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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which must suffice in the full saturation of the haemoglobin corresponding to this area (A. Kostelecka-Myrcha, unpublished data).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 mm³ of blood (RBC 10⁶ 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 $10^6\mu\text{m}^2\text{ mm}^{-3}$) and the amount of haemoglobin per unit of surface area (Hb/TSAE $\text{pg}\mu\text{m}^{-2}$). 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,

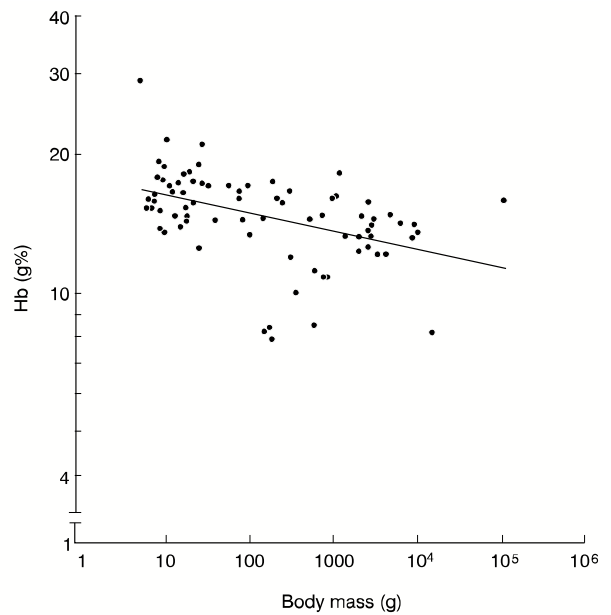


Fig. 1. Relationship between haemoglobin concentration (Hb) and body mass. $y = 17.86x^{-0.04}$ (SE slope 0.009), $n = 82$, $r = -0.45$, $p < 0.05$.

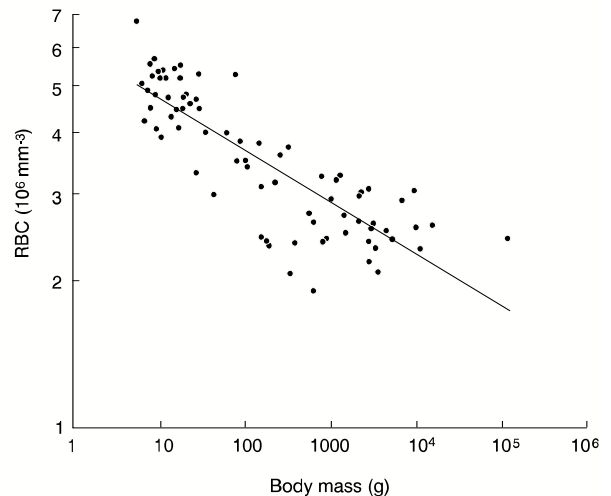


Fig. 2. Relationship between number of erythrocytes per mm^3 of blood (RBC count) and body mass. $y = 6.09x^{-0.107}$ (SE slope 0.008), $n = 79$, $r = -0.84$, $p < 0.05$.

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, $n = 41$, $r = -0.08$, $p > 0.05$).

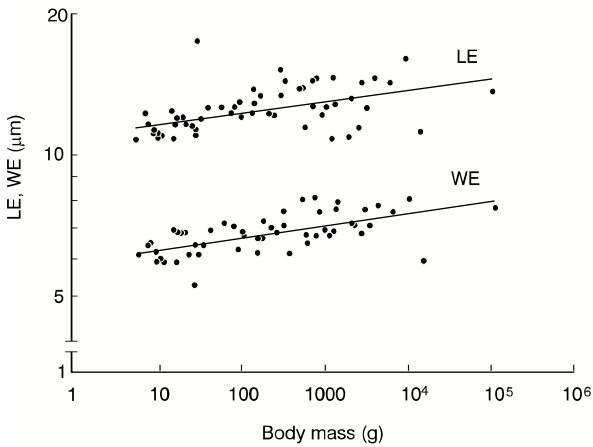


Fig. 3. Relationship between values of erythrocyte length (LE) and width (WE) versus body mass.

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), $n = 56$, $r = 0.60$, $p < 0.05$.

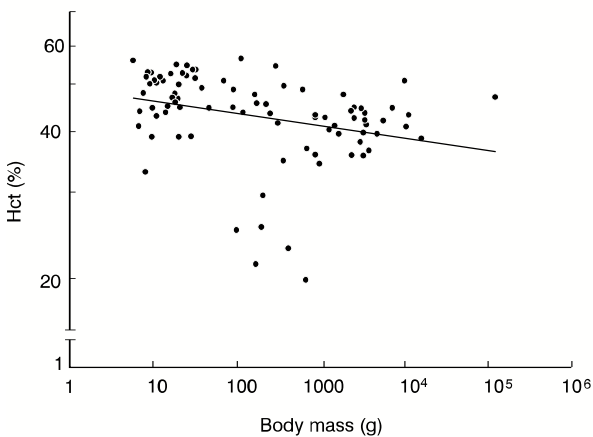


Fig. 4. Relationship between haematocrit value (Hct) and body mass. $y = 48.9x^{-0.02}$ (SE slope 0.009), $n = 87$, $r = -0.28$, $p < 0.05$.

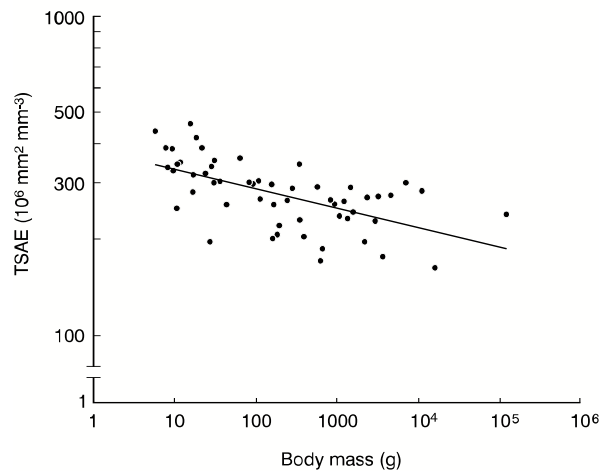


Fig. 5. Relationship between total surface area of erythrocytes per mm^3 of blood (TSAE) and body mass. $y = 382x^{-0.06}$ (SE slope 0.01), $n = 56$, $r = -0.59$, $p < 0.05$.

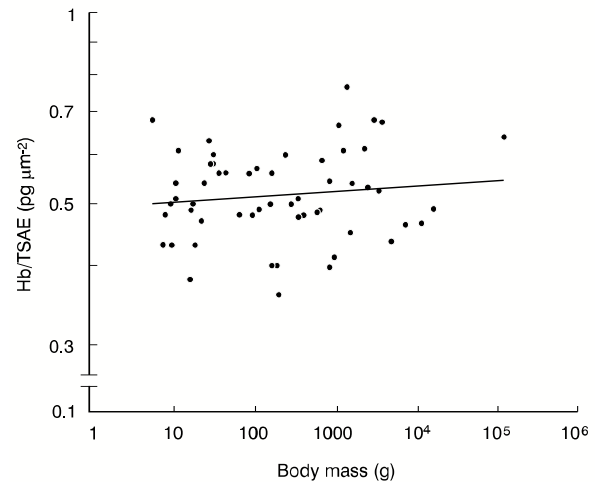


Fig. 6. Relationship between the ratio of amount of haemoglobin to total surface area of erythrocytes (Hb/TSAE) and body mass. $y = 0.49x^{0.009}$ (SE slope 0.009), $n = 56$, $r = 0.13$, $p > 0.05$.

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 ($0.52 \pm 0.09 \text{ pg } \mu\text{m}^{-2}$) does not differ significantly from that for the 21 of less-varied body mass ($0.53 \pm 0.08 \text{ pg } \mu\text{m}^{-2}$) studied by Kostelecka-Myrcha et al. (1993). Nor does it differ significantly from the mean ($0.53 \pm 0.07 \text{ pg } \mu\text{m}^{-2}$) 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 czerwonych krwinek 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 mm³ krwi (Fig. 2) zmniejszają się statystycznie istotnie ze wzrostem masy ciała ptaków, podczas gdy wielkość tych krwinek wzrasta (Fig. 3). Bardzo intensywne zmniejszenie się liczby erytrocytów w jednostce objętości krwi powoduje statystycznie istotne zmniejszenie 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 $0.52 \pm 0.09 \text{ pg } \mu\text{m}^{-2}$. 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 \pm SD	Source of data	Parameters
<i>Regulus regulus</i>	5.8 \pm 0.3	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Aegithalos caudatus</i>	6.7	Palomeque et al. 1980	Hb, RBC, Hct
<i>Certhia brachydactyla</i>	7	Palomeque et al. 1980	Hb, RBC, Hct
<i>Aegithalos caudatus</i>	7.7 \pm 0.7	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Phylloscopus collybita</i>	8	Palomeque et al. 1980	Hct
<i>Troglodytes troglodytes</i>	8.3 \pm 1.3	unpublished data	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Troglodytes troglodytes</i>	8.4	Palomeque et al. 1980	Hb, RBC, Hct
<i>Serinus serinus</i>	9	Palomeque et al. 1980	Hb, RBC, Hct
<i>Certhia familiaris</i>	9.5 \pm 3.3	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Parus montanus</i>	9.7 \pm 1.2	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Parus caeruleus</i>	9.7	Palomeque et al. 1980	Hb, RBC, Hct
<i>Carduelis spinus</i>	10.6	Palomeque et al. 1980	Hb, RBC, Hct
<i>Parus caeruleus</i>	11 \pm 0.3	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Parus palustris</i>	11	unpublished data	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Carduelis spinus</i>	11.9 \pm 0.5	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Carduelis carduelis</i>	12.7	Palomeque et al. 1980	Hb, RBC, Hct
<i>Sylvia atricapilla</i>	13.8	Palomeque et al. 1980	Hb, RBC, Hct
<i>Erithacus rubecula</i>	14.6	Palomeque et al. 1980	Hb, RBC, Hct
<i>Erithacus rubecula</i>	16.2 \pm 1.1	unpublished data	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Parus major</i>	17 \pm 1.3	Kostelecka-Myrcha 1997	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Sylvia atricapilla</i>	17.8 \pm 3	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Fringilla coelebs</i>	18.5	Palomeque et al. 1980	Hb, RBC, Hct
<i>Prunella modularis</i>	18.8 \pm 1.3	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Prunella modularis</i>	19.4	Palomeque et al. 1980	Hb, RBC, Hct
<i>Carpodacus mexicanus</i>	19.6 \pm 1.2	Clemens 1990	Hb, Hct
<i>Emberiza cirius</i>	20	Palomeque et al. 1980	Hb, RBC, Hct
<i>Carduelis chloris</i>	20.5	Palomeque et al. 1980	Hb, RBC, Hct
<i>Fringilla coelebs</i>	22.3 \pm 1.5	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Leucosticte arctoa</i>	24.2 \pm 2.3	Clemens 1990	Hb, Hct
<i>Passer montanus</i>	24.4 \pm 0.5	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Passer melanurus</i>	28*	Fourie & Hattingh 1983	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Emberiza citrinella</i>	29 \pm 0.9	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Passer domesticus</i>	31.5 \pm 2.7	unpublished data	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Pyrrhula pyrrhula</i>	31.6 \pm 1.1	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Oceanites oceanicus</i>	37.2 \pm 1	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Pycnonotus barbatus</i>	45*	Fourie & Hattingh 1983	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Turdus philomelos</i>	66.1 \pm 4.6	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Turdus merula</i>	86	Palomeque et al. 1980	Hb, RBC, Hct
<i>Turdus merula</i>	87.4 \pm 4.1	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Coturnix coturnix</i>	95*	Fourie & Hattingh 1983	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Plautus alle</i>	110 \pm 1.4	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Coturnix coturnix</i>	115	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Sterna vittata</i>	160 \pm 5.1	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Garrulus glandarius</i>	165*	Dąbrowski 1968	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE
<i>Sterna paradisaea</i>	166.8 \pm 4.4	Kostelecka-Myrcha et al. 1993	Hb, RBC, Hct, LE, WE, TSAE, Hb/TSAE

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