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Pulmonary hematological parameters, energetic flight demands and their correlation with oxygen diffusion capacity in the lungs

Parámetros hematológicos pulmonares, demandas energéticas del vuelo y su correlación la capacidad de difusión de oxígeno en los pulmones

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ABSTRACT

Hematological parameters of birds and mammals seem to respond to environmental requirements, such as hypoxia at high altitude and the energetic demands of locomotion and flight. In this work we hypothesize that lung capillary hematocrit and red blood size may be influenced by the energetic requirements of flight. Also, we propose that hematological parameters should vary together with the morphological parameters that determine oxygen diffusion capacity. We analyzed the red blood cell size and the local characteristics of the pulmonary capillary hematocrit correlating these with the pulmonary factors that determines the oxygen diffusion capacity. We deal with seven species, non-flying and flying birds and mammals, with different energetic requirements. The capillary hematocrit was not different in each taxon, but the red blood cell size was smaller in flying mammals and birds than non-flying ones. Correlation of erythrocyte size with the diffusing characteristics of the lungs produced a non-phylogenetic clustering with a group constituting by the bats *Tadarida brasiliensis* y *Myotis chiloensis*, and the bird *Z. auriculata*; revealing similar functional response in unrelated species. Finally, in mammals, a negative correlation between the red blood cell size and the mass-specific oxygen diffusion capacity was obtained. These results suggest that the direction of the hematological and pulmonary adjustments is governed mainly by the requirements of flight independent of phylogenetic origin of the species studied.

Key words: cost of flight, capillary hematocrit, red blood cell size, oxygen diffusion capacity

RESUMEN

Los parámetros hematológicos y pulmonares parecen responder a las exigencias ambientales como la hipoxia y la alta altitud y a los requerimientos energéticos de la locomoción. En este trabajo sometemos a prueba la hipótesis que el hematocrito del capilar pulmonar y el tamaño del glóbulo rojo pueden ser influidos por los requerimientos energéticos del vuelo. También proponemos que los parámetros hematológicos varían en conjunto con los parámetros que determinan la capacidad de difusión de oxígeno. Analizamos el tamaño del glóbulo rojo y las características locales del hematocrito capilar pulmonar correlacionándolos con los factores pulmonares que afectan la capacidad de difusión de oxígeno. Analizamos siete especies de diferente requerimiento energético, corredoras y voladoras. El hematocrito capilar pulmonar no mostró diferencias significativas en aves ni en mamíferos. El tamaño del glóbulo rojo fue menor en los mamíferos y en aves voladoras con respecto a sus pares no voladores. La respuesta conjunta del glóbulo rojo, la superficie respiratoria y la membrana alvéolo-capilar mostró un agrupamiento no filogenético donde se destaca un cluster constituido por mamíferos y aves de vuelo activo (dos murciélagos: *Tadarida brasiliensis* y *Myotis chiloensis* y la tórtola *Zenaida auriculata*). Finalmente, en mamíferos se obtiene una relación inversa entre la capacidad de difusión de oxígeno y el tamaño del glóbulo rojo. En definitiva, los hallazgos sugieren la existencia de ajustes funcionales hematológicos y pulmonares como una respuesta conjunta a las exigencias del vuelo, independientes de su origen filogenético.

Palabras clave: costo de vuelo, hematocrito capilar, tamaño glóbulos rojos, capacidad difusión de oxígeno.

INTRODUCTION

Hematological parameters of birds and mammals seem to respond to environmental requirements, such as hypoxia at high altitude and the energetic demands of locomotion and flight (Novoa et al. 2002). For example, a lower mean cell volume of erythrocytes was reported for small high altitude mammals (Thomomys) than for mammals living at sea level (Lechner 1976). Similarly Rosenmann & Ruiz (1993) reported that *Abrothrix andinus* (Phillipi, 1858)which dwells over 2.000 m of altitude, have high red blood cell counts, increased blood hemoglobin concentration and significant decrease in mean cell volume during seasons of high energetic requirements, while the hematocrit remains constant throughout the year. Also, the hematocrit of resident high altitude species has been reported to be similar to that of species which inhabit low elevations (Morrison et al. 1963a, 1963b, Rosenmann & Ruiz 1993). In birds, which have a high tolerance to hypoxia (Novoa et al. 1991), the hematological response to high altitude is still controversial. In native high-altitude birds some authors have shown higher blood hemoglobin concentrations, red blood counts (Carey & Morton 1976) and hematocrits than for birds of low altitude (Carey & Morton 1976, Keys et al. 1986). However other authors have been reported similar hematological parameters but differences in hemoglobin oxygen affinity (Black & Tenney 1980). Carpenter (1975) and Viscor et al. (1985) argued that the hematocrit of bird is more related to flight than to altitude distribution.

Hematological parameters respond to environmental and energetic demands together with respiratory and cardiovascular modifications, rather than in an isolate form (Carey & Morton 1976, Viscor et al. 1985, Viscor & Fuster 1987). Regarding flight demands, birds exhibit several adaptive features such as an efficient cross-current system in their air way, large tidal volume, short pulmonary circulatory time which maximizes the utilization of hematological factors in gas uptake, large respiratory surface areas and thin air-blood barrier (Maina 1998, 2000a, 2000b, Figueroa et al. in press). Similarly, bats show a number of refinements in the design of the cardiovascular and respiratory systems, which include: large heart and cardiac output (Canals et al. 2005a, Jurgens et al. 1981); small erythrocytes (Wolk & Bogdanowics 1987, Neuweiler 2000), high concentrations of hemoglobin and high oxygen transport capacity (Wolk & Bogdanowics 1987); and optimization of structural lung parameters such as lung volume, density of the respiratory surface and thickness of the alveolar-capillary barrier (Lechner 1985, Maina 1998, 2000a, 2000b, Maina et al. 1991, Canals et al. 2005b, Figueroa et al. in press).

In the lung the hematological parameters can vary by the particulate nature of the blood passing through a complex network of capillaries (Baumgartner et al. 2004) and due to differences in the relative speed of plasma and erythrocytes (Rapaport et al. 1996, Hsia et al. 1999). A progressive increase of about two-to three-fold of pulmonary diffusion capacity from rest to exercise has also been reported (Hsia et al. 1995, 1999). These particular behavior of the erythrocytes in the lung capillaries, suggests that it is possible a different response of capillary blood hematocrit in species with different energetic requirements. In this work we hypothesize that lung capillary hematocrit and red blood size may be influenced by the energetic requirements of flight. Also, we propose that hematological parameters should vary together with the morphological parameters that determine oxygen diffusion capacity.

MATERIAL AND METHODS

We studied five mammals and two bird species. We included two bats (flying mammals), *Myotis chiloensis* (Waterhouse, 1838) (M_b = 6.05 ± 0.10 g (mean ± SD); n = 3) and *Tadarida brasiliensis*(Geoffroy Saint Hilarie, 1824) (M_b = 11.3 ± 0.5 g; n = 4) and three non-flying mammals, *Phyllotis darwini* (Waterhouse, 1837) (M_b = 75.36 ± 4.96 g, n = 3) *Abrothrix olivaceus* (Waterhouse, 1837)(M_b = 26.3 ± 2.0 g, n = 3) and *Abrothrix andinus*. (M_b = 25.5 ± 1.9 g, n = 3) Our bird models were *Zenaida auriculata* (Des Murs, 1847) (M_b = 141.1 ± 1.55 g., n = 3) an active flying species and *Nothoprocta perdicaria* (Kittlitz, 1830) (M_b = 398.33 ± 11.70 g, n = 3) a species that fly sporadically. All birds and rodents individuals used in this study were caught with Sherman traps or mist nets and immediately transported to the laboratory during

spring and summer between 2003 and 2005. The bats were donated by the Institute of Public Health from Chile. Animals were weighed and then killed by means of 100 % CO_2 exposure or by an overdose of anesthetic by intraperitoneal injection following the guidelines of the Ethical Committee of the Faculty of Sciences of the University of Chile. The trachea were exteriorized and cannulated. In the case of birds we avoided injection into the air sacs. A quantity of 2.3 % glutaraldehyde in phosphate buffer (pH 7.4) was introduced in the trachea (Maina 2002a). When the fixative solution exceeded the level of the trachea, we closed it and tied it to the cannula. Immediately following this procedure, the lungs were removed and immersed in the same fixative at 4 °C for a minimum of 2 h. Next, tissues (right and left lungs) were processed for routine electron transmission microscopy. Briefly, two pieces of 1-2 mm thickness were obtained from each lobe in mammals and four randomly chose pieces were obtained from each lung of birds. The pieces were washed with buffer and post-fixed with 1 % osmium tetroxide for 1 hour at 4 °C. Tissues were then dehydrated in graded concentrations of alcohol and infiltrated and embedded in epoxy resin constructing cubes of 2-3 mm^3, obtaining semi-thin sections of 1μm. Tissue samples were stained with 1 % toluidine blue. Ultrathin sections of 60-90 nm of thickness were made and mounted on copper mesh grids. These sections were contrasted with Pb-citrate. Sections were studied through optical and transmission electron microscopy (JEOL/JEM 100SX). Eight to twelve sections were photographed, digitalized and twelve semi-thin and twelve ultra-thin sections per individual were analyzed using Scion Image Software.

From the images that showed lung capillaries, the capillary hematocrit was estimated by means of the stereologic point counting method (Weibel et al 1970/71) as Hto = pe / (pe + pl), where pe and pl are the number of points of a grid that intersect erythrocytes and plasma, respectively. Also, diameter (D_e) and the length of transversal axis of erythrocytes (T_e) were measured using a morphometric software (Scion Image). For practical purposes the diameter was defined as the length of the mayor axis following the curvature of the cell and the transversal axis was traced perpendicular to that in the mid point of the diameter (Fig. 1).

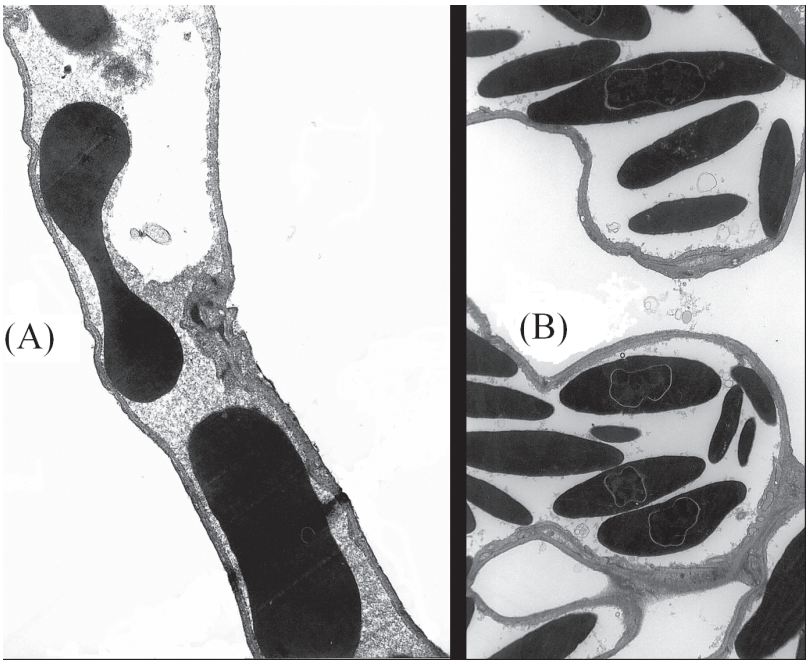

Fig. 1: Pulmonary capillary and red blood cells in (A) the bat *Tadarida brasiliensis* (7000X), and (B) the bird *Nothoprocta perdicaria* (1500X).

Capilar pulmonar y glóbulos rojos en (A) el murciélago *Tadarida brasiliensis* (7000X) y (B) la perdiz *Nothoprocta perdicaria* (1500X).

Hematocrit and red blood cell size data from mammals and birds were analyzed with the Kruskall-Wallis, Wilcoxon signed, and Mann-Whitney U-tests, respectively. The frequency distribution of the hematocrit values (i.e., number of capillary with a particular hematocrit) among the species studied was compared with a χ^2 test for both taxa.

To explore possible relations between pulmonary and hematological parameters, the present red blood cell diameter data and published data of respiratory surface area and thickness of the blood gas barrier from the same individuals of each species (Canals et al. 2005b, Figueroa et al. in press) were analyzed by means of a cluster analysis and a principal component analysis based on standardized values ($z = [\bar{x} - sd] / sd$, sd the standard deviation) for each taxon (birds and mammals). The relationship between the red blood cell size and the mass specific oxygen diffusion capacity of the blood gas barrier (D_LO_2/M_b) was studied with correlation and regression analyses. That is a good estimator of the oxygen conductance independent of the body mass because the nearby linear relationship between D_LO_2 and M_b ($D_LO_2 \alpha M_b^{1.08}$, Weibel et al. 1992). Independent phylogenetic contrasts (Felsenstein 1985) at order level were used considering the molecular phylogenetic hypothesis proposed by Murphy et al. (2001).

RESULTS

We did not find differences in the lung capillary hematocrit in mammals or in birds ($\chi^2_4 = 6.67$, P = 0.155 and Z = 0.567, P = 0.564 in Kruskall-Wallis and Wilcoxon tests for mammals and birds respectively) (Table 1). However, in birds we found a more symmetrical distribution than in mammals ($\chi^2_{20} = 41.05$, P = 0.0037; Fig. 2). While mammals had a negative skewness in the frequency distribution of the capillary hematocrit (-0.47 in average), birds did not show skewness (0.0032). In both taxonomic groups, the frequency distributions of the species were marginally similar ($\chi^2_{12} = 20.71$, P = 0.06 and $\chi^2_4 = 8.51$, P = 0.07 in mammals and birds respectively). Considering the individual capillary segment as the study object, the lung capillary hematocrit ranged between 0 and 99 % in mammals and between 0 and 89 % in birds.

TABLE 1

Lung capillary hematocrit and the dimensions of the red blood cell in five mammalian and two avian species. D_e and T_e are the diameter and the transversal length of the erythrocyte respectively. Different letters indicate statistical differences at $\alpha = 0.05$ in the Kruskall-Wallis a-posteriori non-parametric multiple comparison test

Hematocrito capilar pulmonar y dimensiones de los glóbulos rojos en cinco especies de mamíferos y dos especies de aves. D_e y T_e corresponden al diámetro longitudinal y transversal respectivamente. Letras diferentes indican diferencias significativas con un nivel $\alpha = 0,05$ usando comparaciones múltiples post prueba de Kruskall-Wallis

Species	Capillary hematocrit (%)	D_e (µm)	T_e (µm)
Mammals			
Abrothrix olivaceus	59.6 ± 15.4	5.74 ± 0.40 bc	1.14 ± 0.09 a
Abrothrix andinus	69.8 ± 4.7	4.73 ± 0.21 b	1.54 ± 0.09 ab
Phyllotis darwini	44.0 ± 4.5	7.05 ± 0.22 c	1.23 ± 0.06 ab
Tadarida brasiliensis	65.0± 7.5	4.18 ± 0.12 a	1.22 ± 0.11 ab
Myotis chiloensis	60.4± 7.8	4.38 ± 0.17 ab	2.56 ± 0.13 b
Birds			
Nothoprocta perdicaria	41.8 ± 3.6	9.70 ± 0.11	2.35 ± 0.03
Zenaida auriculata	49.0 ± 11.8	8.77 ± 0.12	1.37 ± 0.02

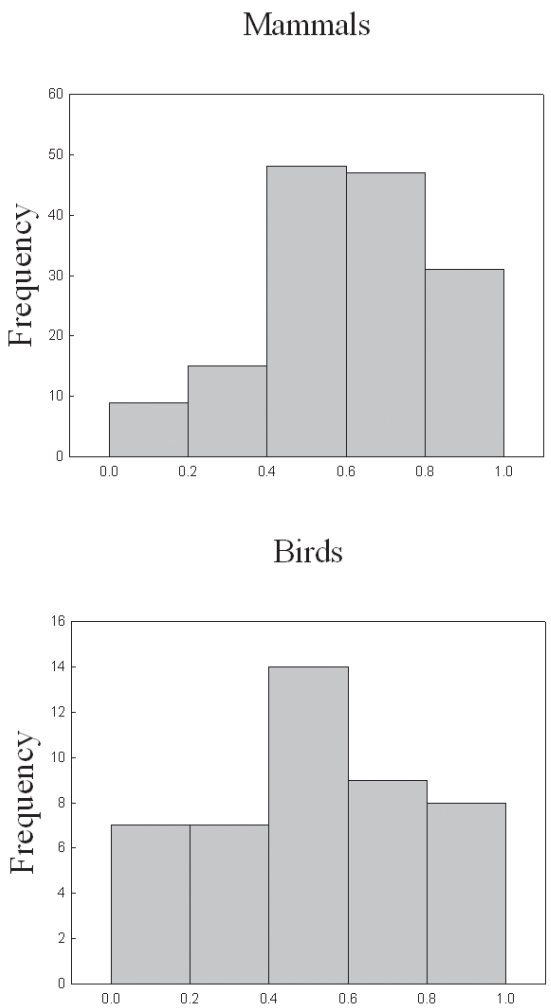

Fig. 2: Frequency histograms of the pulmonary capillary hematocrit in mammals and birds. All intervals were of the same length from 0 to 100% hematocrit: 1 = 0-20 %; 2 = 20-40 %; 3 = 40-60 %; 4 = 60-80 % and 5 = 80-100 %. Here the analysis unit is the capillary section.

Histograma de frecuencias del hematocrito capilar pulmonar en mamíferos y aves. Todos los intervalos del mismo largo, desde 0 a 100 % de hematocrito: 1 = 0-20 %; 2 = 20-40 %; 3 = 40-60 %; 4 = 60-80 %, and 5 = 80-100 %. Aquí la unidad de análisis es la sección capilar.

We found differences in erythrocyte size: χ^2_4 = 10.99, P = 0.026 and χ^2_4 = 10.32, P = 0.035 for D_e and T_e, respectively, in mammals; and Z = 1.73, P = 0.08 (the small P due to the sample size) and Z = 1.73, P = 0.08 D_e and T_e in birds, respectively. The diameter of the red blood cells (D_e) in *Zenaida auriculata* was smaller than in the "non-flying" *Nothoprocta perdicaria*. In the bats *T. brasiliensis* and *Myotis chiloensis*, D_e was small and only comparable with that of *A. andinus* (Table 1).

When we contrasted erythrocyte size with the morphological determinants of the oxygen diffusion capacity of the lungs using a cluster analysis, we found that bats and the active flying bird *Z. auriculata* clustered close together. A similar result was obtained with the principal component analysis (Fig. 3).

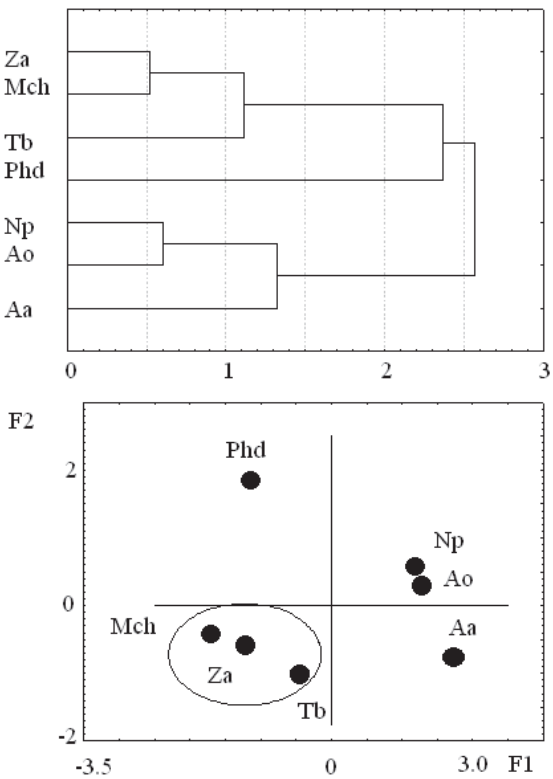

Fig. 3: Cluster analysis (up) and principal component analysis (down) based on standardized values of red blood cell diameter, respiratory surface area and thickness of the blood gas barrier (from Canals et al. 2005b, Figueroa et al. in press). Active flying animals marked with circles; Tb = *Tadarida brasiliensis*, Mch = *Myotis chiloensis*, Phd = *Phyllotis darwini*, Aa = *Abrothrix andinus*, Ao = *Abrothrix olivaceus*, Np = *Nothoprocta perdicaria*, Za = *Zenaida auriculata*.

Análisis de conglomerados (arriba) y análisis de componentes principales (abajo), basado en los valores estandarizados del diámetro del eritrocito, la superficie respiratoria y el grosor de la barrera aire-sangre (de Canals et al. 2005b y Figueroa et al. in press). Encerradas en un círculo los voladores activos; Tb = *Tadarida brasiliensis*, Mch = *Myotis chiloensis*, Phd = *Phyllotis darwini*, Aa = *Abrothrix andinus*, Ao = *Abrothrix olivaceus*, Np = *Nothoprocta perdicaria*, Za = *Zenaida auriculata*.

We found a negative but non significant correlation (r = -0.44, $F_{1,3}$ = 0.75, P = 0.45) of erythrocyte diameter with D_LO_2/Mb in mammals, but when we included additional data from the literature (Table 2) the correlation was significant (r = -0.46; $F_{1,17}$ = 4.71, P = 0.044; Fig. 4). This result did not vary when we considered *M. chiloensis* as an out-groups (r =-0.47, $F_{1,16}$ = 4.56, P = 0.048) and neither when we considered only one average value per taxonomic category (order) (r = -0.79, $F_{1,6}$ = 9.62, P < 0.02). When we analyzed but corrected by phylogeny (independent contrasts) we obtain similar results (r = -0.824, $F_{1,5}$ = 10.567, P < 0.0226). Our bird data show a similar trend, the smaller the red blood cell, the higher D_LO_2/Mb. Unfortunately, the scarcity of available studies in which in which red blood cell size and D_LO_2 avoid us to obtain robust results. With 15 points a non significant but negative correlation was found (r = -0.31, $F_{1,12}$ = 1.29, P = 0.27).

DISCUSSION

The lung capillary hematocrit of the species studied was similar in mammals and birds. It showed great intra-individual variability, ranging from 0 to 99 % in mammals and from 0 to 89 % in birds. This means that there are capillary sections without red blood cells and other capillary sections with a very large number of them. This results agrees with those found in the classic study of Wearn et al. (1934) in which the not random switching of blood flow among pulmonary capillaries was described as the normal behavior of these vessels. Okada et al. (1994) found a considerable switching among capillaries which was not correlated with small variations in arterial pressure or cardiac output. Although the mechanism of switching remains unknown, it is thought that it is correlated with the continuously changing hematocrit of the blood that perfuses the pulmonary capillaries. In a similar vein, in vivo microscopic observation of individual pulmonary capillary segments showed that hematocrit varies constantly from zero to high values when a train of closely spaced red blood cells passes through the segment (Baumgartner et al. 2004).

Although the hematocrit differences among mammals did not reach statistical significance, the lung capillary hematocrit of the bats *M. chiloensis* and *T. brasiliensis* was high, specially considering that the mean pulmonary hematocrit is about a 90 % of that of the systemic great vessels (Hsia et al. 1999). This is an expected result for bats, in which venous hematocrit over 60 % are frequently reported (Neuweiler 2000). In particular in *T. brasiliensis* a venous hematocrit between 68 and 75 % was found (Black & Wiederhielm 1976). In addition, in other species of the genus Myotis hematocrits of 43 % in *M. myotis* (9.3 g) and 60 % in *M. natteri* (12.5 g) were reported (Neuweiler 2000). All these values are in the range of our data and could be attributed to the high oxygen requirements of flight. However, the hematocrit of *A. andinus* was also very high. Although *A. andinus* is a rodent that lives at high altitude which has high red blood cell counts, increased blood hemoglobin concentration and significant decrease in mean cell volume during seasons of high energetic requirements, the hematocrit has been reported constant and ranging from 49.9 to 53 % throughout the year in this species (Rosenmann & Ruiz 1993). If our result is a consequence of the high energetic requirements at high altitudes, we would expect a different response of the capillary hematocrit in the lungs than of the venous hematocrit. However, the lung capillary hematocrit of *A. olivaceus*, which inhabits low altitudes, also showed a high value. Finally, as expected, the hematocrit of *P. darwini* was low and similar to the 42.5 %, reported by Morrison et al. (1963a).

Differences in the red blood cell size among species reported here suggest that this parameter is highly correlated with the locomotion style. In both mammals and bird species the same trend towards to exhibits a small size in active flying animals was found. In addition, the high Andean rodent *A. andinus* and the bats had a very small red blood cell size, suggesting a positive association between erythrocyte size and oxygen demand.

Correlation of erythrocyte size with the diffusing characteristics of the lungs produced a non-phylogenetic clustering with a group constituting by the bats and *Z. auriculata*; revealing similar functional response in unrelated species. This cluster suggests also that

TABLE 2

Red blood cell diameter (D_e), oxygen diffusion capacity air-erythrocyte (DLO_2) and mass-specific oxygen diffusion capacity (D_tO_2/M_b) in several mammals and birds. Data of TGR from this study[1], Gregory (2000)[2], Banerjee et al. (1962)[3], Bartels et al. (1979)[4], Goniakowska-Witalinska (1976)[5], Altman & Dittmer (1974)[6], Bartsch et al. (1937)[7], Mushi et al. (1999)[8], Gulliver (1875)[9]. Data of D_LO_2 and D_LO_2/M_b from Canals et al. (2005b)[10], Figueroa et al. (in press)[11], Maina (2002)[13] and Gehr et al. (1981)[12]. Values of oxygen diffusion capacity D_LO_2 of some species (Canals et al. 2005b and Figueroa et al. in press) were estimated from the tissue oxygen diffusion capacity D_tO_2 by using $D_LO_2 = D_tO_2/10$ (Canals et al. 2005b)

Diámetro del glóbulo rojo (D_e), capacidad de difusión de oxígeno (D_LO_2) y capacidad de difusión de oxígeno masa-específica (D_tO_2/M_b) en mamíferos y aves. Datos de TGR de este estudio[1], Gregory (2000)[2], Banerjee et al. (1962)[3], Bartels et al. (1979)[4], Goniakowska-Witalinska (1976)[5], Altman & Dittmer (1974)[6], Bartsch et al. (1937)[7], Mushi et al. (1999)[8], Gulliver (1875)[9]. Datos de D_LO_2 y D_LO_2/M_b de Canals et al. (2005b)[10], Figueroa et al. (in press)[11], Maina (2002)[13] y Gehr et al. (1981)[12]. Los valores de D_LO_2 de algunas especies (datos de Canals et al. 2005b y Figueroa et al. in press) fueron estimados a partir de la capacidad de difusión de oxígeno de la barrera D_tO_2 a partir de $D_LO_2 = D_tO_2/10$ (Canals et al 2005b)

Species	Mb (g)	D_e (αm)	D_LO_2 ($x10^{-5}$mL O_2 s^{-1} $mbar^{-1}$ g^{-1})	D_LO_2/M_b
($mL\ O_2\ s^{-1}\ mbar^{-1}$)				
Mammals				
Mus musculus[2,12]	42	6.80	0.00213	5.07143
Rattus rattus[2,12]	457	7.50	0.01830	4.00438
Phyllotis darwini[1,11]	75	7.05	0.00469	6.26473
Abrothrix olivaceus[1,10]	26	5.74	0.00075	2.86198
Abrothrix andinus[1,10]	26	4.73	0.00128	5.0434
Cavia porcellus[2,12]	429	7.10	0.01790	4.17249
Myotis chiloensis[1,11]	6	4.38	0.00156	26.0731
Tadarida brasiliensis[1,10]	11	4.18	0.00094	8.32943
Oryctolagus cuniculus[2,12]	3,560	7.50	0.09170	2.57584
Canis familiaris[2,12]	21,350	7.60	1.31275	6.14871
Camelos dromedarius[3,12]	231,700	7.70	4.93700	2.13077
Giraffa camelopardalis[2,12]	383,000	5.50	11.17200	2.91697
Capra hircus[2,12]	20,900	4.00	1.06200	5.08134
Ovis aries[2,12]	21,800	5.20	1.55400	7.12844
Bos taurus[2,12]	700,000	5.80	29.34600	4.19229
Equus caballus[2,12]	510,000	6.20	34.08000	6.68235
Homo sapiens[2,12]	74,000	8.00	2.47000	3.33784
Suncus etruscus[4,12]	3	5.50	0.00018	6.92308
Crocidura russula[4,12]	12	7.00	0.00053	4.34426
Birds				
Zenaida auriculata[1,11]	141	8.77	0.01666	11.819
Nothoprocta perdicaria[1,11]	398	9.70	0.01051	2.6406
Struthio camelus[8,13]	45,000	15.40	2.93000	6.5111
Anser anser[9,13]	3,838	12.80	0.17200	4.4815
Gallus gallus[5,13]	2,141	11.20	0.03300	1.5413
Columba libia[6,13]	216	13.30	0.02000	9.2593
Dromaius novaehollandiae[9,13]	30,000	15.00	0.00500	0.0166
Passer domesticus[7,13]	26	11.29	0.00300	11.765
Sturnus vulgaris[7,13]	73	10.37	0.00500	6.8871
Falco tinnunculus[9,13]	66	13,4	0.00500	7.5758
Larus canus[9,13]	302	12,9	0.01000	3.3113
Larus ridibundus[9,13]	253	12,1	0.01100	4.3478
Streptopelia decaota[9,13]	189	11,9	0.01200	6.3492
Lanius collaris[9,13]	33	11,4	0.00200	6.1162

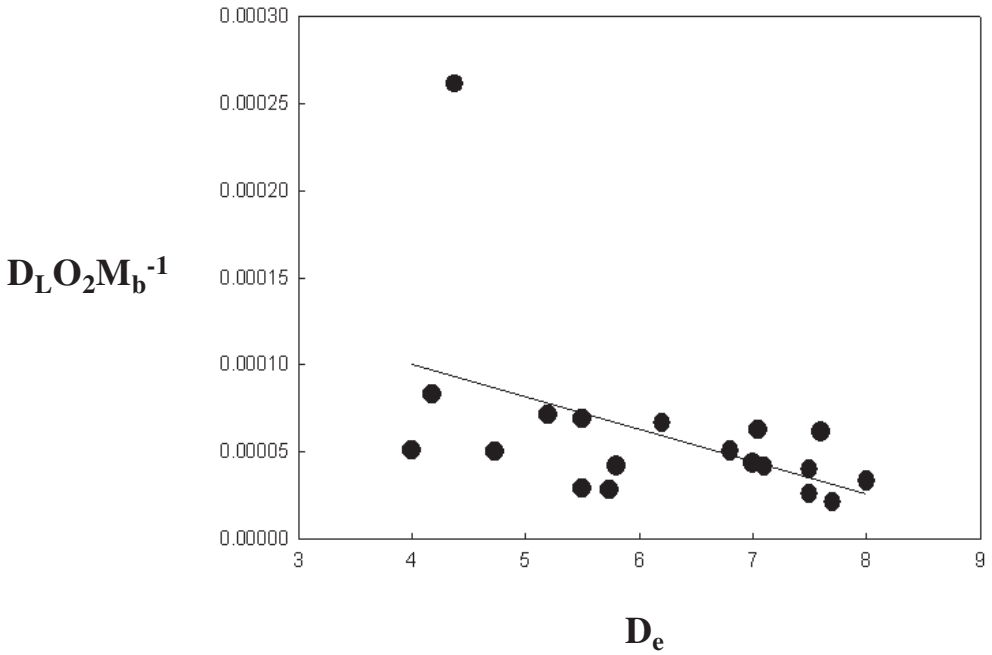

Fig. 4: Regression line between the red blood cell size (D_e) and the mass specific oxygen diffusion capacity of the blood gas barrier (D_LO_2/M_b) in mammals.

Regresión lineal entre el diámetro del glóbulo rojo (D_e) y la capacidad de difusión de oxígeno masa-específica (D_LO_2/M_b) en mamífero.

the direction of the anatomical changes is governed mainly by the requirements of flight. Although the more recent ancestors of mammals and birds diverged at different times from reptiles lineages, birds in the upper Jurassic (150 million years ago) and bats in the Eocene (50 million years ago), and their anatomical pulmonary adjustments associated with flight differ enormously (Maina 2000a, 2000b), at least the anatomical characteristics of the red blood cells and the air-blood barrier vary in the same direction in both taxa. The most important morphological and physiological refinements associated to the oxygen uptake capacity of bats in flight are: large heart with a huge cardiac output (Jurgens et al. 1981, Canals et al. 2005); high hematocrit, hemoglobin concentration, erythrocyte count and blood oxygen-carrying capacity (Wolk & Bogdanowics 1987), thin air-blood barrier and high oxygen diffusion capacity (Maina & King 1984, Maina 2000a, 2000b, Canals et al. 2005); and efficient capillary blood supply to the flight muscles (Mathieu-Costello 1992). The fundamental adaptative features reported in birds are cross-current mechanisms, para-bronchi, air-sacs and unidirectional air flow in the avian airway, short pulmonary circulatory time and, as in bats, large hearts and thin air-blood barriers (Maina 1998, 2000a, 2000b).

Small red blood size and high oxygen diffusion capacity appears to be correlated; the latter as a consequence of a thin air-blood barrier and a large respiratory surface. Although regression analyses of our data did not reach statistical significance, when data from literature were included a clear negative slope between the red blood diameter and the oxygen diffusion capacity was evident in mammals. Although a negative tendency seems to be occurring in birds, it did not reach a significant level, probably because of the small number of data. Small red blood size and as a consequence a high area/volume ratio have been associated with a facilitated oxygen diffusion, an increase of the hemoglobin concentration and an increase in erythrocyte count without increasing the blood viscosity (Promislow 1991, Rosenmann & Ruiz 1993), all these factors operating in the same direction of a thin air-blood barrier and a large respiratory surface, and in consequence a high oxygen conductance.

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