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The ratio of amount of haemoglobin to total surface area of erythrocytes in mammals

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The literature provides all the data needed to calculate the ratio between the amount of haemoglobin and the total surface area of erythrocytes in 54 species of mammals ranging in body mass from 2.5 g to more than 1000 kg. Analysis shows that the concentration of haemoglobin (Hb; g%) does not depend on the body mass of the mammals studied. The number of erythrocytes in 1 mm^3 of blood (RBC; $10^6 \times mm^{-3}$) is significantly lower, and the diameter of these cells significantly higher, among larger mammals as opposed to smaller ones. The result is that the total surface area of erythrocytes in 1 mm^3 of blood (TSAE; $mm^2 \times mm^{-3}$) is significantly lower among larger mammals, while the Hb/TSAE ratio ($pg \times \mu m^{-2}$) is significantly greater. These results point to the smaller size of erythrocytes of smaller mammals permitting much greater numbers to exist, thereby producing a greater TSAE and smaller Hb/TSAE ratio. The greater total surface area of red blood cells per unit volume of blood in small mammals can in turn be presumed to allow for full saturation of haemoglobin by oxygen, even where the period of contact between erythrocytes and air in the lungs is shorter than in their larger counterparts.

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Introduction

It is widely known that the concentration of haemoglobin determines the oxygen capacity of blood. However, of greater physiological importance is the amount of oxygen supplied to the tissues per unit time, thereby allowing the organism's demand for energy at a given time to be satisfied.

The concentration of haemoglobin in blood (Hb) can be considered not to depend on the body mass of mammals (Kostelecka-Myrcha 1973, Promislow 1991). The supply of oxygen to their tissues – more intensive in small than large mammals – may thus be considered regulated above all by different circulation times. In the face of this, there are probably different contact times for erythrocytes with oxygen in the lungs of mammals of differing body mass. Oxygen may only be bound by haemoglobin, and then released to the tissues, after it has passed through the erythrocyte membrane. For this reason, the total surface area of erythrocytes per unit volume of blood (TSAE) must depend on the contact time of erythrocytes with oxygen in the lungs, and on the body mass of mammals.

Previous analysis of the variability of red blood indices indicates that the amount of haemoglobin per unit surface area of erythrocytes (Hb/TSAE) is smaller in mammals of lower body mass (Kostelecka-Myrcha 1973). Later work concerning developing birds of different species, at different seasons of the year and in relation to the body masses of adult individuals, revealed that the value of the ratio Hb/TSAE determines the opportunities for full use of haemoglobin in the course of oxygen transport (Kostelecka-Myrcha 1997).

The aim of this work is to determine the amount of haemoglobin per unit area of erythrocytes in mammals of different body masses, for which the concentration of haemoglobin is known. Data was also collected on the numbers and sizes of red blood cells used in assessing the total surface area of erythrocytes.

Material and methods

In studying different haematological indices in mammals, several authors give a value for the diameter of erythrocytes which they have incorrectly regarded as independent of body mass. For example, the values for the diameters of red cells of some mammals given by Altman and Dittmer (1961) are erroneous. Cited by other authors, these errors are included in "classic" monographs (like Schmidt-Nielsen 1984). Thus, for example, the value for the diameter of erythrocytes in shrews and humans are given as being the same. In reality they are in fact known to be just over half. The obtainment of the complete data needed to calculate Hb/TSAE in different mammal species (diameters of erythrocytes included) was no easy task. In fact, the data collected refer to 54 species from among 10 orders of the mammals.

The literature provides all the data necessary for calculating the Hb/TSAE ratio for 54 species of mammals belonging to 10 orders. These range in body mass from ca 2.5 g to more than 1000 kg (Appendix). The measure of the total surface area of erythrocytes (TSAE) was the product of their numbers in 1 mm^3 of blood and a measure of the surface area of a single red blood cell. The latter measure was in turn taken to be easily-measured diameter of the cell squared (Kostelecka-Myrcha 1973). It is clear from the work of Götze (1923, cited by Korzhuev 1964) that the failure to account for the correction due to the biconcavity of erythrocytes in broad comparative studies may give rise to only a small error of several per cent in assessments of their surface area. At the same time, it is also known that the diameter of an erythrocyte determines the size of its surface area, while the thickness does not have a major influence (Fung *et al.* 1981). The adoption of this simple measure of surface area is thus entirely adequate from the point of view of comparative research.

To determine the Hb/TSAE ratio, the amount of haemoglobin present in 1 mm^3 of blood is calculated, on the basis of known contents per 100 ml (g%) that are measured by standard methods. The relationships between the log-transformed body masses of mammals and (1) the concentration of haemoglobin (Hb; g%), (2) the number of erythrocytes in 1 mm^3 of blood (RBC; $10^6 \times mm^{-3}$) and (3) their diameter (μm), as well as (4) of the total surface area of erythrocytes (TSAE; $mm^2 \times mm^{-3}$) and (5) the Hb/TSAE ratio ($pg \times \mu m^{-2}$) were expressed with the aid of linear regression and their correlation coefficients, adopting 0.05 as the significance level.

In the case of the two parameters determining values of the Hb/TSAE ratio (ie Hb and TSAE), as well as the ratio itself, the above statistical calculations were also performed for two subsets of data including the light mammals (weighing up to 1000 g) and the heavy species (of more than 1000 g). The aim was to establish whether the relationship with body mass was as much visible in these two sub-groups as in the whole dataset.

Results

Concentrations of haemoglobin (Hb) were not found to depend on body mass in the mammals studied (Fig. 1). Where the body masses are greater, the number of erythrocytes per 1 mm^3 of blood (RBC) are significantly lower (Fig. 2), while the diameters of these cells are significantly greater (Fig. 3). As a result, the total surface area of erythrocytes in 1 mm^3 of blood (TSAE) is even lower in larger and larger mammals, to an extent that achieves statistical significance (Fig. 4). In turn, the ratio Hb/TSAE is ever larger in mammals of greater and greater size (Fig. 5). In other words, in small mammals, there is a significantly smaller amount of haemoglobin per unit surface area of erythrocytes than is the case in larger species. Smaller erythrocytes in small mammals can be present in much greater numbers and at the same time ensure the maintenance of such haematocrit (Hct %) values as do not indicate a functionally significant raising of the viscosity of blood.

Worth noting is the considerable variability in the values for the studied indices that are noted in animals of defined body mass. Earlier research of a detailed nature revealed that this reflected the changing environmental and physiological situation of the organism and is of significance in regulating the process of oxygen transport in each species, and even each individual (Kostelecka-Myrcha 1967, 1973).

In relation to the results presented above, the work of Dunaway and Lewis (1965), as well as Promislow (1991), points to the lack of any dependent relationship

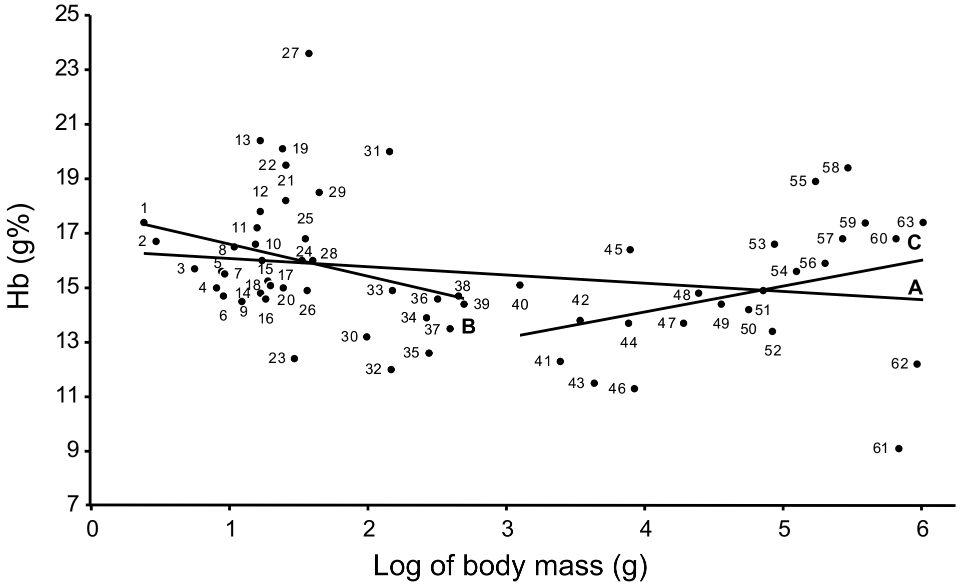

Fig. 1. The concentration of haemoglobin (Hb; g%) in relation to body mass in mammals. Numbers indicate mammal species given in Appendix. A: $y = -0.30x + 16.38$, $r = -0.21$, $n = 63$, $p = 0.098$; B (body mass ≤ 1000 g): $y = -1.18x + 17.79$, $r = -0.29$, $n = 39$, $p = 0.072$; C (body mass > 1000 g): $y = 0.95x + 10.32$, $r = 0.33$, $n = 24$, $p = 0.110$.

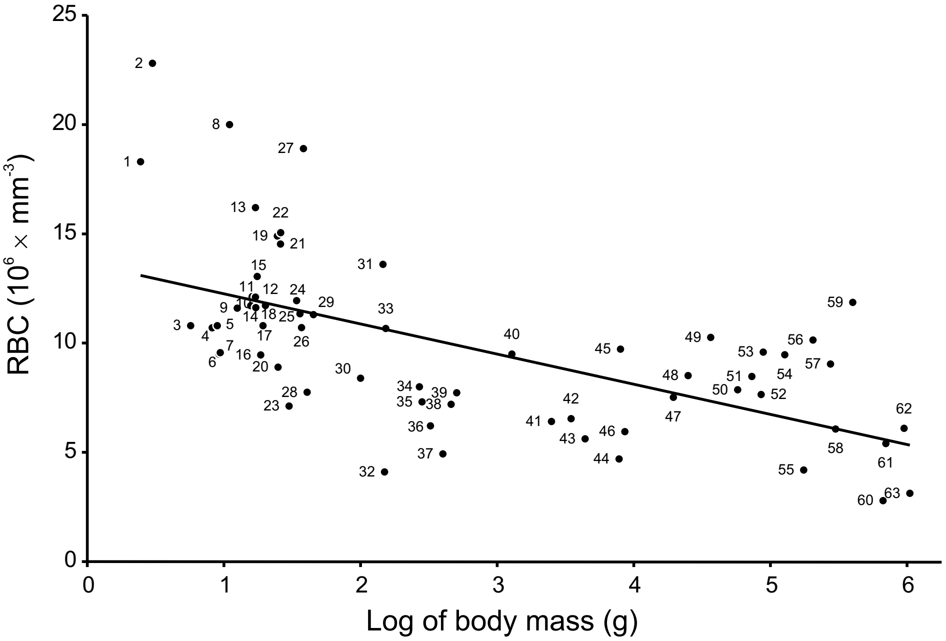

Fig. 2. The number of erythrocytes per 1 mm^3 of blood (RBC; $10^6 \times mm^{-3}$) in relation to body mass in mammals. Numbers indicate mammal species given in Appendix. $y = -1.38x + 13.63$, $r = -0.60$, $n = 63$, $p < 0.0001$.

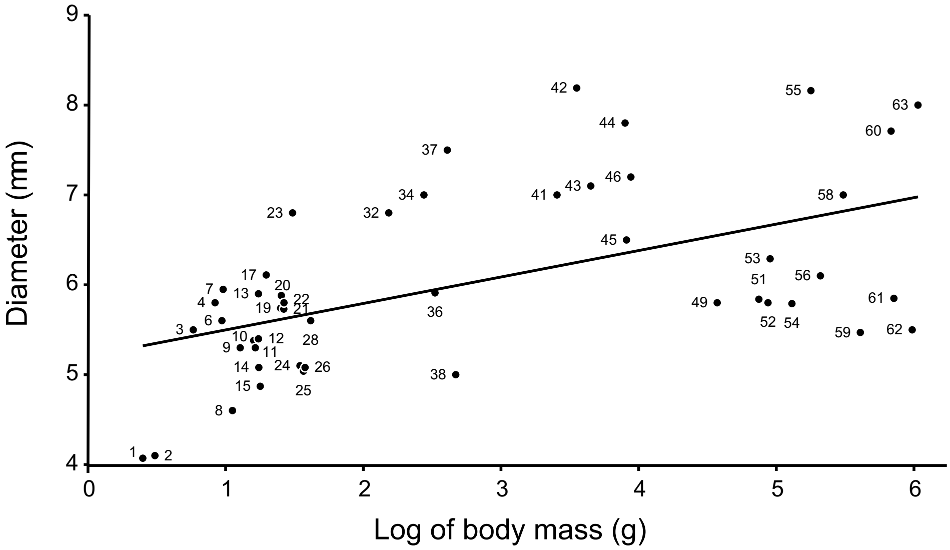

Fig. 3. The diameter of erythrocyte (μm) in relation to body mass in mammals. Numbers indicate mammal species given in Appendix. $y = 0.29x + 5.21$, $r = 0.54$, $n = 48$, $p < 0.0001$.

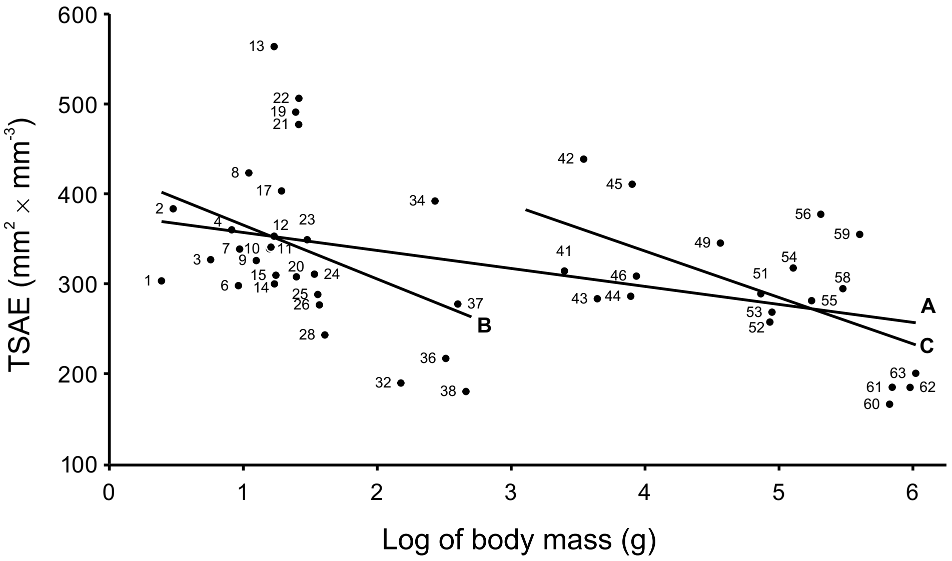

Fig. 4. The total surface area of erythrocytes per 1 mm^3 of blood (TSAE; mm^2 × mm^{-3}) in relation to body mass in mammals. Numbers indicate mammal species given in Appendix. A: $y = -19.97x + 377$, $r = -0.42$, $n = 48$, $p = 0.003$; B: $y = -60.03x + 425$, $r = -0.39$, $n = 29$, $p = 0.039$; C: $y = -51.66x + 543$, $r = -0.61$, $n = 19$, $p = 0.006$. B and C as in Fig. 1.

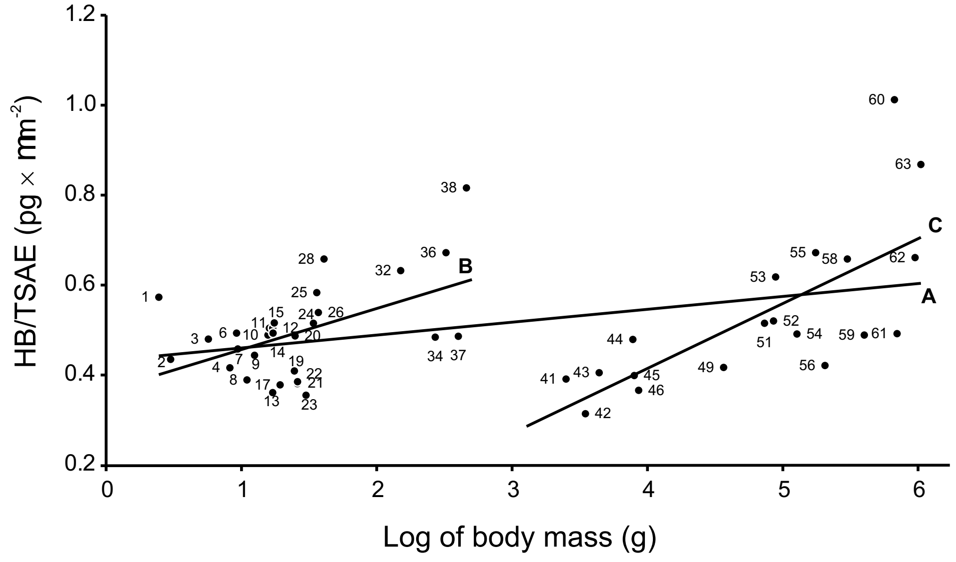

Fig. 5. The ratio of amount of Hb per unit area of erythrocytes (Hb/TSAE; pg × μm^{-2}) in relation to body mass in mammals. Numbers indicate mammal species given in Appendix. A: $y = 0.03x + 0.43$, $r = 0.38$, $n = 48$, $p = 0.008$; B: $y = 0.09x + 0.37$, $r = 0.51$, $n = 29$, $p = 0.005$; C: $y = 0.14x - 0.16$, $r = 0.72$, $n = 19$, $p = 0.001$. B and C as in Fig. 1.

between red blood parameters and the systematic allegiances of a given species, while at the same time confirming such a relationship with body mass in mammals (Kostelecka-Myrcha 1973, Promislow 1991).

Discussion

The work carried out confirmed the supposition that the Hb/TSAE ratio is related to body mass of mammals in a statistically-significant way, ie the lower the body mass the lower the ratio. Since concentrations of haemoglobin are similar in all mammals (ca 16 g%), the differences in the ratio are accounted for by the total surface area of erythrocytes alone.

The amount of oxygen transported per unit volume of blood per unit time is above all regulated by differences in the circulation time. This is due to oxygenation capacity per unit volume as determined by a largely-constant concentration of Hb. The circulation time is shorter in small mammals than in larger ones – a phenomenon which results from the much higher frequency of their hearts (Stahl 1967, Schmidt-Nielsen 1984) in association with a relatively unvarying index for this organ (Prothero 1979). The capillary transit time (t_c) is therefore probably also shorter, being a component part of the circulation time. Thus the contact time between erythrocytes and air in the lungs should really be shorter among small mammals, providing that their lungs have a structure and function similar to that in larger mammals. It is known that, per unit body mass, lung volume (V_L), pulmonary capillary volume (V_C) and total alveolar surface area (S_A) are equal in mammals species (Gehr *et al.* 1981). The diffusion volume of the lungs (D_{LO2}) has also been found constant among mammals when related to unit body mass (Gehr *et al.* 1981, Taylor *et al.* 1981, Weibel *et al.* 1981). The pulmonary "air-blood" barrier itself, and the erythrocyte membrane, do not limit the rate of diffusion of oxygen (Forster 1964, Weibel *et al.* 1981). All these data thus point to a structural and functional similarity of the lungs of all mammals.

The amount of oxygen flowing per unit lung diffusion volume (V_{O2max}/D_{LO2}) is thus first and foremost dependent on the rate of its uptake by blood. Capillary transit time (t_c) can serve as a measure of this rate, because this is in fact the time during which haemoglobin should become totally saturated with oxygen. In small mammals, as opposed to large ones, the process must take place in a much shorter time. During the shorter residence time of the erythrocytes in the lungs, a unit surface area of these cells has a chance to encounter a smaller number of oxygen molecules, which can only saturate a correspondingly smaller amount of Hb. For this reason, a greater total surface area of erythrocytes (TSAE) – resulting in a smaller Hb/TSAE ratio – probably allows for the full oxygen saturation of the same amount of haemoglobin as in large mammals, as well as for rapid delivery of the gas to the tissues. The process is probably associated with a higher speed of enzymatic reactions, as confirmed experimentally, for example in the case of carbonic anhydrase of small mammals (Larimer and Schmidt-Nielsen 1960).

A similar mechanism may also be presumed to allow for full haemoglobin saturation in mammals adapted to life at high altitudes. Korzhuev (1964) cites data of various authors concerning the concentration of Hb, number and size of erythrocytes in the *Lama glama* and *L. vicugna*. A similar concentration of Hb (17.9 g%) in these animals and among lowland species allows for advancing a hypothesis that all their haemoglobin is used in the transport of oxygen. As is well-known, the physiology of a lowland mammal finding itself in the mountains engages in a compensatory raising of the amount of haemoglobin in blood. This is because only a part of it is saturated by oxygen in conditions of the lower partial pressure of this gas. At the same time, high-mountain mammals have smaller, oval erythrocytes ($7.3 \times 3.6\ \mu m$), in much greater numbers (ca $14.5 \times 10^6 \times mm^{-3}$), than lowland mammals of similar body mass. It is therefore highly probable that the greater total surface area of erythrocytes and greater haemoglobin oxygen affinity among high-mountain mammals are what allow for the oxygen saturation of all their haemoglobin. This occurs in a situation in which a unit surface area of red blood cells is in contact with a smaller number of oxygen molecules in their lungs, in capillary transit time. Thus, it is the size of the TSAE in mammals that determines the Hb/TSAE ratio, something that probably corresponds with the number of oxygen molecules per unit area of erythrocytes during their contact with air in the lungs.

Among birds, in contrast, the Hb/TSAE ratio is constant in all species, even in differing physiological and environmental situations (Kostelecka-Myrcha 1997). In this second group of endothermic animals, the Hb concentration depends on body mass (Kostelecka-Myrcha and Chołostiakow-Gromek 2001), as well as the season of the year (Kostelecka-Myrcha 1997), and changes very markedly in the course of nestling development (Kostelecka-Myrcha 1985). Appropriate changes in the number and size of erythrocytes ensure that changes in TSAE are always directly proportional to those in the Hb concentrations, with the result that the Hb/TSAE ratio remains constant (Kostelecka-Myrcha 1997). The constant amount of haemoglobin per unit area of erythrocytes may be presumed optimal from the point of view of their oxygen saturation in the lungs of birds. It would seem that their lungs ensure constant conditions for this process, via the presence of air sacs and the cross-current exchange of gas between the air and the blood in the pulmonary capillaries (Scheid and Piiper 1971, Schmidt-Nielsen 1975). Thus, changes in the value for the total surface area of erythrocytes allow for full oxygen saturation of haemoglobin in the differently-constructed lungs of mammals and birds.

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Appendix. Values of red blood cell indices used for the calculation of the total surface area of erythrocytes (TSAE) and the Hb/TSAE ratio in mammals. Hb – concentration of haemoglobin, RBC – number of erythrocytes per 1 mm^3 of blood.

No.	Species	Order	Body mass (g)	Hb (g%)	RBC ($10^6 \times mm^{-3}$)	Diameter (μm)	Source	TSAE ($mm^2 \times mm^{-3}$)	Hb/TSAE ($pg \times \mu m^{-2}$)
1	2	3	4	5	6	7	8	9	10
1.	*Suncus etruscus*	Insectivora	2.45	17.4	18.3	4.07	Jürgens *et al*. 1981	303.137	0.573
2.	*Sorex minutus*	Insectivora	3.0	16.7	22.8	4.1	Wołk 1974	383.268	0.435
3.	*Micromys minutus*	Rodentia	5.7	15.7	10.8	5.5	Wołk 1990	326.700	0.480
4.	*Myotis daubentoni*	Chiroptera	8.2	15.0	10.7	5.8	Wołk 1990	359.948	0.416
5.	*Crocidura russula*	Insectivora	9.0	15.6	10.8		Jürgens *et al*. 1981		
6.	*Sicista betulina*	Rodentia	9.2	14.7	9.5	5.6	Wołk 1990	297.920	0.493
7.	*Pitymys pinetorum*	Rodentia	9.4	15.51	9.56	5.95	Foreman 1956	338.447	0.458
8.	*Sorex araneus*	Insectivora	11.0	16.5	20.0	4.6	Wołk 1974	423.200	0.389
9.	*Neomys anomalus*	Insectivora	12.5	14.5	11.6	5.3	Wołk 1974	325.844	0.444
10.	*Neomys fodiens*	Insectivora	15.7	16.6	11.71	5.38	Wołk 1974	338.938	0.489
11.	*Clethrionomys glareolus*	Rodentia	16.1	17.2	12.13	5.3	Kostelecka-Myrcha 1967	340.731	0.504
12.	*Neomys fodiens*	Insectivora	17.0	17.8	12.1	5.4	Wołk 1974	352.836	0.504
13.	*Eptesicus serotinus*	Chiroptera	17.0	20.4	16.2	5.9	Wołk and Ruprecht 1988	563.922	0.361
14.	*Lagurus lagurus*	Rodentia	17.1	14.8	11.62	5.08	Kostelecka-Myrcha 1967	299.870	0.493
15.	*Pitymys subterraneus*	Rodentia	17.5	16.0	13.05	4.87	Kostelecka-Myrcha 1967	309.505	0.516
16.	*Apodemus sylvaticus*	Rodentia	18.6	14.59	9.46		Pérez-Suárez *et al*. 1990		
17.	*Peromyscus leucopus*	Rodentia	19.3	15.25	10.8	6.11	Foreman 1956	403.186	0.378
18.	*Pitymys duodecimcostatus*	Rodentia	20.1	15.08	11.72		Pérez-Suárez *et al*. 1990		
19.	*Eptesicus serotinus*	Chiroptera	24.6	20.1	14.9	5.74	Wołk and Ruprecht 1988	490.919	0.409
20.	*Apodemus flavicollis*	Rodentia	24.9	15.0	8.9	5.88	Wołk 1990	307.712	0.487
21.	*Eptesicus serotinus*	Chiroptera	25.9	18.2	14.53	5.73	Wołk 1990	447.062	0.381
22.	*Eptesicus serotinus*	Chiroptera	26.0	19.5	15.05	5.8	Wołk 1990	506.282	0.385
23.	*Cricetulus grisens*	Rodentia	30.0	12.4	7.12	6.8	Moore 1966	348.880	0.355

Appendix – continued.

1	2	3	4	5	6	7	8	9	10
24.	*Microtus arvalis*	Rodentia	34.0	16.0	11.94	5.1	Kostelecka-Myrcha 1967	310.558	0.515
25.	*Microtus agrestis*	Rodentia	36.0	16.8	11.34	5.04	Kostelecka-Myrcha 1967	288.054	0.583
26.	*Microtus oeconomus*	Rodentia	37.0	14.9	10.71	5.08	Wołk 1970	276.386	0.539
27.	*Molossus ater*	Chiroptera	38.2	23.6	18.9		Jürgens *et al*. 1981		
28.	*Artibeus jamaicensis*	Chiroptera	40.7	16.0	7.75	5.6	Valdivieso and Tamsitt 1971	243.040	0.658
29.	*Phyllostomus discolor*	Chiroptera	45.2	18.5	11.3		Jürgens *et al*. 1981		
30.	*Amnospermophilus harasii*	Rodentia	100.0	13.2	8.39		Hall 1965		
31.	*Rousettus aegyptiacus*	Chiroptera	146.0	20.0	13.6		Jürgens *et al*. 1981		
32.	*Mesocricetus auratus*	Rodentia	150.0	12.0	4.1	6.8	Chicewicz and Dulemba 1968	181.584	0.632
33.	*Spermophilus tridecemlineatus*	Rodentia	153.0	14.9	10.67		Hall 1965		
34.	*Rattus norvegicus* (Wistar)	Rodentia	270.0	13.9	8.0	7.0	Barański and Barkowa 1956	392.000	0.484
35.	*Spermophilus tereticaudus*	Rodentia	282.0	12.6	7.31		Hall 1965		
36.	*Sciurus vulgaris*	Rodentia	325.0	14.59	6.21	5.91	Dimitrova 1979	216.903	0.672
37.	*Cavia porcellus*	Rodentia	400.0	13.5	4.93	7.5	Lewis 1992	277.312	0.486
38.	*Chinchilla lanigera*	Rodentia	460.0	14.7	7.2	5.0	Kitts *et al*. 1971	180.000	0.816
39.	*Sciurus carolinensis*	Rodentia	505.0	14.4	7.73		Hall 1965		
40.	*Cynomys ludovicianus*	Rodentia	1280.0	15.1	9.5		Hall 1965		
41.	*Oryctolagus cuniculus*	Lagomorpha	2500.0	12.3	6.41	7.0	Sheeler and Barber 1964	314.090	0.391
42.	*Marmota monax*	Rodentia	3478.0	13.8	6.54	8.19	Musacchia *et al*. 1955, Hall 1966	438.677	0.314
43.	*Macaca nemestrina*	Primates	4400.0	11.5	5.62	7.1	Rahlmann *et al*. 1967	283.304	0.405
44.	*Myocastor coypus*	Rodentia	7800.0	13.7	4.7	7.8	Ferrara 1951, Hall 1966	285.948	0.479
45.	*Vulpes fulva*	Carnivora	8000.0	16.4	9.72	6.5	Korzhuev 1964	410.670	0.399
46.	*Macaca nemestrina*	Primates	86 00.0	11.3	5.95	7.2	Rahlmann *et al*. 1967	305.448	0.366
47.	*Neofelis neubulosa*	Carnivora	19 500.0	13.7	7.52		Pospišil *et al*. 1987		
48.	*Lynx lynx*	Carnivora	25 000.0	14.8	8.51		Pospišil *et al*. 1987		
49.	*Panthera pardus saxicolor*	Carnivora	36 500.0	14.4	10.26	5.8	Korzhuev 1964, Pospišil *et al*. 1987	345.146	0.417

Appendix – concluded.

1	2	3	4	5	6	7	8	9	10
50.	*Acinonyx jubatus*	Carnivora	57 500.0	14.2	7.86		Pospišil *et al*. 1987		
51.	*Rangifer tarandus*	Artiodactyla	73 200.0	14.9	8.47	5.84	Gorodeckii 1962	288.847	0.515
52.	*Rangifer tarandus*	Artiodactyla	85 400.0	13.4	7.65	5.8	Gorodeckii 1962	257.346	0.520
53.	*Rangifer tarandus*	Artiodactyla	88 500.0	16.6	9.59	6.29	Gorodeckii 1962	268.367	0.618
54.	*Rangifer tarandus*	Artiodactyla	127 400.0	15.6	9.47	5.79	Gorodeckii 1962	317.473	0.491
55.	*Tursiops tursio*	Cetacea	175 000.0	18.9	4.19	8.16	Korzhuev 1964	281.048	0.672
56.	*Panthera leo leo*	Carnivora	205 000.0	15.9	10.14	6.1	Korzhuev 1964, Pospišil *et al*. 1987	377.309	0.421
57.	*Panthera tigris altaica*	Carnivora	275 000.0	16.8	9.04		Pospišil *et al*. 1987		
58.	*Ursus arctos*	Carnivora	300 000.0	19.4	6.07	7.0	Korzhuev 1964, Seal *et al*. 1967	294.490	0.658
59.	*Equus caballus* Arabian hors	Perissodactyla	400 000.0	17.38	11.86	5.47	Gill and Kompanowska-Jezierska 1986	354.861	0.489
60.	*Odobenus rosmarus*	Pinnipedia	668 000.0	16.8	2.79	7.71	Wołk 1990	165.846	1.012
61.	*Bos taurus*	Artiodactyla	700 000.0	9.1	5.4	5.85	Wołk 1990	184.801	0.492
62.	*Bison bonasus*	Artiodactyla	950 000.0	12.2	6.1	5.5	Wołk 1990	184.525	0.661
63.	*Odobenus rosmarus*	Pinnipedia	1 049 000.0	17.4	3.13	8.0	Wołk 1990	200.320	0.868