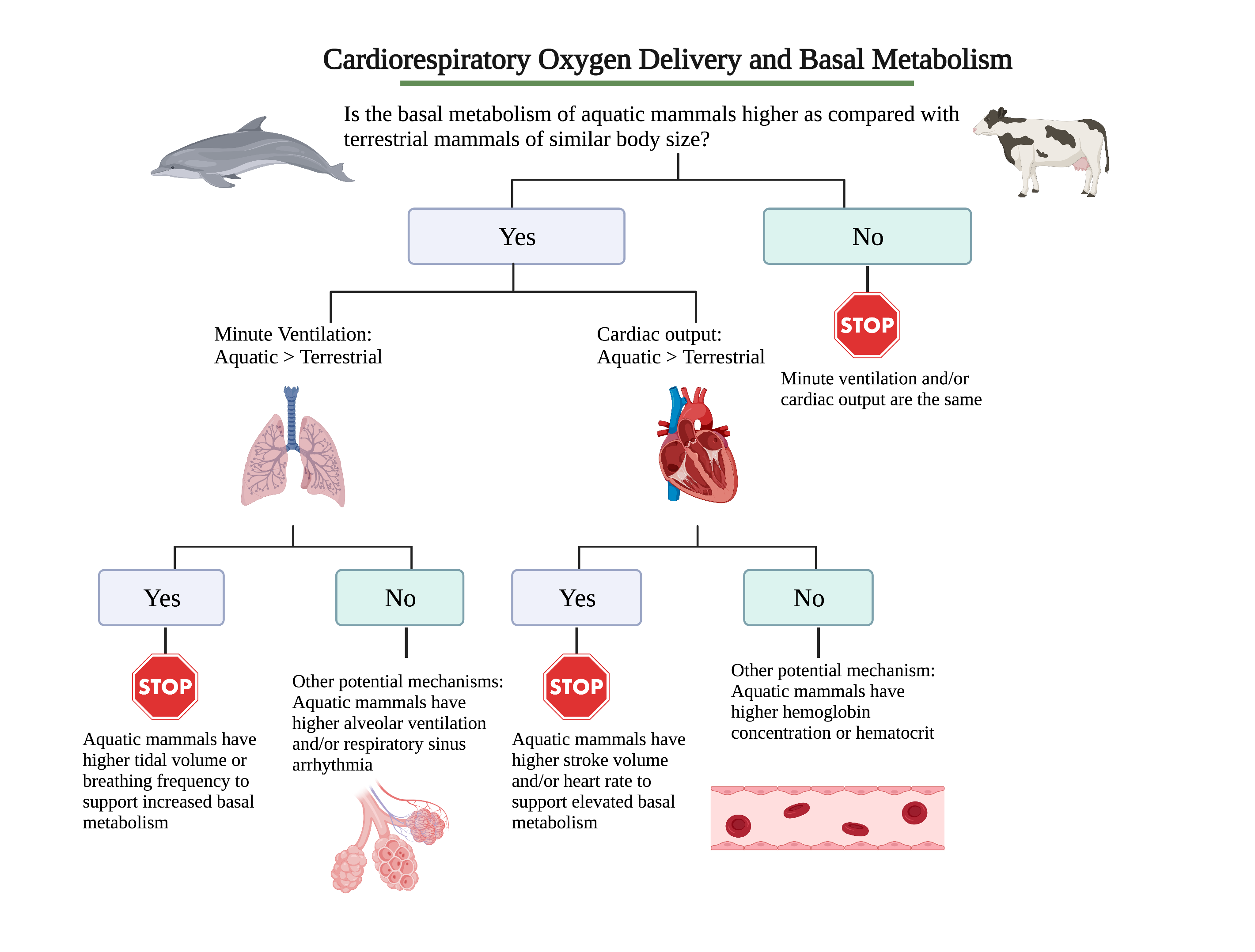
**Table 1.** The total (terrestrial + aquatic) number of orders, genera, and species represented in terms of basal metabolic rate (RMR), breathing frequency (*f*R), tidal volume (*V*T), heart rate (*f*H), and stroke volume (SV). Number in parenthesis is the number for aquatic mammals. Average body mass (*M*b, kg) is stated, with the range in parentheses.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  | **Mean *M*b (range)** | |
| **Full data set** | **Orders** | **Family** | **Genus** | **Species** | **Terrestrial** | **Aquatic** |
| **BMR** | 13 (4) | 32 (10) | 55 (18) | 63 (20) | 154±585 (10-3833) | 483±1187 (10-5318) |
| ***f*R** | 7 (4) | 27 (13) | 65 (27) | 81 (30) | 455±869 (11-4550) | 715±1351 (11-6650) |
| ***VT*** | 6 (3) | 16 (7) | 28 (15) | 31 (16) | 158±174 (13-550) | 1122±1901 (28-6350) |
| ***f*H** | 7 (4) | 23 (13) | 46 (25) | 60 (29) | 565±1118 (18-5000) | 759±1208 (11-5552) |
| **SV** | 6 (2) | 13 (4) | 20 (7) | 20 (7) | 722-1279 (25-4080) | 746±1661 (36-4500) |

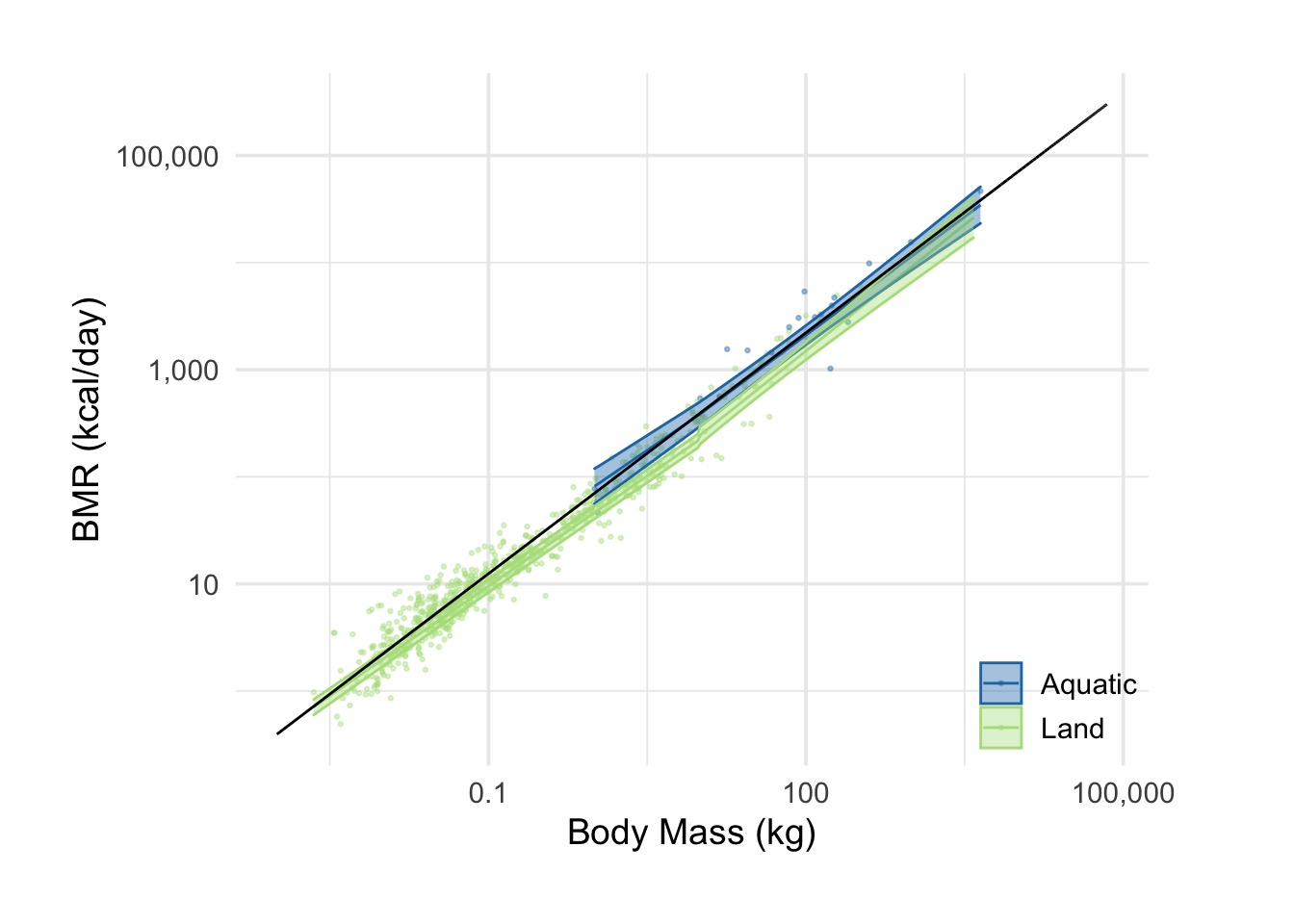
**Table 2.** Allometric model results from general linear mixed-effects (GLM) model with nested random effects of family and order to estimate log10-transformed (log10) basal metabolic rate (BMR, kJ • day-1), heart rate (*f*H, beats • min-1), stroke volume (SV, mL), breathing frequency (*f*R, breaths • min-1), and tidal volume (*V*T, mL). Explanatory variables include log10-transformed body mass ([log10]*M*b), habitat (a parameter that alters the intercept for terrestrial mammals), and a cross-term for log10-transformed *M*b and habitat (the slope). GLM model includes order/family as random factor for the intercept. Table includes parameter estimates (± s.d., with confidence limits in parenthesis) of the full model. \* and † indicates significant p-value either < 0.05 or < 0.01, respectively, of each specific parameter (using a Type II Wald c2 test). Additional results can be found in the appendix and the specific section is “Appendix section”. The reduced model is the one considered for this study and excludes juvenile mammals and those sedated during the study. The full model includes juvenile and sedated mammals, and is used for comparison only in this table.

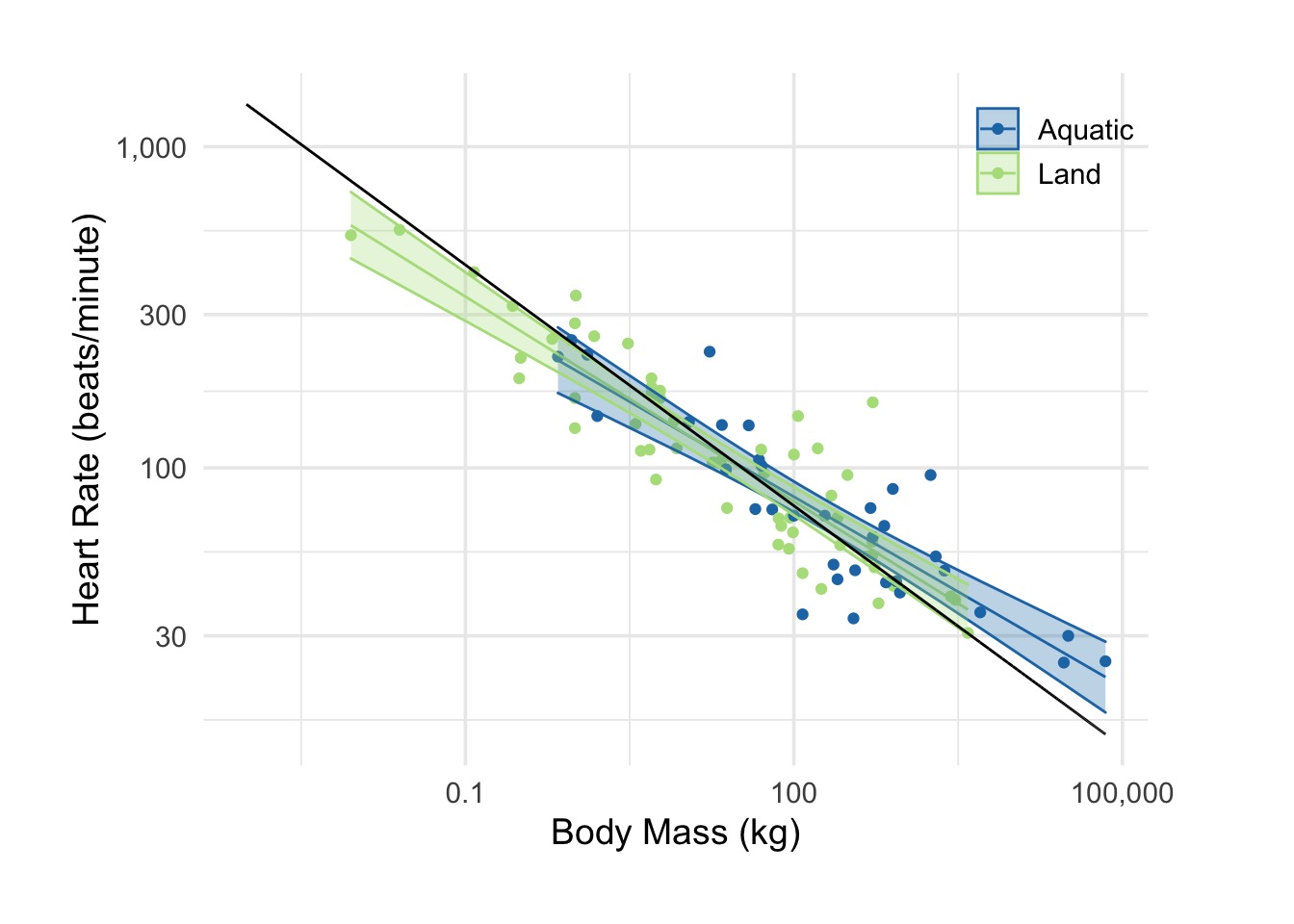
|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Model | Intercept | [log10]*M*b | Habitat (terrestrial) | [log10]*M*b x habitat | Appendix section |
| **Reduced model** |  |  |  |  |  |
| **[log10]RMR** | 2.04±0.14 (1.77:2.30) | 0.66±0.05 (0.56:0.77)† | -0.55±0.13 (-0.81:-0.29)† | 0.17±0.07 (0.03:0.31)\* | 1.2 |
| **[log10]*f*R** | 1.41±0.24 (0.95:1.88) | -0.34± 0.08 (-0.51:-0.17)† | 0.10±0.26 (-0.41:0.62)† | 0.17±0.11 (-0.04:0.39) | 2.2 |
| **[log10]*f*H** | 2.19±0.10 (1.99:2.39) | -0.16±0.04 (-0.24:-0.08)† | 0.01±0.14 (-0.26:0.29) | -0.02±0.06 (-0.13-0.09) | 3.2 |
| **[log10]SV** | -0.002±0.0.19 (-0.36:0.37) | 1.07±0.06 (0.95:1.20)† | 0.20±0.20 (-0.18:0.59) | -0.07±0.08 (-0.23:0.08) | 4.2 |
| **[log10]*V*T** | 1.14±0.18 (0.78:1.51) | 1.10±0.07 (0.98:1.24)† | 0.07±0.24 (-0.40:0.55) | -0.21±0.10 (-0.42:-0.02)\* | 5.2 |
| **Full model** |  |  |  |  |  |
| **[log10]RMR** | 2.04±0.14 (1.77:2.30) | 0.66±0.05 (0.56:0.77)† | -0.55±0.13 (-0.81:-0.29)† | 0.17±0.07 (0.03:0.31)\* | 1.2 |
| **[log10]*f*R** | 1.24±0.20 (0.84:1.64) | -0.28± 0.07 (-0.42:-0.14)† | 0.24±0.24 (-0.22:0.71)† | 0.13±0.10 (-0.07:0.32) | 2.2 |
| **[log10]*f*H** | 2.28±0.10 (2.07:2.49) | -0.19±0.04 (-0.27:-0.11)† | -0.02±0.16 (-0.33:0.29) | 0.02±0.06 (-0.11-0.14) | 3.2 |
| **[log10]SV** | -0.08±0.21 (-0.48:0.32) | 1.08±0.07 (0.93:1.23)† | 0.20±0.24 (-0.26:0.66) | -0.06±0.10 (-0.25:0.13) | 4.2 |
| **[log10]*V*T** | 1.51±0.18 (1.15:1.87) | 0.97±0.07 (0.83:1.10)† | -0.19±0.23 (-0.65:0.27) | -0.13±0.10 (-0.32:0.07) | 5.2 |
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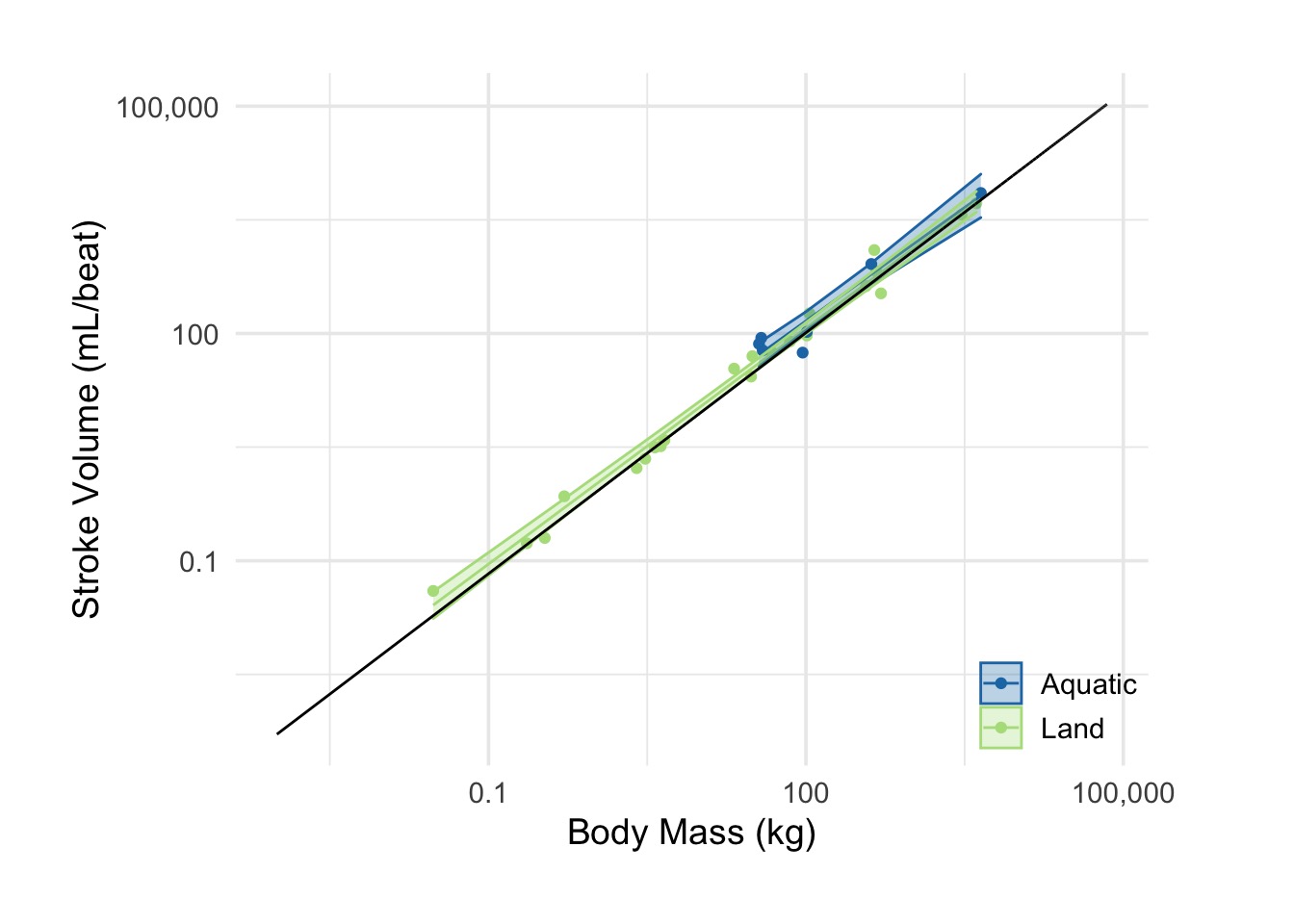
**Figure 1.** The hypotheses tested in the current study. Oxygen flow from the atmosphere to the cell is expected to be different if basal metabolic rate (BMR) is different between aquatic and terrestrial mammals.

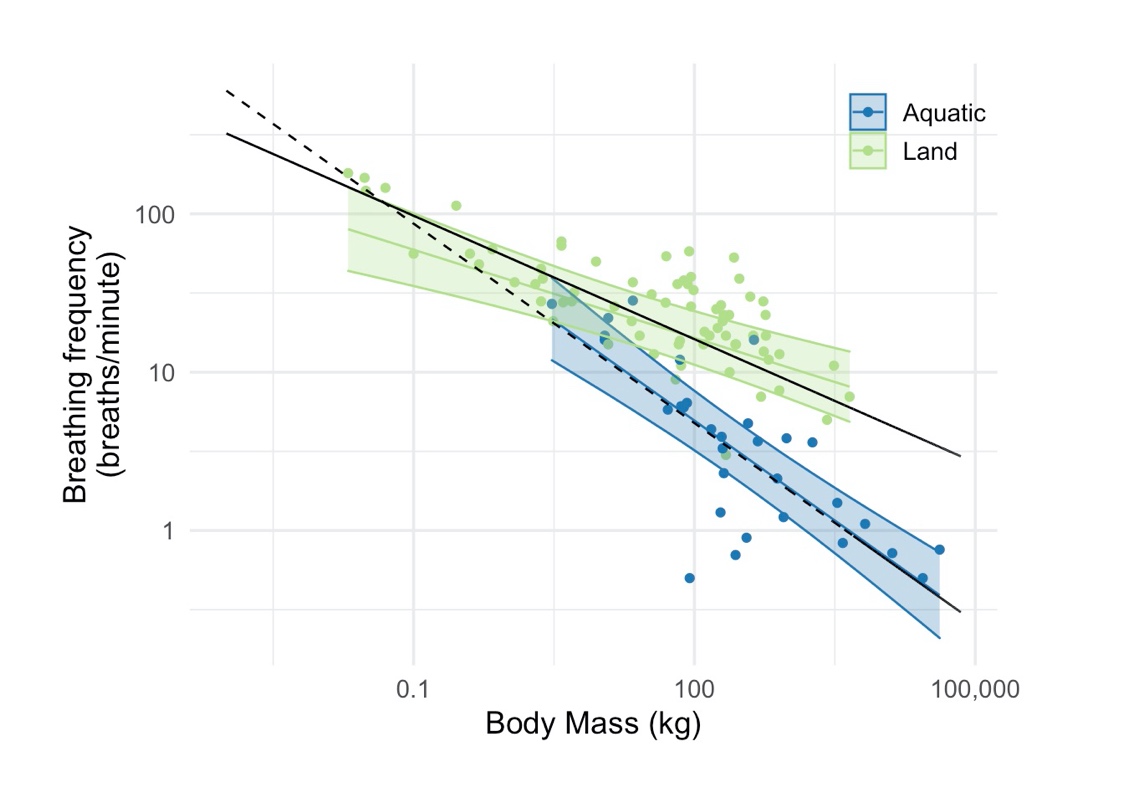


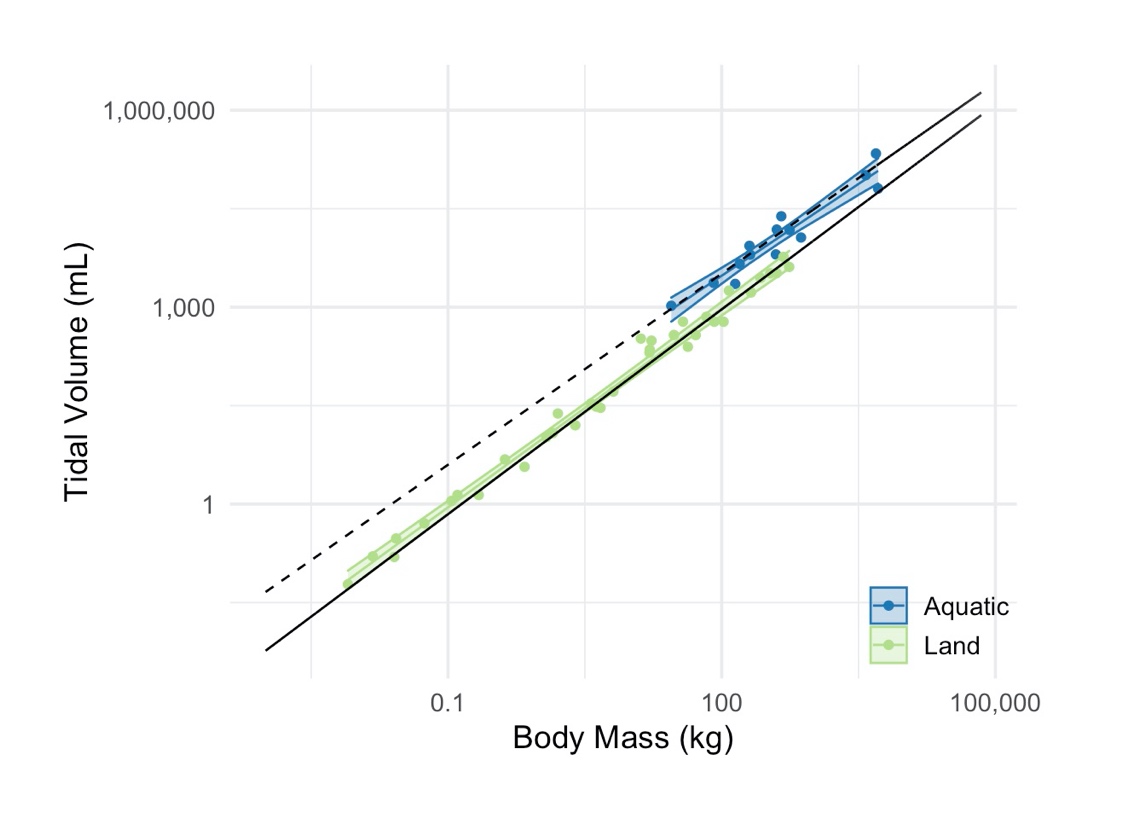
**Figure 2. A)** Basal metabolic rate (BMR, kcal • day-1), B) resting heart rate (beats • min-1), C) stroke volume (ml • beat-1), D) breathing frequency (breaths • min-1), E) tidal volume (ml • breath-1), and against body mass (kg) for terrestrial and aquatic mammals.The solid (terrestrial) and broken (aquatic) black lines are the prediction equations from the literature: A) BMR terrestrial = 70 • body mass0.75 (Kleiber, 1947), B) heart rate terrestrial = 241 • body mass-0.25 (Stahl, 1967), C) stroke volumeterrestrial = cardiac output • heart rate = [181 • body mass0.81] • [241 • body mass-0.25]-1 (Stahl, 1967), D) breathing frequency terrestrial = 53.5 • body mass-0.26 (Stahl, 1967), E) breathing frequency aquatic = 33 • body mass-0.42 (Mortola and Limoges, 2006), tidal volume terrestrial = 76.9 • body mass1.04 (Stahl, 1967) and tidal volume aquatic = 0.0372 • body mass0.92 (Fahlman et al., 2020a).



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**Authors' contributions**

AF, and JAS conceived of the study. JAS, AB, and AF developed the hypothesis, RSH, and DLD obtained the historical data, RSH, SDR, TW, DLD, AS, BS, SD and AF analyzed the data. SDR, TW, AS, BS, and SD carried out the statistical analysis. RSH and AF and drafted the paper, with feedback from co-authors. All authors gave final approval for publication.

**Supplementary materials**

Please refer to this [link](https://stacyderuiter.github.io/mammal-allometry/) for supplementary materials.

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