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Body mass dependence of the haemoglobin content to surface area ratio of avian erythrocytes

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Abstract. Data from 75 bird species weighing between 6 g and > 16 kg confirmed a supposition that the amount of haemoglobin per unit surface area of erythrocyte was not dependent on body mass. It showed a constancy across the range reflecting adjustment of the total surface area of erythrocytes in relation to blood haemoglobin concentration. This conclusion is based on an inverse correlation between the numbers and sizes of red blood cells.

Key words: birds, body mass, haemoglobin, erythrocytes

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INTRODUCTION

Greater body mass in bird species, ranging in weight between 6 and c. 170 g, has been found to be associated with both significantly lower blood haemoglobin concentrations and a significantly smaller total surface area of erythrocytes (Kostelecka-Myrcha et al. 1993). A consequence is that the amount of haemoglobin per unit surface area of erythrocytes does not differ in relation to body mass among these birds. During the time that erythrocytes are present in the lungs, their surfaces come into contact with a defined number of oxygen molecules which must suffice in the full saturation of the haemoglobin corresponding to this area (A. Kostelecka-Myrcha, unpublished data). It may be presumed that the constancy of the ratio between the amount of haemoglobin and the surface areas of erythrocytes determines the possibility for haemoglobin in birds to be fully saturated with oxygen (Kostelecka-Myrcha 1997), in the constant conditions in their lungs. These are due to the presence of air sacs and counter-current gaseous exchange (Schmidt-Nielsen 1975).

If the stated hypothesis of the same Hb/TSAE ratio in all birds is true, then adding other authors results, concerning any birds, to own results should support the truth of the hypothesis. It was possible to find data for 54 species of birds in literature on the subject.

MATERIALS AND METHODS

Data gathered previously, collected using uniform methodology, related to only 21 species of birds ranging in body mass from 6 to 167 g (Kostelecka-Myrcha et al. 1993). These were augmented by data from other authors on 54 species of larger birds. So information was thus obtained on birds of 75 species (Appendix), both nidifugous and nidicolous, belonging to 12 orders. Body masses ranged from 6 g to more than 16 kg, with a value also included for an Ostrich *Struthio camelus* weighing more than 125 kg.

Analyses considered the dependence on body mass of: the concentration of haemoglobin (Hb g%), the number of erythrocytes per mm^3 of blood (RBC 10^6 mm^{-3}), the haematocrit value (Hct %), the length and width of erythrocytes (LE, WE in μm), a measure of the total surface area of erythrocytes in 1 mm^3 of blood (TSAE $10^6\ \mu m^2\ mm^{-3}$) and the amount of haemoglobin per unit of surface area (Hb/TSAE pg μm^{-2}). The measure for the total surface area of erythrocytes was calculated knowing their linear dimensions and the number in 1 mm^3 of blood. The measure adopted in calculating the surface area of a single cell was the product of its length and breadth. Multiplication of the obtained value by the number of erythrocytes in a mm^3 of blood gave the total surface area of erythrocytes (TSAE). One obvious condition to be met in adopting this measure of surface area in comparative studies was constancy of shape across a range of body sizes of birds. To check on this, consideration was also given to the relationship between body mass and the erythrocyte length/width ratio (LE/WE), as well as the length/width ratio of nuclei (LN/WN) (Kostelecka-Myrcha et al. 1993).

All the above relationships were characterized using correlation coefficients and curvilinear regressions presented in a coordinate system with both sides log-transformed.

Haemoglobin concentrations were actually available for 73 species, haematocrit values for 74 and the number of erythrocytes per mm^3 of blood for 70 species. The ratio of amount of haemoglobin to total surface area of erythrocytes was possible to be calculated only for 51 species, those for which lengths and widths of erythrocytes were known.

Data for the same species studied by different authors were not combined.

RESULTS

Concentrations of haemoglobin (Hb) are steadily (and significantly) lower in bird species of ever greater body mass (Fig. 1). At the same time, the number of erythrocytes per mm^3 of blood is also significantly lower in larger birds (Fig. 2). In fact the extent to which the number of erythrocytes is lower in birds of larger mass is sufficient to ensure that — in spite of the fact that red blood cell dimensions LE and WE are greater and greater in ever larger bird species (Fig. 3) — the haematocrit value is ever lower with greater body size (Fig. 4). For this reason, the total surface area of erythrocytes (TSAE) is significantly lower at larger body sizes (Fig. 5). As the differences in TSAE noted across the body-size range are in proportion to differences in the Hb concentration across that range, the Hb/TSAE ratio does not differ significantly across the size range (Fig. 6). Finally, the lack of any significant relationships between body mass and either the cell or nuclear length/width ratios (LE/WE, LN/WN) allows it to be presumed that erythrocytes, though differing in size, are of uniform shape (LE/WE: $y = 1.85x^{-0.001}$, SE slope 0.004, $n = 56$, $r = -0.05$, $p > 0.05$; LN/WN: $y = 2.29x^{-0.004}$, SE slope 0.006, $n = 41$, $r = -0.08$, $p > 0.05$).

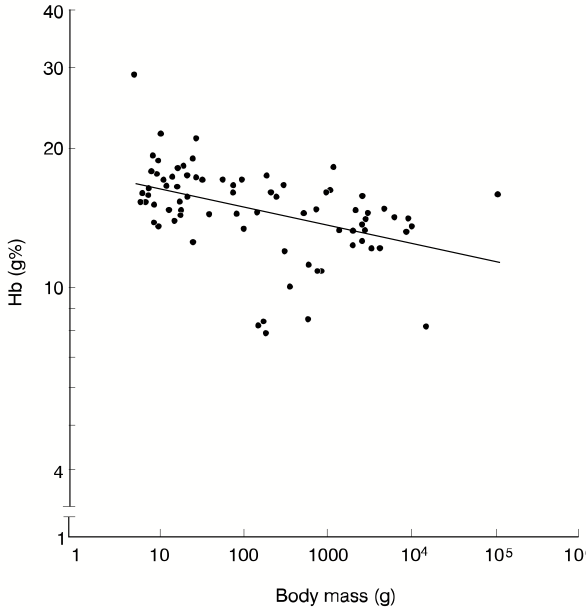

Fig. 1. Relationship between haemoglobin concentration (Hb) and body mass. $y = 17.86x^{-0.04}$ (SE slope 0.009), $n = 82$, $r = -0.45$, $p < 0.05$.

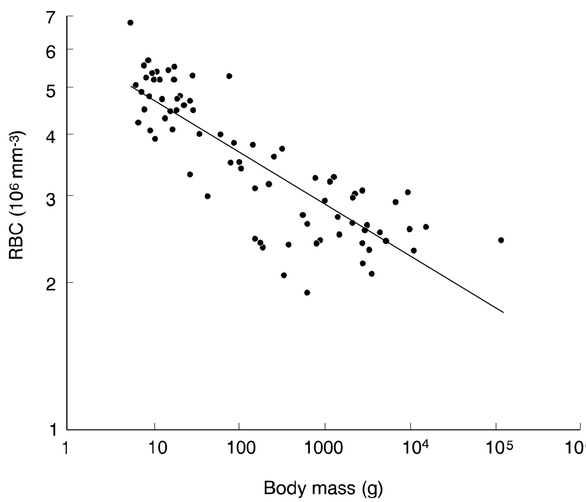

Fig. 2. Relationship between number of erythrocytes per mm^3 of blood (RBC count) and body mass. $y = 6.09x^{-0.107}$(SE slope 0.008), $n = 79$, $r = -0.84$, $p < 0.05$.

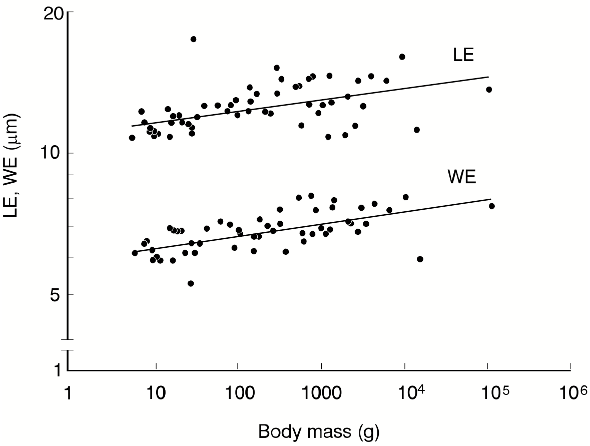

Fig. 3. Relationship between values of erythrocyte length (LE) and width (WE) versus body mass.
LE: $y = 10.95x^{0.02}$ (SE slope 0.005), n = 56, r = 0.52, $p < 0.05$.
WE: $y = 5.92x^{0.02}$ (SE slope 0.004), n = 56, r = 0.60, $p < 0.05$.

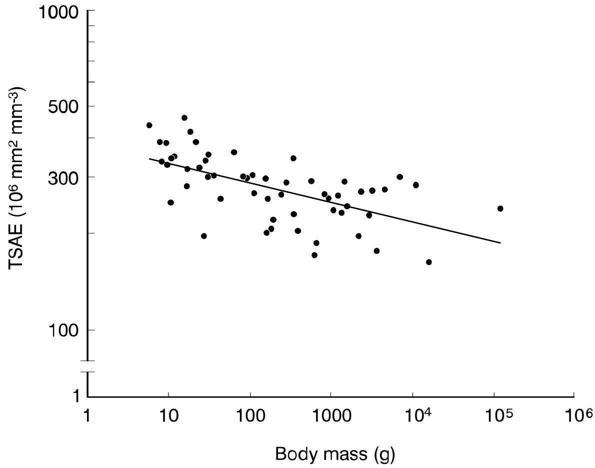

Fig. 5. Relationship between total surface area of erythrocytes per mm^3 of blood (TSAE) and body mass. $y = 382x^{-0.06}$ (SE slope 0.01), n = 56, r = -0.59, $p < 0.05$.

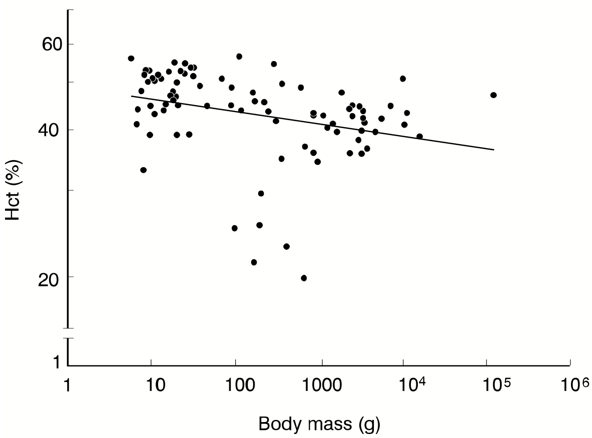

Fig. 4. Relationship between haematocrit value (Hct) and body mass. $y = 48.9x^{-0.02}$ (SE slope 0.009), n = 87, r = -0.28, $p < 0.05$.

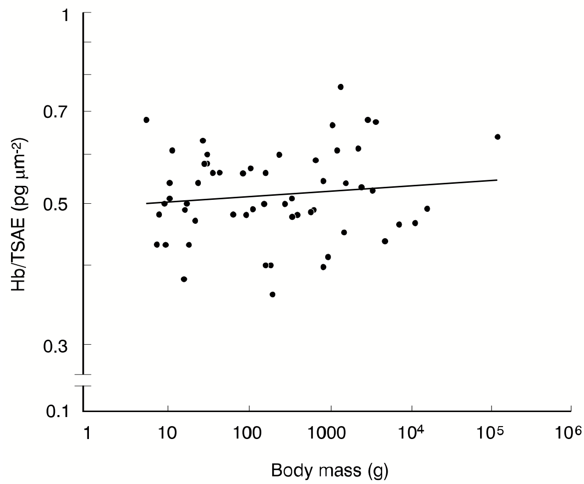

Fig. 6. Relationship between the ratio of amount of haemoglobin to total surface area of erythrocytes (Hb/TSAE) and body mass. $y = 0.49x^{0.009}$ (SE slope 0.009), n = 56, r = 0.13, $p > 0.05$.

DISCUSSION

The analyses confirmed and supported the earlier findings on the relationships in birds between body mass and various red blood cell indexes (Kostelecka-Myrcha et al. 1993). Some of the relationships even appeared more unequivocal than before. Hb concentrations were steadily lower in successively larger birds to a nearly-statistically-significant degree across the original, narrow range of body masses (6–167 g). In contrast, across the widened range of body masses to > 16 kg, the relationship took on clear statistical significance. Similarly, the value of haematocrit, which showed downward trend only with the increase of the body mass to 167 g, in this analysis shows statistically significant dependence.

The ratio of amount of haemoglobin to total surface area of erythrocytes does not depend on body mass. The mean values of this ratio for 51 species (0.52 ± 0.09 pg μm^{-2}) does not differ significantly from that for the 21 of less-varied body mass (0.53 ± 0.08 pg μm^{-2}) studied by Kostelecka-Myrcha et al. (1993). Nor does it differ significantly from the mean (0.53 ± 0.07 pg μm^{-2}) obtained for the 564 birds of various species studied previously in relation to body mass, nestling age and season of the year (Kostelecka-Myrcha 1997).

Mean values were characterised by standard deviation and compared using Student t-tests with a 0.05 significance level.

The analysis confirms the constancy in the amount of haemoglobin per unit surface area of erythrocyte in birds. It also supports the supposition that this is achieved through adjustment of the TSAE value in relation to haemoglobin concentration, on the basis of an inverse correlation between the number and sizes of erythrocytes (Kostelecka-Myrcha 1997).

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STRESZCZENIE

[Stosunek ilości hemoglobiny do sumarycznej powierzchni erytrocytów u ptaków, w zależności od ich masy ciała]

Zbadano zależności wartości wskaźników czerwonokrwinkowych od masy ciała ptaków. Do analizy tej włączono dane własne, uzyskane we wcześniejszych badaniach (Kostelecka-Myrcha et al. 1993) i dostępne dane literaturowe. Ogółem zebrano informacje dla 75 gatunków ptaków, o masie ciała od 6 g do ponad 16 kg.

Poszczególne zależności scharakteryzowano za pomocą współczynników korelacji i regresji krzywoliniowych.

Stwierdzono, że koncentracja hemoglobiny (Hb, Fig. 1) i liczba erytrocytów w 1 mm^3 krwi (Fig. 2) zmniejszają się statystycznie istotnie ze wzrostem masy ciała ptaków, podczas gdy wielkość tych krwinek wzrasta (Fig. 3). Bardzo intensywne zmniejszanie się liczby erytrocytów w jednostce objętości krwi powoduje statystycznie istotne zmniejszanie się wartości hematokrytu (Fig. 4) i sumarycznej powierzchni erytrocytów (TSAE, Fig. 5). Zmiany wielkości tej powierzchni przebiegają

wprost proporcjonalnie do zmian koncentracji Hb i dlatego stosunek Hb/TSAE nie zależy od masy ciała ptaków (Fig. 6). Jego średnia wartość wynosi 0.52 ± 0.09 pg μm^{-2}. Nie różni się ona statystycznie istotnie od wcześniej otrzymanej średniej dla 564 osobników różnych gatunków ptaków, przebadanych w zależności od wieku piskląt, sezonu roku i masy ciała, w wąskim zakresie jej zmienności — od 6 g do 167 g (Kostelecka-Myrcha 1997).

Przedstawiona analiza potwierdza więc przypuszczenie z 1997 roku (ibidem), że ilość hemoglobiny przypadająca na jednostkę powierzchni erytrocytów (Hb/TSAE) jest u ptaków stała, i że stałość ta jest wynikiem dostosowywania się wielkości TSAE do koncentracji Hb. U podstaw tego ważnego mechanizmu, zapewniającego zawsze pełne wysycenie hemoglobiny tlenem, leży ujemna korelacja między liczbą a wielkością erytrocytów.

Appendix. List of 75 bird species, their body mass (g), and sources of data the study is based on. * — body mass from Busse (1990).

Species	Body mass ± SD	Source of data	Parameters
Regulus regulus	5.8 ± 0.3	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Aegithalos caudatus	6.7	Palomeque et al. 1980	Hb, RBC, Hct
Certhia brachydactyla	7	Palomeque et al. 1980	Hb, RBC, Hct
Aegithalos caudatus	7.7 ± 0.7	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Phylloscopous collybita	8	Palomeque et al. 1980	Hct
Troglodytes troglodytes	8.3 ± 1.3	unpublished data	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Troglodytes troglodytes	8.4	Palomeque et al. 1980	Hb, RBC, Hct
Serinus serinus	9	Palomeque et al. 1980	Hb, RBC, Hct
Certhia familiaris	9.5 ± 3.3	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Parus montanus	9.7 ± 1.2	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Parus caeruleus	9.7	Palomeque et al. 1980	Hb, RBC, Hct
Carduelis spinus	10.6	Palomeque et al. 1980	Hb, RBC, Hct
Parus caeruleus	11 ± 0.3	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Parus palustris	11	unpublished data	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Carduelis spinus	11.9 ± 0.5	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Carduelis carduelis	12.7	Palomeque et al. 1980	Hb, RBC, Hct
Sylvia atricapilla	13.8	Palomeque et al. 1980	Hb, RBC, Hct
Erithacus rubecula	14.6	Palomeque et al. 1980	Hb, RBC, Hct
Erithacus rubecula	16.2 ± 1.1	unpublished data	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Parus major	17 ± 1.3	Kostelecka-Myrcha 1997	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Sylvia atricapilla	17.8 ± 3	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Fringilla coelebs	18.5	Palomeque et al. 1980	Hb, RBC, Hct
Prunella modularis	18.8 ± 1.3	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Prunella modularis	19.4	Palomeque et al. 1980	Hb, RBC, Hct
Carpodacus mexicanus	19.6 ± 1.2	Clemens 1990	Hb, Hct
Emberiza cirlus	20	Palomeque et al. 1980	Hb, RBC, Hct
Carduelis chloris	20.5	Palomeque et al. 1980	Hb, RBC, Hct
Fringilla coelebs	22.3 ± 1.5	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Leucosticte arctoa	24.2 ± 2.3	Clemens 1990	Hb, Hct
Passer montanus	24.4 ± 0.5	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Passer melanurus	28*	Fourie & Hattingh 1983	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Emberiza citrinella	29 ± 0.9	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Passer domesticus	31.5 ± 2.7	unpublished data	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Pyrrhula pyrrhula	31.6 ± 1.1	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Oceanites oceanicus	37.2 ± 1	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Pycnonotus barbatus	45*	Fourie. & Hattingh 1983	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Turdus philomelos	66.1 ± 4.6	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Turdus merula	86	Palomeque et al. 1980	Hb, RBC, Hct
Turdus merula	87.4 ± 4.1	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Coturnix coturnix	95*	Fourie & Hattingh 1983	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Plautus alle	110 ± 1.4	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Coturnix coturnix	115	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Sterna vittata	160 ± 5.1	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Garrulus glandarius	165*	Dąbrowski 1968	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Sterna paradisaea	166.8 ± 4.4	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE

Species	Body mass ± SD	Source of data	Parameters
Corvus monedula	190*	Dąbrowski 1968	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Pica pica	200*	Dąbrowski 1968	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Falco tinnunculus	220*	Kirkwood et al. 1979	Hb, Hct
Larus ridibundus	245*	Balasch et al. 1974,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Columba livia f. domestica	285*	Kostelecka-Myrcha 1997	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Circus pygargus	300*	Ferrer et al. 1987	Hct
Columba livia	350*	Balasch et al. 1974,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Tyto alba	350*	Fourie. & Hattingh 1983	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Corvus frugilegus	400*	Dąbrowski 1968	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Circus aeruginosus	600*	Lavin et al. 1992	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Corvus corone	650*	Dąbrowski 1968	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Alectoris graeca	675*	Balasch et al. 1973	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Milvus migrans	850*	Balasch et al. 1976,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Aythya ferina	850*	Balasch et al. 1974,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Hieraaetus pennatus	850*	Ferrer et al. 1987	Hct
Buteo buteo	950*	Balasch et al. 1976,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Larus argentatus	1100*	Balasch et al. 1974,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Corvus corax	1250*	Balasch et al. 1974,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Phasianus colchicus	1400*	Balasch et al. 1973,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Numida meleagris	1521 ± 98	Fourie & Hattingh 1980,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Ardea cinerea	1600*	Fourie & Hattingh 1983	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Hieraaetus fasciatus	1850*	Ferrer et al. 1987	Hct
Gallus gallus g.	2300*	Balasch et al. 1973,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Phoenicopterus chilensis	2300*	Puerta et al. 1989	Hb, RBC, Hct
Phalacrocorax carbo	2500*	Balasch et al. 1974,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Bubo bubo	2500*	Ferrer et al. 1987	Hct
Stephanoaetus coronatus	2950*	Balasch et al. 1976	Hb, RBC, Hct
Phoenicopterus ruber ruber	3000*	Puerta et al. 1992	Hb, RBC, Hct
Anas platyrhynchos	3030 ± 253	Magath & Higgins 1934,	
		Palomeque & Planas 1977,	
		Girard & Grima 1980	Hb, RBC, LE, WE, TSAE, Hb/TSAE
Aquila heliaca adalberti	3200*	Ferrer et al. 1987	Hct
Aquila heliaca	3200*	Balasch et al. 1976	Hb, RBC, Hct
Ciconia ciconia	3300 ± 267	Alonso et al. 1991	Hb, RBC, Hct
Sarcoramphus papa	3375*	Balasch et al. 1976,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Phoenicopterus ruber roseus	3500*	Puerta et al. 1989	Hb, RBC, Hct
Pavo cristatus	3800*	Balasch et al. 1973	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Aquila chrysaetos	4800*	Balasch et al. 1976,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Grus grus	5500 ± 516	Puerta et al. 1990	Hb, RBC, Hct
Gyps fulvus	7250*	Balasch et al. 1976,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Otis tarda	10000*	Jimenez et al. 1987	Hb, RBC, Hct
Pelecanus onocrotalus	10500*	Puerta et al. 1991	Hb, RBC, Hct
Vultur gryphus	11500*	Balasch et al. 1976,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Meleagris gallopavo	16300 ± 1980	Girard & Grima 1980,	
		Palomeque & Planas 1977	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
Struthio camelus	125000*	Palomeque et al. 1991	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE