

## Allometric and Phylogenic Comparisons of Circulating Leukocyte Concentrations between and within Birds and Mammals

Review Article

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### Abstract

The blood concentrations of leukocytes and the major classes of leukocytes were compared across over 200 species of birds and over 300 species of mammals based on phylogenic relations, body weight and diet. The concentration of leukocytes was markedly higher in birds than mammals reflecting elevated concentrations of all major classes but particularly those of lymphocytes, monocytes, eosinophils and basophils. Overall, there were no differences between blood leukocyte concentrations in placental and marsupial mammals. There were differences between leukocytes concentrations within the placental mammals, for instance being lower in mammalian species within the taxa *Glires* than in *Laurasiatberia* and *Primate-morpha* which in turn are lower than in *Afrotheria* and *Xenarthra*. There were also differences in leukocyte concentrations in birds being higher in species with the taxa *Afroaves* than in *Australaves*. There were phylogenic differences in the percentages of the leukocyte classes. For instance, in placental compared marsupial mammals, the percentage neutrophils is elevated, the percentage lymphocytes is depressed and neutrophil to lymphocyte (N:L) ratio was much higher. Moreover, the percentage heterophils is high, the percentage lymphocytes is low and heterophil to lymphocyte (H:L) ratio is greater in birds from the taxa *Paleognathae* than the *Neognathae*. There was a positive relationship between concentrations of leukocytes or neutrophils and log body weight.

### Introduction

The present study examines the relationship between blood leukocyte concentrations together with differential leukocyte counts and the ratio of neutrophils (mammals) or heterophils (birds) to lymphocytes (N/H:L ratio) relative to the following: phylogenic/evolutionary relationships, log body weight and ecological parameters (diet, habitat) in birds and mammals. It is well recognized that there are pathological shifts in these leukocyte parameters. For instance, the N:L ratio is reported to be a useful clinical parameter in human medicine being “a useful marker to predict subsequent mortality in patients admitted” for ST segment elevation myocardial infarction [1], together with after percutaneous coronary intervention [2] and following hepatic resection for colorectal liver metastases [3]. Moreover, there are also marked physiological shifts in leukocyte concentrations.

There is, for instance, a linkage between stress and immune functioning in mammals; this having been advanced since the 1940s (reviewed [4]). In birds, the relationship was first noted

in poultry. Corticosterone administration was accompanied by increases in the blood concentrations of heterophils (over 3 fold), decreases in the lymphocyte concentration (85 % decrease) and large changes in the H:L ratio (>20 fold) in chickens [5] with the relationship ( $R^2$ ) between the dosage of corticosterone and heterophils, lymphocytes and H:L ratio being 0.41, 0.66 and 0.88 respectively (calculated from 5). The percentages of both heterophils and lymphocytes are similarly changed by stressors and the glucocorticoid dexamethasone in young turkeys [6]. “For the ecologist, therefore, high ratios of heterophils or neutrophils to lymphocytes (‘H:L’ or ‘N:L’ ratios) in blood samples reliably indicate high glucocorticoid levels” and hence stress [7]. This is supported, for instance, by the marked increases in the percentage represented by heterophil and decreases in lymphocyte percentages in blood parasite infected warblers [8]. Moreover, there are shifts in leukocytes populations one to two hours following capture in great tits; there being large increases in heterophils and concomitant decreases in both lymphocytes and eosinophils [9]. Moreover, there is an increase in H:L ratio in response to endotoxin and flight in pigeons [10] and with transportation stress in domesticated (e.g. goats – [11];

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horses – [12]) and wild mammals (e.g. badgers – [13]). A strong relationship between stress and blood N: L ratios has been reported in chronically but not acutely stressed rats [14]; the latter but not the former having elevated circulating concentrations of corticosterone.

As leukocyte numbers shift to meet physiological challenges, it is hypothesized that there are selective/evolutionary pressures for optimal basal values in different species. The phylogenetic, allometric or ecological relationships for leukocytes in mammals and birds are examined in the present study.

## Materials and Methods

### Databases

A series of databases were assembled for blood concentrations of leukocytes using the published or calculated mean for the species based on rigorous and systematic series of searches of the literature. The databases for blood concentrations of leukocytes are available for the following: mammals (Supplementary table A and B) and birds [15]. Information on body weights was for birds from [16] and for mammals from [17].

### Analyses

Data were analyzed by taxonomic groups based on the following for birds [18-21] and for mammals [22, 23]. However, for the latter, it should be noted that recent studies support the grouping *Laurasiatheria* but do not support the *Euarchontoglires* encompassing the *Glires* (rodents/lagomorphs) and *Euarchonta* (including primates and tree shrews) [24]. Moreover, while the *Cetacea* (marine mammals such as whales and dolphins) are generally viewed as a branch of the *Artiodactylans* [21, 25], the *Artiodactyla* and *Cetacea* will be considered separately in the present study due to ecological, size and other differences.

### Statistics

Data were analyzed by taxa using one-way analysis of variance, with mean separated by Tukey's range test or for comparisons between two taxa by Student's *t* test. The relationship between data on leukocytes and log body weights were compared by linear regression.

## Results

Table 1 summarizes differences between leukocytes in birds and mammals. The circulating concentrations of leukocytes were 72.3 % higher ( $p < 0.01$ ) in birds than mammals with greater ( $p < 0.01$ ) numbers of neutrophils (44.5 %), lymphocytes (57.5 %), monocytes (50.7 %), eosinophils (132.8 %) and basophils (392.9 %). The increases in neutrophils and lymphocytes between mammals and birds was very similar; the  $\Delta$  neutrophils being 1820 per  $\mu\text{L}$  blood and  $\Delta$  lymphocytes being 1868 per  $\mu\text{L}$  blood. In contrast, there were no differences in the percentage of either lymphocytes or monocytes between mammalian and avian species. There were some difference in the percentages of neutrophils/heterophils, eosinophils and basophils but these were of a smaller magnitude than for absolute concentrations. The percentage of neutrophils was lower ( $p < 0.01$ ) in birds than mammals while the percentages of both eosinophils and basophils were greater ( $p < 0.01$ ). Parenthetically, the coefficients of variation (CV) were markedly lower when the differential leukocyte count was expressed as a percentage rather than as a concentration. For instance, the CV for neutrophil across mammalian species and heterophils across avian species were respectively 38.7% and 37.7% for percentages and 71.1% and 72.5% of absolute concentrations. The neutrophil/heterophil to lymphocyte ratio (H/N:L) was similar comparing mammals and birds but 21.9% higher ( $p < 0.01$ ) in mammals than birds.

The differences between blood concentrations of leukocytes and

**Table 1. Comparison between leukocytes between mammals and birds [Mean  $\pm$  (number of species n=) S.E.M.]**

Parameter	Class Mammalia	Class Aves
Leukocyte concentration ( $\times 10^3$ . # $\mu\text{L}^{-1}$ )	7.89 $\pm$ (311) 0.22 <sup>a</sup>	13.6 $\pm$ (207) 0.65 <sup>b</sup>
Leukocyte concentration #. $\mu\text{L}^{-1}$		
Neutrophils <sup>‡</sup>	4089 $\pm$ (273) 227 <sup>a</sup>	5909 $\pm$ (164) 334 <sup>b</sup>
Lymphocytes	3251 $\pm$ (273) 166 <sup>a</sup>	5119 $\pm$ (164) 274 <sup>b</sup>
Monocytes	288 $\pm$ (273) 30 <sup>a</sup>	434 $\pm$ (164) 31 <sup>b</sup>
Eosinophils	338 $\pm$ (273) 33 <sup>a</sup>	787 $\pm$ (164) 109 <sup>b</sup>
Basophils	56 $\pm$ (273) 7.5 <sup>a</sup>	276 $\pm$ (164) 25.5 <sup>b</sup>
Differential leukocyte		
Neutrophils/heterophils <sup>‡</sup> (%)	48.5 $\pm$ (285) 1.1 <sup>b</sup>	44.4 $\pm$ (199) 1.2 <sup>a</sup>
Lymphocytes (%)	42.9 $\pm$ (286) 1.1	43.1 $\pm$ (199) 1.2
Monocytes (%)	3.6 $\pm$ (284) 0.2	3.7 $\pm$ (196) 0.2
Eosinophils (%)	4.3 $\pm$ (281) 0.2 <sup>a</sup>	6.0 $\pm$ (196) 0.5 <sup>b</sup>
Basophils (%)	0.8 $\pm$ (274) 0.1 <sup>a</sup>	2.8 $\pm$ (196) 0.3 <sup>b</sup>
N/H:L ratio	1.78 $\pm$ (284) 0.085 <sup>b</sup>	1.46 $\pm$ (207) 0.134 <sup>a</sup>

<sup>‡</sup> Neutrophils in mammals and heterophils in birds

<sup>a, b</sup> Different superscript indicates difference ( $p < 0.01$ ) by Students *t*-test

the differential leukocyte percentages in different mammalian groups are summarized in Tables 2 and 4 respectively. There was no difference in the blood concentrations of leukocytes between marsupial and placental mammals (Table 2). There were insufficient numbers of egg laying mammals for statistical analysis. Within the placental mammals, the blood concentrations of leukocytes were lowest in rodents and lagomorphs (Super-order *Glires*), elevated ( $p < 0.01$ ) in species in the super-orders *Primates* and *Laurasiatheria* and highest elevated ( $p < 0.01$ ) in species in the Super-orders *Afrotheria* and *Xenarthra* (Table 2). Within the Super-order *Laurasiatheria*, the lowest blood concentrations of leukocytes were in Orders *Chiroptera* and *Soricomorpha* while the highest were in species in the orders *Erinaceomorpha* and *Carnivora* (Table 2).

There were no differences in the blood concentration of leukocytes between species of birds the Sub-classes *Paleognathae* and *Neognathae* (Table 3). In contrast, the concentration of leukocytes was higher in the species within the Landbird assemblage than the *Charadriiformes* ( $p < 0.05$ ) (Table 3) and in the *Afroaves* than the *Australaves* (Table 3). There were no differences between taxa within the Waterbird radiation (between the orders - *Ciconiiformes*, *Pelecaniformes*, *Procellariiformes* and *Sphenisciformes*) (data not shown).

The N:L ratio was lower ( $p < 0.01$ ), in marsupial than placental mammals; being less than half. Moreover, the N:L ratio was greater in species within the Super-orders *Laurasiatheria* and *Xenarthra* (Table 2); the former reflecting the very high ratios in species within the Orders *Carnivora* and *Cetacea*. There were

no differences in H:L ratio between avian groups except it was greater ( $p < 0.05$ ) in Sub-class *Paleognathae* than *Neognathae* (Table 3).

There were differences ( $p < 0.01$ ) in the percentages of both neutrophils and lymphocytes between marsupial than placental mammals (Table 4). Within the placental mammals, the percentage of neutrophils were higher ( $p < 0.01$ ) in the species in the Super-order *Xenarthra* and *Laurasiatheria* and lowest in the Super-order *Afrotheria* and *Glires* (Table 4). Conversely, the percentage of lymphocytes were lowest in the species in the Super-order *Xenarthra*, *Laurasiatheria* and *Primates* and highest in *Glires* (Table 4). There were also differences with monocytes (highest in the Super-order *Afrotheria*), eosinophils (highest in the Super-order *Laurasiatheria*) and basophils (highest in the Super-order *Primates*). There were also differences within the Super-order *Laurasiatheria* with neutrophils was highest (and lymphocytes lowest) in species in the Orders *Carnivora* and Order *Cetacea*; monocytes lowest in the Order *Chiroptera*; eosinophils highest in species in the Orders *Cetacea* and *Erinaceomorpha* and basophils lowest in species in the Order *Chiroptera* and highest in Orders *Chiroptera* and *Erinaceomorpha* and *Perissodactyla* (Table 4).

There were some differences in differential leukocyte concentration in different avian groups. The heterophil percentage was markedly higher ( $p < 0.05$ ), and the percentage lymphocytes concomitantly lower ( $p < 0.05$ ), in Sub-class *Paleognathae* than in the *Neognathae* (Table 3). There were no differences in the heterophil or lymphocyte concentration between Anseriform and Galliform birds or the major groups shown within the Neoaves (Table 5).

**Table 2. Comparison between leukocytes within mammalian taxa [Mean  $\pm$  S.E.M.]**

Group (number of species n=)	Leukocyte concentration ( $\times 10^3$ . # $\mu\text{L}^{-1}$ )	Neutrophils: Lymphocyte (N:L) ratio
Within Class <i>Mammalia</i> <sup>Δ</sup>		
Sub-class <i>Metatheria</i> (marsupial mammals) (58)	7.1 $\pm$ 0.45	0.85 $\pm$ 0.09 <sup>a</sup>
Infra-class <i>Eutheria</i> (placental mammals) (277)	8.0 $\pm$ 0.24	1.84 $\pm$ 0.10 <sup>b</sup>
Within Placental Mammals		
Super-order <i>Afrotheria</i> (6)	11.9 $\pm$ 1.78 <sup>c</sup>	1.64 $\pm$ 0.74 <sup>ab</sup>
Super-order <i>Xenarthra</i> (8)	11.1 $\pm$ 1.45 <sup>c</sup>	1.95 $\pm$ 0.40 <sup>b</sup>
Super-order <i>Laurasiatheria</i> (212)	7.9 $\pm$ 0.27 <sup>b</sup>	2.09 $\pm$ 0.14 <sup>b</sup>
Super-order <i>Primates</i> <sup>†</sup> (19)	9.3 $\pm$ 0.55 <sup>b</sup>	1.47 $\pm$ 0.22 <sup>ab</sup>
Super-order <i>Glires</i> <sup>‡</sup> (38)	6.5 $\pm$ 0.52 <sup>a</sup>	1.01 $\pm$ 0.20 <sup>a</sup>
Within Super-order <i>Laurasiatheria</i>		
Order <i>Erinaceomorpha</i> (5)	9.2 $\pm$ 1.17 <sup>b</sup>	1.33 $\pm$ 0.39 <sup>a</sup>
Order <i>Soricomorpha</i> (5)	4.7 $\pm$ 1.12 <sup>a</sup>	1.40 $\pm$ 0.61 <sup>ab</sup>
Order <i>Chiroptera</i> (31)	5.9 $\pm$ 0.70 <sup>a</sup>	1.10 $\pm$ 0.44 <sup>a</sup>
Order <i>Carnivora</i> (51)	10.0 $\pm$ 0.37 <sup>b</sup>	3.32 $\pm$ 0.21 <sup>d</sup>
Order <i>Perissodactyla</i> (15)	8.7 $\pm$ 0.51 <sup>ab</sup>	1.77 $\pm$ 0.18 <sup>b</sup>
Order <i>Artiodactyla</i> (65)	7.2 $\pm$ 0.58 <sup>ab</sup>	1.49 $\pm$ 0.12 <sup>ab</sup>
Order <i>Cetacea</i> (15)	7.7 $\pm$ 0.76 <sup>ab</sup>	2.64 $\pm$ 0.38 <sup>c</sup>

<sup>Δ</sup> There were insufficient data on species within the *Monotremata* to allow meaningful comparisons

<sup>†</sup> Order *Primates* + *Scandentia*

<sup>‡</sup> Orders *Rodentia* + *Lagomorpha*

<sup>a, b</sup> Different superscript within a column indicates difference ( $p < 0.01$ )

**Table 3. Comparison between leukocytes within birds [Mean ± S.E.M.].**

Group (number of species n=)	Leukocyte concentration (x 10 <sup>3</sup> . # μL <sup>-1</sup> )	Heterophils: Lymphocyte (H:L) ratio
Sub-class <i>Paleognathae</i> (5)	11.6 ± 1.36	2.34 ± 0.42 <sup>b</sup>
Sub-class <i>Neognathae</i> (202)	13.7 ± 0.66	1.46 ± 0.14 <sup>a</sup>
Within Super-order <i>Galloanserae</i>		
<i>Anseriformes</i> (10)	18.3 ± 1.58	1.36 ± 0.59
<i>Galliformes</i> excluding poultry (9)	13.4 ± 2.56	0.55 ± 0.09
Within Super-order <i>Neoaves</i>		
<i>Charadriiformes</i> (24)	8.0 ± 0.94 <sup>a</sup>	1.76 ± 0.69
Landbird assemblage (86)	15.4 ± 0.93 <sup>b</sup>	1.59 ± 0.27
<i>Gaviformes</i> / <i>Guiformes</i> (including <i>Otididae</i> )/Waterbird radiation/assemblage <sup>∞</sup> (32)	13.2 ± 1.62 <sup>ab</sup>	1.52 ± 0.15
Within Landbird assemblage		
<i>Afroaves</i>	17.0 ± 1.31 <sup>b</sup>	1.99 ± 0.45
( <i>Accipitriformes</i> , <i>Coraciiformes</i> , <i>Strigiformes</i> , <i>Trogoniformes</i> ) (50)		
<i>Australaves</i> ( <i>Falconiformes</i> , <i>Passeriformes</i> , <i>Psittaciformes</i> ) (49)	12.9 ± 1.13 <sup>a</sup>	1.23 ± 0.32

<sup>∞</sup> Core Gruiformes/Waterbird radiation (together with *Cuculidae*, *Otididae*)(*Ciconiiformes*, *Gaviformes*, *Pelicaniformes*, *Procellariiformes*, *Sphenisciformes*)

<sup>a, b</sup> Different superscript within a column indicates difference (p<0.01)

**Table 4. Comparison between differential leukocyte percentages within major mammalian taxa [Mean ± S.E.M.].**

Taxa (number of species n=)	Neutrophil (%)	Lympho-cyte (%)	Monocyte (%)	Eosinophil (%)	Basophil (%)
Within Class <i>Mammalia</i> <sup>Δ</sup>					
Sub-class <i>Metatheria</i> (marsupials) (48)	37.0 ± 2.10 <sup>a</sup>	52.5 ± 2.28 <sup>b</sup>	4.00 ± 0.79	3.80 ± 0.41	0.56 ± 0.16
Infra-class <i>Eutheria</i> (placental mammals) (234)	50.8 ± 1.19 <sup>b</sup>	40.6 ± 1.21 <sup>a</sup>	3.42 ± 0.20	4.30 ± 0.32	0.84 ± 0.081
Within placental mammals ( <i>Eutheria</i> )					
Super-order <i>Afrotheria</i> (6)	41.8 ± 9.37 <sup>a</sup>	43.6 ± 8.87 <sup>ab</sup>	9.0 ± 3.76 <sup>b</sup>	4.2 ± 0.71 <sup>ab</sup>	0.79 ± 0.58 <sup>ab</sup>
Super-order <i>Xenarthra</i> (8)	55.7 ± 5.6 <sup>b</sup>	35.9 ± 5.7 <sup>a</sup>	3.4 ± (8) 1.0 <sup>a</sup>	4.1 ± (8) 0.9 <sup>ab</sup>	0.47 ± (8) 0.20 <sup>a</sup>
Super-order <i>Laurasiatheria</i> (166)	53.9 ± 1.32 <sup>b</sup>	37.2 ± 1.36 <sup>a</sup>	2.9 ± 0.16 <sup>a</sup>	4.9 ± 0.41 <sup>b</sup>	0.87 ± 0.10 <sup>ab</sup>
Super-order <i>Primates</i> <sup>†</sup> (19)	52.2 ± 3.5 <sup>ab</sup>	38.8 ± 3.2 <sup>a</sup>	3.5 ± 0.31 <sup>a</sup>	3.59 ± 0.91 <sup>ab</sup>	1.45 ± 0.53 <sup>b</sup>
Super-order <i>Glires</i> <sup>‡</sup> (35)	37.4 ± 3.42 <sup>a</sup>	55.7 ± 3.26 <sup>b</sup>	4.4 ± 0.80 <sup>a</sup>	1.8 ± 0.26 <sup>a</sup>	0.556 ± 0.17 <sup>a</sup>
With Super-order <i>Laurasiatheria</i>					
Order <i>Erinaceomorpha</i> n=	40.6 ± 8.96 <sup>ab</sup>	47.5 ± 8.42 <sup>c</sup>	2.36 ± 0.25 <sup>ab</sup>	7.30 ± 1.27 <sup>bc</sup>	1.34 ± 0.54 <sup>b</sup>
Order <i>Soricomorpha</i> (3)	48.4 ± 8.28 <sup>b</sup>	42.3 ± 8.9 <sup>bc</sup>	4.67 ± 1.67 <sup>c</sup>	3.77 ± 1.39 <sup>ab</sup>	0.833 ± 0.426 <sup>ab</sup>
Order <i>Chiroptera</i> (31)	34.6 ± 3.20 <sup>a</sup>	59.5 ± 3.10 <sup>d</sup>	1.72 ± 0.31 <sup>a</sup>	2.35 ± 0.42 <sup>a</sup>	1.00 ± 0.19 <sup>b</sup>
Order <i>Carnivora</i> (55)	66.9 ± 1.23 <sup>d</sup>	23.7 ± 1.11 <sup>a</sup>	3.49 ± 0.27 <sup>bc</sup>	4.47 ± 0.49 <sup>ab</sup>	0.62 ± 0.09 <sup>ab</sup>
Order <i>Perissodactyla</i> (11)	58.2 ± 2.30 <sup>bcd</sup>	34.7 ± 1.90 <sup>b</sup>	3.15 ± 0.41 <sup>abc</sup>	2.72 ± 0.43 <sup>a</sup>	1.13 ± 0.305 <sup>b</sup>
Order <i>Artiodactyla</i> (50)	50.9 ± 1.76 <sup>bc</sup>	40.6 ± 1.76 <sup>bc</sup>	3.19 ± 0.29 <sup>abc</sup>	4.75 ± 0.94 <sup>ab</sup>	1.18 ± 0.22 <sup>b</sup>

<sup>Δ</sup> There was insufficient data on species within the *Monotremata* to allow meaningful comparisons

<sup>†</sup> Orders *Primates* + *Scandentia*

<sup>‡</sup> Orders *Rodentia* + *Lagomorpha*

<sup>a, b</sup> Different superscript within a column indicates difference (p<0.01)

However, the heterophil percentage was somewhat greater in the *Afroaves* than in *Australaves* ( $p < 0.05$ ) while the percentage lymphocytes was concomitantly lower ( $p < 0.05$ ) (Table 5). There were no differences between avian groups in the percentages of monocytes, eosinophils and basophils (Table 3).

There were a series of clear relationships between blood leukocyte parameters and log body weight (Table 6). There were positive allometric relationships ( $p < 0.002$ ) for the blood concentrations of leukocytes in both mammals and birds; for both the concentrations and percentages of neutrophils (mammals) and heterophils (birds) and for the percentage of lymphocytes in both mammals and birds. Indeed, the allometric relationship explaining over 20% of variance in the percentage of neutrophils in both mammals and birds. There were also allometric relationships for monocytes (birds), eosinophils (mammals) and basophils (birds).

## Discussion

The present data support a level of control of the numbers and percentages leukocyte within birds and mammals. This is remarkable given the very short lifespan of the leukocytes and the classes of these. For instance, the lifespan of neutrophils in the circulation is short being estimated by *in vivo* labelling as 5.4 days in humans [26] and 11.4 hours in mice [27].

The present analysis provides evidence for differences in leukocyte numbers and differential leukocyte concentrations with phylogenetic relationship between and among birds and mammals. The blood concentration of leukocytes was higher in birds than mammals reflecting increases in all of the classes but in particular lymphocytes, monocytes, eosinophils and basophils (Table 1). This is to the best of our knowledge the first report of taxa differences in leukocyte number (and leukocyte classes) between and within mammals and birds. There were higher concentrations

and the percentages of eosinophils and basophils in birds than mammals. The establishing of these differences was made possible by the large data base employed. The basis of the lower numbers of leukocytes in mammals is not readily apparent but may reflect greater efficiency and/or lower basal metabolic rate in mammals. There is need to establish whether there are functional differences.

The present analysis provides the first evidence for allometric relationships for leukocyte numbers and differential leukocyte concentrations/percentages in both mammals and birds. The immune system would be expected to scale with the size of an organism [28]. On theoretic grounds, transmission rates for pathogens have been related to the body weight of the host in an allometric manner [29] with the transmission coefficient threshold scaling allometrically [30]. Moreover, allometric scaling has been demonstrated on the pathogenesis of diseases – the times from infection to either the first symptoms or death for five pathogens [31]. It is reasonable to suggest that the circulating concentrations of neutrophils would increase with the duration of exposure of host animals to pathogens as would be seen with allometric scaling. Moreover, as the infective dose of a pathogen would be expected to scale with body, it might be predicted that more large animals would have sub-clinical infections and consequently high concentrations of neutrophils.

Neutrophils are important components of the innate immune system. They are recruited to site of bacterial, fungal or protozoan infection. Activated neutrophils undergo apoptosis and is removed by macrophage (reviewed: [32-34]). The circulating concentration of neutrophils depends on the rate of production, release from the bone marrow, clearance/loss from the blood (reviewed: [35]) and obviously also blood volume with a “neurostat” or homeostatic set point postulated. The present data is supportive of the concept of the “neurostat”.

**Table 5. Comparison between differential leukocyte percentages within major avian taxa [Mean  $\pm$  S.E.M.].**

Taxa (number of species n=)	Heterophil (%) <sup>‡</sup>	Lympho-cyte (%)	Monocyte (%)	Eosinophil (%)	Basophil (%)
Sub-class <i>Palaeognathae</i> (4)	65.4 $\pm$ 1.3 <sup>b</sup>	26.0 $\pm$ 3.8 <sup>a</sup>	3.3 $\pm$	3.9 $\pm$ 1.9	1.3 $\pm$ 0.9
Sub-class <i>Neognathae</i> (192)	44.1 $\pm$ 1.2 <sup>a</sup>	43.4 $\pm$ 1.2 <sup>b</sup>	3.7 $\pm$ 0.2	6.1 $\pm$ 0.5	2.8 $\pm$ 0.3
Within Super-order <i>Galloansae</i>					
<i>Anseriformes</i> (9)	41.2 $\pm$ 6.9	50.9 $\pm$ 6.2	2.8 $\pm$ 0.9	3.9 $\pm$ 1.3	1.5 $\pm$ 0.3
<i>Galliformes</i> <sup>1</sup> (12)	34.2 $\pm$ 3.8	54.5 $\pm$ 3.5	5.4 $\pm$ 1.0	3.2 $\pm$ 0.8	3.0 $\pm$ 0.83
Within Super-order <i>Neoaves</i>					
<i>Charadriiformes</i> (14)	43.5 $\pm$ 3.7	41.9 $\pm$ 4.4	4.7 $\pm$ 1.0	5.1 $\pm$ 1.1	3.0 $\pm$ 0.7
Landbird radiation (78)	43.1 $\pm$ 2.1	42.3 $\pm$ 1.8	4.1 $\pm$ 0.3	6.8 $\pm$ 0.8	3.8 $\pm$ 0.7
Water bird assemblage, <i>Cuculiformes</i> and <i>Gruiformes</i> <sup>∞</sup> (58)	46.1 $\pm$ 2.0	41.6 $\pm$ 2.1	3.7 $\pm$ 0.4	6.6 $\pm$ 1.0	1.9 $\pm$ 0.3
Within Landbird radiation					
<i>Afroaves</i> (43)	47.3 $\pm$ 2.5 <sup>b</sup>	37.2 $\pm$ 1.9 <sup>a</sup>	4.4 $\pm$ 0.5	7.8 $\pm$ 0.9	3.9 $\pm$ 1.2
<i>Australaves</i> (35)	38.0 $\pm$ 3.5 <sup>a</sup>	48.5 $\pm$ 2.9 <sup>b</sup>	3.8 $\pm$ 0.5	5.6 $\pm$ 1.4	3.7 $\pm$ 0.78

<sup>∞</sup> Core Gruiformes/Waterbird radiation (together with *Cuculidae*, *Otididae*)(*Ciconiiformes*, *Gaviformes*, *Pelicaniformes*, *Procellariiformes*, *Sphenisciformes*)

<sup>a, b</sup> Different superscript within a column indicates difference ( $p < 0.01$ ).



Table 6. Relationships between leukocyte parameters and log<sub>10</sub> body weight.

	Adjusted R <sup>2</sup> (observations)	F = (p =)	Y intercept	Slope
Leukocyte concentrations versus Log <sub>10</sub> B. Wt.				
Mammals	0.0599 (340)	22.6 (2.947E <sup>-06</sup> )	5.37	0.69
Birds	0.0473 (200)	10.9 (0.001936)	4.84	0.3
Neutrophils/heterophil concentrations versus Log <sub>10</sub> B. Wt.				
Mammals	0.169 (264)	54.4 (2.129E <sup>-12</sup> )	1.03	0.82
Birds	0.089 (167)	17.3 (0.00005048)	0.6	1.8
Lymphocyte concentrations versus Log <sub>10</sub> B. Wt.				
Mammals	0.003 (264)	1.71 (0.191)		
Birds	-0.0027 (167)	0.56 (0.455)		
Monocyte concentrations versus Log <sub>10</sub> B. Wt.				
Mammals	0.028 (263)	15.3 (0.000118)	0.11	0.061
Birds	-0.006 (166)	0.064 (0.801)		
Eosinophil concentrations versus Log <sub>10</sub> B. Wt.				
Mammals	0.051 (263)	8.24 (0.0039)	0.10	0.048
Birds	-0.006 (166)	0.0044 (0.947)		
Basophil concentrations versus Log <sub>10</sub> B. Wt.				
Mammals	0.0036 (263)	1.95 (0.163)		
Birds	0.0169 (166)	3.84 (0.0519)		
Neutrophils/heterophils % versus Log <sub>10</sub> B. Wt.				
Mammals	0.235 (264)	87.8 (2.477E <sup>-18</sup> )	25.14	6.23
Birds	0.207 (199)	52.8 (8.267E <sup>-12</sup> )	13.72	10.52
Lymphocytes % versus Log <sub>10</sub> B. Wt.				
Mammals	0.290 (264)	116.4 (5.931E <sup>-23</sup> )	69.17	-6.94
Birds	0.097 (199)	22.4 (4.248E <sup>-06</sup> )	63.6	-6.9
Monocyte % versus Log <sub>10</sub> B. Wt.				
Mammals	0.003 (264)	1.73 (0.190)		
Birds	0.039 (191)	7.80 (0.0034)	6.24	-0.86
Eosinophil % versus Log <sub>10</sub> B. Wt.				
Mammals	0.034 (264)	11.0 (0.00103)	1.91	0.58
Birds	-0.031 (190)	0.58 (0.447)		
Basophil % versus Log <sub>10</sub> B. Wt.				
Mammals	-0.003 (264)	0.0078 (0.930)		
Birds	0.110 (190)	24.3 (1.818E <sup>-06</sup> )	9.93	-2.43

Significant differences (p<0.005) are shown in bold.

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