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Relative size of hearts and lungs of small bats

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We estimated the heart and lung size of several species of small bats (*Tadarida brasiliensis, Mormopterus kalinowski, Myotis chiloensis*, *Histiotus macrotus*, *H. montanus*, *Lasiurus borealis* and *L. cinereus*) and compared these values to those of bats of larger size and other mammals. Our results confirmed that bats have the largest relative heart and lung size of all mammals. This is associated with the high energetic costs of flight. As expected, the mass-specific lung and heart sizes of small bats were larger than those of large bats. However, although relative heart mass decreased according to body mass, $M_b^{-0.21}$, lung volume was nearly isometric with body mass (exponent = 0.90). This exponent was close to unity, and between exponents reported previously (0.77 and 1.06). This suggests that small bats compensate the energetic cost of flight mainly by changes in cardiovascular morphology. The relative heart mass of both *H. macrotus* and *H. montanus* was particularly large, representing 1.71 and 2.18% of total body mass, respectively. These values correspond to 121.3 and 162.7%, respectively, of the expected values from allometric relationships. In these big-eared bats, the large hearts could be attributed to the energetic costs induced by the ears' drag.

Key words: heart, lung, allometric relationships, *Histiotus*, Chile

INTRODUCTION

Bats are the only mammals that have developed active flight. In this group, this energetically expensive form of locomotion is associated with several morphophysiological factors. These include: well developed flight muscles (Mathieu-Costello *et al.*, 1992), large heart and lung size (Jurgens *et al.*, 1981; Maina and King, 1984; Maina, 2000*b*), high heart rate and wing beat frequencies (Thomas, 1987), high cardiac output, high oxygen diffusing capacities (Maina, 2000*a*, 2000*b*), large capillary surface areas (Mathieu-Costello *et al.*, 1992), optimization of the blood gas barrier (Maina, 2000*a*, 2000*b*) and physical optimization of the airway (Canals *et al.*, 2004).

All these adaptations constitute a very efficient machinery for acquisition and delivery of oxygen to different tissues, associated with high maximum metabolic rates (Maina, 2000*b*). However, oxygen consumption is also related to several other factors such as phylogeny, life history, wing morphology, diet, thermal biology and body size (see Cruz-Neto *et al.*, 2001; Cruz-Neto and Jones, 2003; Rezende *et al.*, 2004). From such studies it may be expected that these factors also affect differentially key organs of the cardiovascular and respiratory systems. For example, Jurgens *et al*. (1981) showed different lung volume-body mass and heart size-body mass allometric relationships between bats and other mammals (see also Maina, 2000*a*, 2000*b*).

The allometric relationships between lung and heart size with body size have been estimated mostly for species of bats with body mass above 20 g (see Maina, 2000*b*); the inclusion of more bats outside this range could significantly vary these relationship. Furthermore, bats are the second most diverse order of mammals, and this diversity is associated with variable sources, such as diet (from frugivores to sanguivores), life history, wing morphology, and habitat. If these factors impose energetic constraints on bats, we could expect differences in key organs of the cardiovascular and respiratory systems.

The aim of this study is to estimate the heart and lung size of small bats, comparing them to those of bats of larger size and other mammals.

MATERIALS AND METHODS

Fifty-four individuals of seven species were examined: the molossids, *Tadarida brasiliensis* (*n* = 15; body mass, M_b = 11.25 ± 1.13 g ($\bar{x}$ ± SD) and *Mormopterus kalinowski* (*n* = 2; M_b = 3.10 ± 1.13), and the vespertilionids, *Myotis chiloensis* (*n* = 22; M_b = 6.88 ± 0.47 g), *Histiotus macrotus* (*n* = 4; M_b = 9.65 ± 0.61), *H. montanus* (*n* = 1; M_b = 12.50), *Lasiurus borealis* (*n* = 5; M_b = 7.87 ± 1.10) and *L. cinereus* (*n* = 5; M_b = 12.76 ± 2.74). All specimens were captured during the regular program for rabies control and donated to us by the Chilean Institute of Public Health.

Animals were sacrificed and radiographs of the thorax were taken. The heart was extracted and weighed the following day through a standard thoracotomy. All radiographs were obtained with a standardized technique of 300 mA, 0.05 s and 50 KV and with 1 m of object-focus distance, a sufficient distance to make magnification negligible.

The lung volume was estimated from radiographs with a previously developed method (Canals *et al*., 2005). On the images of the lungs, a straight line (RL) between both costophrenic recesses was traced, and several measurements were made: i) the width of RL (W) as a lateral measurement; ii) the height between RL and the top of the left (H_1) and the right (H_2) lung; and iii) left (w_1) and right (w_2) lung width at the middle point of diaphragm domes (Fig. 1). Considering the average between w_1 and w_2 as an estimator of the dorso-ventral diameter of the lungs (i.e., in lungs with nearly circular basal sections) a box containing the lungs and mediastinum organs was built. Canals *et al*. (2005) showed that lungs filled 49.6% of the volume of this box and therefore:

$$V_L = 0.496 \times V_{RX} \approx 1/2 \times V_{RX}$$

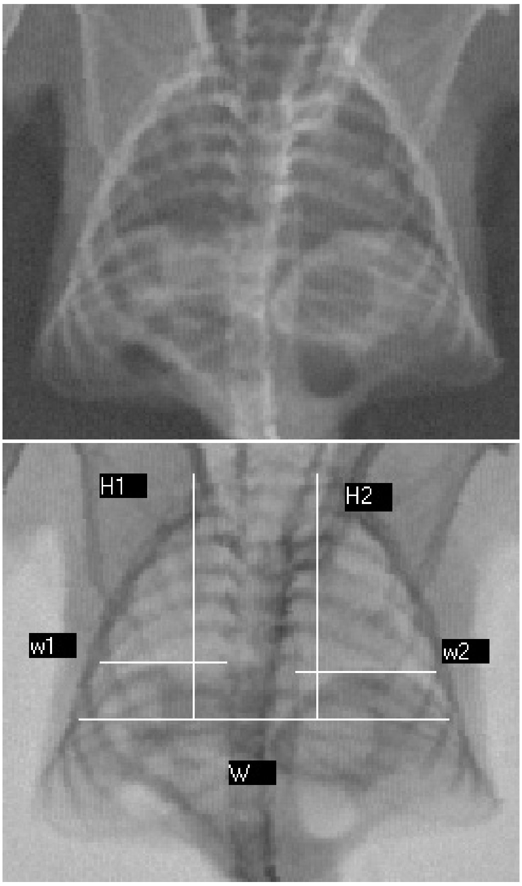

FIG. 1. Thorax radiograph of *Histiotus macrotus*. At the bottom are the reference lines used to estimate the lung volume

was a good estimator of the lung volume, where:

$$V_{RX} = W \times (\frac{H_1 + H_2}{2}) \times (\frac{w_1 + w_2}{2})$$

represented the volume of the box containing the lungs.

Heart mass and lung volume were compared with the expected values from the allometric relationships

$$M_H = 0.01471 \times M_b^{0.0883}$$

for heart mass (Jurgens *et al.*, 1981) and:

$$V_L = 0.16 \times M_b^{0.7731}$$

for lung volume of bats (Maina *et al.*, 1991). Also, lung volume was compared with values predicted for all mammals by:

$$V_L = 0.046 \times M_b^{1.06}$$

(Gher *et al.*, 1981). To test differences between observed and expected values, the observed/expected ratio (R) was computed and the hypothesis H_0: $R \leq 1$ vs. H_1: $R > 1$ was tested with Student's *t*-tests.

Regression analyses (potential model) were performed using our data and values from the literature (Jurgens *et al.*, 1981; Maina *et al.*, 1991) to estimate new allometric relationships between heart mass and lung volume with body mass.

To compare mass-specific heart masses (relative heart mass, RHM) and mass-specific lung size (relative lung volume, RLV) between the species of this study, one-way ANOVA analyses or Kruskal-Wallis tests were used when appropriate. Multiple comparisons with the Tukey test or its non-parametric equivalent were also performed. To study possible phylogenetic effects on heart mass, independent of body mass, the ratio between the observed and expected values from allometry was analyzed with an unbalanced nested ANOVA, considering taxa (i.e., families: molossids vs. vespertilionids) and species as factors.

RESULTS

Heart masses (M_H) of the studied species were larger than expected from the allometric relationship for bats:

$$M_H = 0.01471 \times M_b^{0.0883}$$

where M_b is body mass. When M_H was divided by the expected values derived from the allometric relationship of Jurgens *et al.* (1981) ratios were larger than unity in most cases, 1.235 ± 0.235 ($t = 7.06$, $n = 49$, $P < 0.001$ — Table 1).

When we used both Jurgens' and our species we obtained the following relationship:

$$M_H = 0.02273 \times M_b^{0.791 \pm 0.058}$$

(both variables in grams and the exponent expressed as $\bar{x} \pm$ SE; $F_{1,\ 10} = 188.1$, $P < 0.001$, $r^2 = 0.949$ — see Fig. 2).

We found significant differences in the relative heart mass (RHM) of different species (Kruskal-Wallis: $H = 10.75$, $P < 0.05$). RHM of *M. kalinowski* was larger than that of *T. brasiliensis* and *M. chiloensis*, and the RHM of *H. macrotus* was larger than *T. brasiliensis* ($P < 0.05$ in multiple

TABLE 1. Heart size ($\bar{x}$ ± SD) of bats. M_H is the heart mass, RHM is the relative heart size (M_H/M_b, in %), and R is the observed/expected ratio of heart mass as derived from the allometric relationship: $M_H = 0.02273 \times M_b^{0.791 \pm 0.058}$ (this study)

Species	*n*	M_b (g)	M_H (g)	RHM	R
Tadarida brasiliensis	15	11.25 ± 1.13	0.145 ± 0.033	1.29 ± 0.23	0.943 ± 0.176
Mormopterus kalinowski	2	3.10 ± 1.13	0.057 ± 0.018	1.88 ± 0.10	1.041 ± 0.022
Myotis chiloensis	21	6.88 ± 0.47	0.096 ± 0.015	1.40 ± 0.20	0.921 ± 0.137
Histiotus macrotus	4	9.65 ± 0.61	0.166 ± 0.035	1.71 ± 0.03	1.213 ± 0.237
H. montanus	1	12.50	0.272	2.18	1.627
Lasiurus borealis	5	7.87 ± 1.10	0.120 ± 0.020	1.55 ± 0.27	1.046 ± 0.169
L. cinereus	5	12.76 ± 2.74	0.173 ± 0.042	1.40 ± 0.04	1.042 ± 0.279
*Pipistrellus pipistrellus**	2	4.85 ± 0.18	–	1.26 ± 0.24	–
*Myotis myotis**	4	20.60 ± 0.90	–	0.98 ± 0.08	–
*Molossus ater**	4	38.20 ± 1.40	–	0.97 ± 0.01	–
*Phyllostomus discolor**	4	45.20 ± 1.34	–	0.94 ± 0.09	–
*Rousettus aegyptiacus**	3	146.00 ± 7.50	–	0.84 ± 0.08	–

* — data from Jurgens *et al.* (1981)

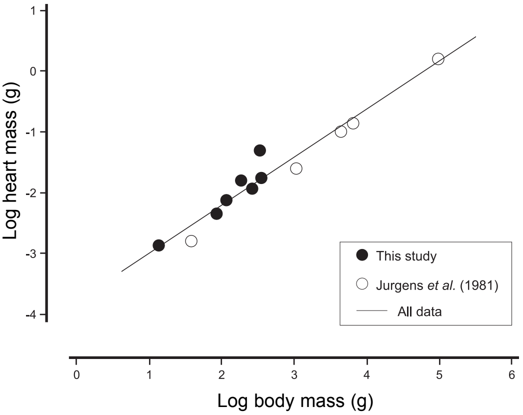

FIG. 2. Allometric relationship between heart mass and body mass for several bats (Log is natural logarithm)

comparisons). When we analyzed the observed/expected ratio (from our allometric relationship) to remove the effect of body size on heart mass, we found a marginally statistical significance ($F_{5,\ 44}$ = 2.27, P = 0.06), sustained only by the differences between *H. macrotus* and both *M. chiloensis* and *T. brasiliensis* (P < 0.05 in the Tukey test — Fig. 3). When we analyzed phylogenetic effects on that ratio we did not find family (taxon) influence ($F_{1,\ 5}$ = 0.31, P > 0.05) but we confirmed species effects ($F_{4,\ 44}$ = 2.74, P < 0.05).

As expected, the lung volume of our bats was larger than that expected for all mammals from the allometric relationship:

$$V_L = 0.046 \times M_b^{1.06}$$

where M_b is in kg and V_L in liters. When the lung volumes measured in this study were divided by the expected values from Gher's allometry, values were larger than unity: 1.727 ± 0.262 (t = 16.5, n = 23, P < 0.01). However, when compared with the expected lung volume for bats from:

$$V_L = 0.16 \times M_b^{0.7731}$$

(where M_b is in grams and V_L in ml), the lung volume of our species was lower than expected. The observed/expected ratio was 0.600 ± 0.109 (t = 8.90, n = 17, P < 0.01). Including our species and four species of large bats from Maina *et al.* (1991), we obtained the general allometric relationship:

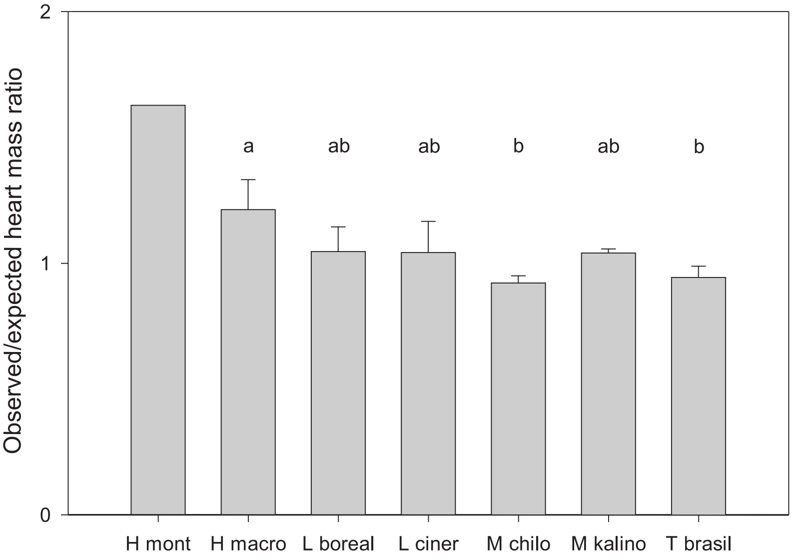

FIG. 3. Observed/expected ratios for the heart mass of *Tadarida brasiliensis* (T brasil), *Mormopterus kalinowski* (M kalino), *Myotis chiloensis* (M chilo), *Histiotus macrotus* (H macro), *H. montanus* (H mont), *Lasiurus borealis* (L boreal) and *L. cinereus* (L ciner). Species differences are indicated by different letters above the bars. *Histiotus montanus* was not used in the analysis (n = 1)

$$V_L = 0.0714 \times M_b^{0.9028\pm0.019}$$

(M_b in grams and V_L in ml; $F_{1,9} = 2166.1$, $P << 0.001$; $r^2 = 0.996$ — Fig. 4). We did not note significant differences in relative lung volume between the studied species (Table 2).

Discussion

Our results confirm that bats have larger relative heart and lung size than all other mammals. This is associated with the high energetic cost of flight. As expected, the mass-specific lung and heart sizes of small bats were larger than those of big bats. However, while the relative heart mass decreased according to $M_b^{-0.21}$, the lung volume was nearly isometric with body mass. This exponent (b = 0.90) falls between Maina's (0.77) and Gehr's (1.06) exponents.

There were differences in the direction of the deviations from the expected from the different allometries. While heart mass of small bats was larger than expected from allometric relationships for bats (Jurgens *et al.*, 1981), the lung size of small bats was smaller than expected from the allometric relationship for their lung volume (Maina *et al.*, 1991). Furthermore, relative lung volume was similar in all the studied species. This suggests that small bats compensate the energetic cost of flight mainly by changes in their cardiovascular system, with large hearts and correspondingly greater large cardiac outputs (Snyder, 1976; Jurgens *et al.*, 1981). In concordance, it has been found that bats have relatively high hemoglobin concentrations and hematocrits. For example, a venous hematocrit of 68% and a hemoglobin concentration of 24.4 g/dl has been reported for *T. brasiliensis* (Maina, 1998). While elevated hematocrit and hemoglobin concentration may enhance aerobic capacity through an increased oxygen transport, this advantage may be compromised by a greater energetic demand to drive a more viscous blood through the vascular system (Maina, 1998), requiring a large heart.

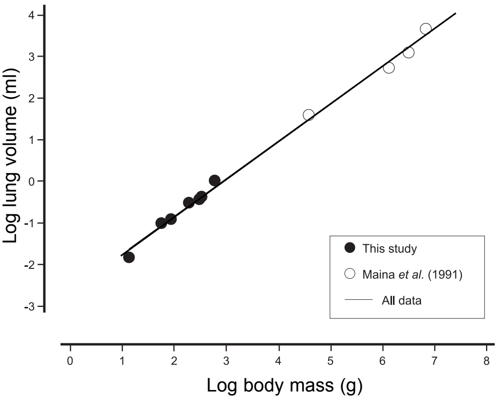

Fig. 4. Allometric relationship between lung volume and body mass for several bats (Log is the natural logarithm)

Both *H. macrotus* and *M. kalinowski* had relatively larger hearts than *T. brasiliensis* and *M. chiloensis*. However, when controlled for body mass, only the heart mass of *H. macrotus* was different from that of *T. brasiliensis* and *M. chiloensis*. This fact indicates that the differences in heart mass are in part a consequence of the nonlinear relationship between body mass and oxygen consumption. Heart size is determined by physiological demands and is not linearly related to body mass. Furthermore, bats have a closer correlation of heart mass with oxygen consumption than has been found in larger animals (Jurgens *et al.*, 1981).

Species of different phylogenetic origin were included in this study, Vespertilionidae and Molossidae; these were compared with species of Phyllostomatidae, Molossidae, Vespertilionidae and Pteropidae (Jurgens *et al.*, 1981; Maina *et al.*, 1991). Comparisons between congeneric taxa, for example between the vespertilionids, *M. chiloensis* (6.9 g) with *Myotis myotis* (20.6)

TABLE 2. Body mass (M_b) and lung volume (V^*_L) of several bats. RV_L is the relative lung size (V_L/M_b)

Species	*n*	M_b (g)	V^*_L (cm^3)	RV_L (cm^3/g)
Tadarida brasiliensis	4	11.95 ± 1.36	0.654 ± 0.091	0.055 ± 0.011
Mormopterus kalinowski	2	3.10 ± 1.13	0.162 ± 0.024	0.054 ± 0.021
Myotis chiloensis	8	6.95 ± 0.54	0.406 ± 0.071	0.058 ± 0.009
Histiotus macrotus	3	9.80 ± 0.666	0.602 ± 0.094	0.061 ± 0.005
H. montanus	1	12.50	0.696	0.056
Lasiurus borealis	2	6.80 ± 2.05	0.455	0.064 ± 0.004
L. cinereus	3	16.06 ± 7.62	1.025 ± 0.389	0.066 ± 0.010
*Phyllostomus hastatus**	4	97.8 ± 2.56	4.95 ± 0.26	0.051 ± 0.007
*Pteropus lylei**	7	456.0 ± 20.87	15.37 ± 1.93	0.034 ± 0.011
*P. alecto**	1	667.0	22.20	0.033
*P. poliocephalus**	1	928.0	39.24	0.042

* — data from Maina *et al*. (1991); lung volume measured by means of water displacement method

and the molossids, *T. brasiliensis* (11.3) with *Molossus ater* (38.2) and *M. kalinowski* (3.1) did not show differences other than those expected from differences in body size. Our phylogenetic analysis did not detect differences between molossids and vespertilionids, but it showed specific differences sustained by extreme values. *Histiotus* species seem to have larger hearts than expected from the allometric relationship (Fig. 3), which could be a consequence of their phylogenetic position and similar morphology and life style. The RHM of both *H. macrotus* and *H. montanus* were particularly large, 1.71 and 2.18% of body mass, which correspond to 121.3 and 162.7% of the values expected from allometric relationships, respectively.

Although the sample size was small, one specimen of *H. montanus* and four specimens of *H. macrotus*, the relative heart size of both species was consistently high. These species are commonly known as big-eared bats. Both species can live in dense woodlands, but also inhabit areas with few trees. In Chile, they are commonly present in savannas and zones with shrubs and woodlands. They are generally found in small colonies in mines, caves, roofs and tree holes (Mann, 1978; Redford and Eisenberg, 1992). They have wing loadings (WL) and aspect ratios (AR) similar to those of *M. chiloensis* and *L. borealis*. Preliminary estimations for WLs and ARs are 7.0 N/m^2 and AR = 6.8, and 7.167 N/m^2 and AR = 6.6 for *H. macrotus* and *H. montanus*, respectively (M. Canals, unpubl. data). For *L. borealis* WL = 7.4 N/m^2 and AR = 6.6 (Patterson and Hardin, 1969) and for *M. chiloensis* WL = 6.8 N/m^2 and AR = 5.76, have been reported (Canals *et al*., 2002; Iriarte-Díaz *et al*., 2002). The ears of *H. macrotus* are about 3 cm long, and those of *H. montanus* about 2 cm long, representing 29–42.8% and 22–33% of the total body length, respectively (Mann, 1978). During flight these bats can afford to have large, drag-producing ears, like *Plecotus auritus* (Norberg, 1987). Field observations suggest that both species have a low flight speed (Mann, 1978) as expected from the allometric relationship:

$$v = 2.9 \times WL^{0.44}$$

where v = flight speed (Norberg, 1987). This, added to the drag-producing ears, makes locomotion among shrubs energetically expensive. Their large heart could be a cardiovascular response to this life style.

The heart and lung are key organs in the strategy for specialization for flight in bats. Within the mammalian scheme, the heart and lung are remarkably refined and operating close to their maximal performance (narrow-based and high-keyed strategy — Maina, 1998). The most important specializations are: large hearts (Snyder 1976; Jurgens *et al.*, 1981), high hematocrit, hemoglobin concentration, erythrocyte count and blood oxygen capacity (Wolk and Bogdanowicz, 1987) and thin blood-gas barrier and large lungs (Maina and King, 1984; Maina, 1998, 2000*b*). Moreover, all anatomical and physiological specializations enhance the oxygen uptake capacity of bats in flight to levels similar to those of birds (Thomas, 1987). Most likely, the main factor determining the size of these organs is related to oxygen requirements, which are allometrically correlated with body size, and only secondarily modulated by resource abundance, foraging behavior, life style and phylogeny.

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