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The allometry and scaling of the size of vertebrate eyes

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Abstract

We compiled data from the literature and colleagues to examine the relationship between eye axial length and body weight for vertebrates as well as birds, mammals, reptiles, and fishes independently. After fitting the data to logarithmic and semi-logarithmic models, we found that axial length of vertebrate eyes does obey a conventional logarithmic relationship with body weight rather than a semi-logarithmic relationship as suggested by the results of previous studies [Handbook of Sensory Physiology, VII/5: The Visual System in Vertebrates, Springer-Verlag, Berlin, 1977; The Allometry of the Vertebrate Eye, Dissertation, University of Chicago, UMI, Ann Arbor, T28274, 1982]. The regression slopes and intercepts appear to be characteristic of various animal groups. The axial length of the eye is largest in birds and primates, smaller in other mammals (especially rodents) and reptiles, and widely varying in fishes.

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1. Introduction

What is a large eye and what is a small eye, in relation to body size? In order to answer this question, one must first find a measure of eye size. The axial length of the eye serves as a valid measure of eye size for two reasons: first, a considerable amount of information on eye size has been gathered in this form, and second, there is a close relationship between axial length and focal length of vertebrate eyes (Murphy & Howland, 1987). The focal length determines the size of the image on the retina, and although the spatial sampling frequency may vary across a retina and between taxa, nonetheless, the focal length is related to the amount of visual information reaching the brain. This makes axial length a particularly meaningful measure.

Allometry refers to the scaling of size of animals and their parts. It is well known that animals are not isometric; that is, their organs generally do not scale in a linear fashion with their bodies. For example, cartoonists often exploit the fact that the eyes of babies are much larger in proportion to body size than the eyes of adults. The most commonly used allometric equation

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employs not a linear but a logarithmic scaling of both body size and the size of the organ under study. The equation is written in one of two equivalent forms:

or

where the intercept constant of Eq. (1) is the logarithm of the proportionality constant of Eq. (2). The slope constant is often referred to as the "body mass exponent". All of these concepts are well reviewed and discussed by Schmidt-Nielsen (1984).

Researchers studying allometry in animals have usually attempted to relate the size of the organ to some functional property of that organ. For example, the sizes of bones might scale so that they would be columns of equivalent strength, in which case the square of the diameter of bones would scale with the mass of the animal (Schmidt-Nielsen, 1984). Regarding sensory organs, it has been possible to relate the dimensions of the semi-circular canals to the frequency spectrum of the motions of the animals possessing them (Howland & Masci, 1973; Mayne, 1965).

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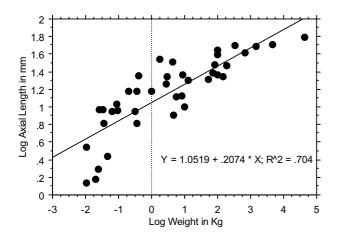


Fig. 1. Relationship between the axial length of the eye and body weight in 40 vertebrates, mainly birds and mammals, redrawn from Hughes (1977).

The eyes, however, present a unique problem in that no theory accounts for their scaling with body size. It is known empirically that the brain weight scales with the 0.66 power of the body size in many vertebrates, and given that weight is proportional to the third power of length, the brain's linear dimension therefore scales with the 0.22 power of the animal's weight (Schmidt-Nielsen, 1984). Since the retina is a part of the brain, its diameter should also scale with the 0.22 power of body weight, and the other dimensions of the eye, such as axial length, may scale with weight in the same way.

The size of vertebrate eyes has been studied by Hughes (1977). His data appear in Fig. 1; there is a curvilinear relationship between the logarithm of axial length and the logarithm of body weight. In this data set, the slope constant of Eq. (1) appears to decrease with increasing body weight. One can obtain a straightline relationship between axial length and body weight if a semi-logarithmic plot of axial length vs. log body weight is used instead of a double logarithmic plot. However, Hughes's data set is rather small and includes mostly birds and mammals. It is possible that the conventional allometric equations would better describe a more inclusive data set. The purpose of this study was to expand on Hughes's data set and determine whether or not the conventional log-log allometric relationship holds for vertebrate eye size.

2. Methods

We compiled existing data on eye axial lengths and body weights of vertebrates from the literature (Allyn, 1947; Altman & Dittmer, 1962; American Kennel Club, 1938; Andersen & Munk, 1971; Bellairs, 1970; Carlander, 1969; Christie, 1985; Duke-Elder, 1963; Gay, 1914; Grzimek, 1975, 1990; Halliday & Adler, 1986;

Howland & Sivak, 1984; Hueter, 1991; Hughes, 1977, 1979; Hutchinson, 1935; Kroger & Fernald, 1994; Lord Jr., 1956; Martin & Brooke, 1991; Mathis, Schaeffel, & Howland, 1988; Murphy et al., 1990; Murphy, Evans, & Howland, 1985; Nellis, Sivak, McFarland, & Howland, 1989; Nelson, 1984; Neuweiler, 1962; Northmore & Granda, 1991; Norton & McBrien, 1992; Patten, 1960; Perrins, 1990; Perrins & Middleton, 1985; Pettigrew, Dreher, Hopkins, McCall, & Brown, 1988; Rochon-DuVigneaud, 1943; Rouse, 1973; Sivak & Howland, 1987; Sivak, Howland, & McGill-Harelstad, 1987; Sivak, Howland, West, & Weerheim, 1989; Terres, 1980; Troilo & Judge, 1993; Wheeler, 1985; Whitaker, 1980), from colleagues (Andrew Bass, Cheri Brown, Margaret Marchaterre, Mary Lou Miller, all of Cornell University; Christopher Murphy, University of Wisconsin; Frank Schaeffel, University of Tuebingen; personal correspondence), and from our own measurements of dissected specimens (using calipers) and prepared slides. When available, schematic eyes as well as measured photographs were used to obtain axial lengths. Our entire data set along with notes regarding data quality and method of measurement or calculation appears in the Appendix A. While we acknowledge that calculations such as those described below necessarily add error to the data, we believed the benefits of obtaining as large a data set as possible outweighed the costs.

For some of the animals, the axial length was derived from the eye mass of the animal. This was done by plotting log (axial length) vs. log (eye weight) for animals for which we had both axial length and eye mass. The resulting equation for the regression line through these points was used to calculate other axial lengths. For many of the birds, axial lengths were derived in a similar manner, though iris size was used instead of eye mass. For other animals, especially the reptiles, amphibians, and fishes, a weight was not available for a particular animal whose axial length we had. Often only the length of the animal was given and the weight had to be derived. This was done through the following relationship:

$$W_2 = (W_1^3 L_2 / L_1)^{1/3} (3)$$

where W_1 and L_1 are the length and weight of a related animal. L_2 is the length of the animal of unknown weight. The relationship is based on the fact that L is proportional to $W^{1/3}$ and that for animals with similar body shapes, as in related species, the proportion $L_1/L_2 = W_1^{1/3}/W_2^{1/3}$ should hold true.

In obtaining data from fishes, we encountered another problem. Fishes grow throughout their lives (as do some reptiles and amphibians), so an axial length obtained from one source for a particular species might be from a different age in the fish's life than the weight obtained from a different source. In order to find axial lengths and weights of fishes from the same point in

time, dissections of *Porichthys notatus* (the plainfin midshipman) preserved in 10% formalin were performed. This ensured that at least a subset of our fish data consisted of axial length and weight measurements from the same individual fish. Weights were obtained before dissection of the eyes to find the axial lengths.

We then attempted to fit the data with logarithmic and semi-logarithmic models. We also examined the eye sizes of particular animal groups by finding the equations of the regression lines for birds, mammals (as well as rodents and primates separately), reptiles, and fishes, then used these equations to calculate the predicted log axial lengths from the actual body weights. When we had more than one set of measurements on the same species, we averaged the data in the form of log weight and log axial length so as not to give extra weight to any given species. Amphibians were included in the vertebrate data set but were not analyzed separately because of the small number of species for which we found data. For each group, an analysis of variance was performed to determine whether the slope was significantly different from zero, and for the log-log regressions, analyses of covariance (ANCOVAs) were performed to determine whether the slopes and intercepts differed significantly from those of the total vertebrate regression. To determine whether each taxon's log axial length was underestimated or overestimated by the vertebrate regression line (i.e. whether the members of each taxon have large or small eyes compared to vertebrates as a whole), we used a Wilcoxon signed rank test to examine the differences between the actual log axial length values and those predicted by the vertebrate regression line. All

statistical analyses were performed using the computer program StatView (Abacus Concepts, Berkeley, CA).

3. Results

Our data and regression statistics for all vertebrates as well as for each taxon studied alone appear in Table 1. The conventional allometric equation (1) appeared to fit the data as well as a semi-logarithmic plot. In all cases except fishes, primates and reptiles, the proportion of variance explained by the model was greater for the logarithmic model than for the semi-logarithmic model. The conventional equation also had the advantages of a more even distribution of the data along each axis. Therefore, all figures are shown as double logarithmic plots in the form of Eq. (1).

A logarithmic regression plot of axial length and body weight for all vertebrates is given in Fig. 2. The curvilinear shape of Hughes' graph (Fig. 1) has flattened with the inclusion of many more vertebrates. However, the slopes and intercepts are identical to one decimal place. The distributions of weights and axial lengths when plotted logarithmically are both close to normal, as shown in Fig. 3.

The regression equation for all vertebrates allows us to predict the axial length for any given animal and compare it to the true axial length value to determine whether an eye is relatively large or small compared to vertebrates as a whole. Relative to the regression line, then, the largest eye in Fig. 2 is that of the 2-kg eagle owl at 35 mm, and the relatively smallest eye is that of the

Table 1 Mean logarithms of eye axial lengths and body weights, as well as regression statistics from logarithmic and semi-logarithmic models for all 292 vertebrates, 70 birds, 145 mammals (including 25 rodents and 11 primates), 18 reptiles, and 54 fishes studied

Data set	Statistic	Log axial	Log body	Regression s	statistics			
		length (mm)	weight (kg)	Model	Slope	Intercept	Slope p-value	r^2
Vertebrates	Mean	1.138	0.572	Log	0.196	1.026	< 0.0001	0.666
	SD	± 0.350	±1.456	Semi-log	7.408	14.006	< 0.0001	0.654
Birds	Mean	1.146	-0.145	Log	0.188	1.173	< 0.0001	0.637
	SD	±0.221	±0.937	Semi-log	6.346	16.745	< 0.0001	0.516
Mammals	Mean	1.202	1.183	Log	0.225	0.935	< 0.0001	0.835
	SD	± 0.390	±1.505	Semi-log	8.335	11.816	< 0.0001	0.728
Rodents	Mean	0.757	-0.585	Log	0.262	0.910	< 0.0001	0.713
	SD	±0.318	±1.026	Semi-log	3.946	9.614	< 0.0001	0.738
Primates	Mean	1.223	0.709	Log	0.117	1.140	0.0001	0.826
	SD	±0.136	±1.059	Semi-log	4.134	14.467	< 0.0001	0.876
Reptiles	Mean	0.876	0.051	Log	0.149	0.868	< 0.0001	0.630
•	SD	±0.236	±1.256	Semi-log	2.458	8.160	0.0011	0.444
Fishes	Mean	1.080	0.208	Log	0.256	1.027	< 0.0001	0.452
	SD	±0.350	±0.917	Semi-log	9.834	14.232	< 0.0001	0.559

Amphibians are included in the vertebrate group but not analyzed separately. Thus, the data set contains representatives from each of the five classes of vertebrates.

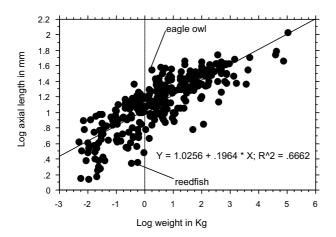


Fig. 2. Logarithmic regression of axial length vs. body weight for 292 vertebrates. The form of the plot is the same as Fig. 1, but additional data are included. The eagle owl had the largest positive residual, whereas the reedfish had the largest negative residual.

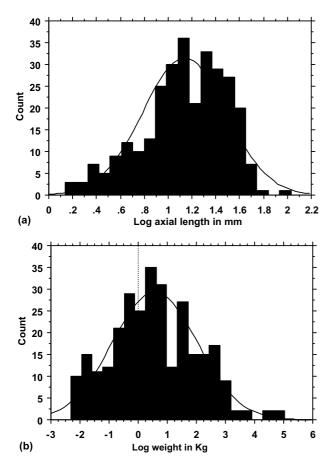


Fig. 3. Distributions of the logarithms of body weight and eye axial length in 292 vertebrates.

0.5-kg reedfish at 2.25 mm. Regression plots of log axial length vs. log weight for each group studied are given in Fig. 4. A plot of all regression lines including the total vertebrate regression line is given in Fig. 5.

3.1. Birds

The regression plot for birds alone appears in Fig. 4a. An ANCOVA found that the slope of this line does not differ significantly from the slope of the total vertebrate regression line (F = 0.104; p = 0.75); however, the intercepts are significantly different (F = 32.027; p < 0.0001), meaning that the regression line for birds is parallel but not coincident with the regression line for all vertebrates. A comparison of actual log axial weights of birds with those predicted from the all-vertebrates regression using a Wilcoxon signed rank test showed that the probability that these were drawn from the same population was <0.0001. Therefore, bird eyes are 36% larger than those of vertebrates in general.

3.2. Mammals

Fig. 4b gives the regression plot for all mammals studied. According to an ANCOVA, the slope and of this regression line differs significantly from that of the vertebrate. A comparison of actual log axial weights of mammals with those predicted from the all-vertebrates regression using a Wilcoxon signed rank test showed that the probability that these were drawn from the same population was p < 0.0001. These results show that mammals have axial lengths that are 15% larger than those of vertebrates as a whole.

Among the mammals, rodents alone are shown in Fig. 4c and primates alone in Fig. 4d. For rodents, the slope of the regression line does not differ significantly from that of the vertebrate regression line, but the intercept is significantly different (slope: F = 2.565, p = 0.1103; intercept: F = 5.758, p = 0.0170). For primates, neither the slope nor the intercept differ from those of the vertebrate regression line, implying that the primate and vertebrate regression lines are coincident. A comparison of actual log axial weights of rodents with those predicted from the all-vertebrates regression using a Wilcoxon signed rank test showed that the probability that these were drawn from the same population was p < 0.0004. For primates, this difference was also significant, but the mean of the residuals was positive rather than negative (Wilcoxon signed rank test, p < 0.0004). The vertebrate regression overestimates the axial lengths of rodents and underestimates those of primates; thus, rodents have 61% as large eyes and primates have 35% larger eyes than those of vertebrates as a whole.

3.3. Reptiles

Reptile regression data appear in Fig. 4e. The slope of the reptile regression line did not differ significantly from that of the general vertebrate line (F = 1.419; p = 0.2345), but the intercept did differ significantly (F = 10.406; p = 0.0014). A comparison of actual log

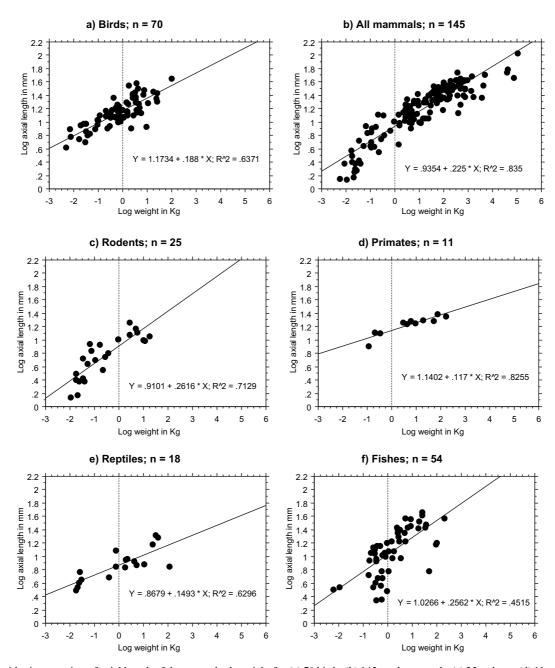


Fig. 4. Logarithmic regression of axial length of the eye vs. body weight for (a) 70 birds, (b) 145 total mammals, (c) 25 rodents, (d) 11 primates, (e) 18 reptiles, and (f) 54 fishes.

axial weights of reptiles with those predicted from the all-vertebrates regression using a Wilcoxon signed rank test showed that the probability that these were drawn from the same population was <0.0021. Reptiles therefore have eyes that are 70% as large as those of vertebrates as a group.

3.4. Fishes

Data for fishes appear in Fig. 4f; they show a remarkable range of variation in eye size as a function

of species. The r^2 values for fishes were the lowest of all the vertebrate groups for both regression models; only the semi-logarithmic regression for reptiles and birds were lower. Possibly as a result of this great variability, the differences between the actual and predicted log axial lengths were not significantly different (p > 0.25 Wilcoxon signed rank test) and neither the slope nor the intercept was significantly different from that of the vertebrate regression line (slope: F = 3.288, p = 0.0707; intercept: F = 0.001, p = 0.9760).

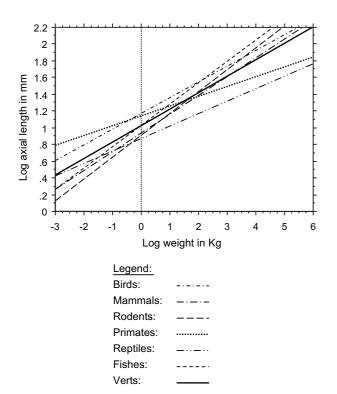


Fig. 5. Regression lines for each taxon (dotted lines) in comparison to the entire vertebrate data set (solid line). Equations for the regression lines are given in Figs. 2 and 4.

4. Discussion

A desirable transform for the sizes of animals or their parts is one that does not emphasize small or large sizes over each other and distributes the axial lengths and weights either evenly or in a bell-shaped curve along the axis. In a limited data set (Hughes, 1977), it appeared that the logarithm of body weight was linearly related to the axial length of the eye, but upon collecting data for more vertebrates we found that the conventional double logarithmic formula of Eq. (1) described the relationship between eye axial length and body weight well. Our regression equation for all vertebrates can be stated in the following form:

Axial length (mm) =
$$10.61 * Weight (kg)^{0.1964}$$
 (4)

which confirms the prediction that eye size should scale with roughly the 0.2 power of body weight.

The curvilinearity of the Hughes data disappears when a large sample of vertebrates is studied but returns when only mammals are examined, showing that mammals accounted for much of the deviation from the conventional allometric relationship. This finding merits further investigation; perhaps different models fit different families of animals, rather than one logarithmic model for all vertebrates or all families of the same class. Ritland (1982) found a similar result for eye diameter and body length as opposed to eye axial length and body

weight. Mammals had a pronounced concave curve on a log-log plot (decreasing slope with increasing log weight), and birds had a slight concave curve, whereas the reptilian and amphibian lines were straight (Ritland, 1982). The concavity of the mammalian graph was largely attributable to insectivores, microchiropterans, and caenolestid marsupials, as well as the smaller rodents and edentates, all of which had relatively small body sizes and large slopes (eye size/body size). Furthermore, each group of mammals had a linear log-log graph, but the combination of different groups with different slopes gave the composite graph a curvilinear appearance (Ritland, 1982).

The high amount of variation in the fish regression, for instance, is largely the result of fifteen species that lie below the regression line. Removing these species increased the r^2 value for the log-log plot from 0.452 to 0.828. Of these species, at least ten have particularly long bodies, such as the green moray, reedfish, and lamprey. Increasing a fish's body length is one way to increase body mass without increasing head size (and therefore eye size), so long-bodied fishes such as eels may not obey the same allometric relationships as other fishes do.

4.1. Conclusions

The regression line for all vertebrates provides a measure of relative eye size for any given body weight. Animals whose axial lengths lie above the regression line have relatively large eyes, and those below it have relatively small eyes. After comparing the regression lines for vertebrates as a whole and for each group alone, we conclude that birds and primates have relatively large eyes and that both rodents and reptiles have small eyes. Fish eye sizes, on the other hand, are so variable that no general conclusion can be drawn regarding their relative sizes. Of course, the relative eye size of any animal listed in the Appendix A may be estimated by comparing its axial length with the predicted axial length of the smallest taxon within which it falls.

What, then, is the significance of having a long or short axial length? The main consequence of a longer eye is a greater resolving power. Regardless of how eye size is measured (e.g. axial length, diameter, volume), resolving power increases with absolute eye size (Walls, 1967, p. 175). However, there is an added advantage to having not only a large eye but a long eye: the increased distance between the cornea/lens and the retina increases the size of the image (Walls, 1967, p. 175). A large image is quite useful for animals that rely on vision to find food and escape from predators.

Therefore, a future direction of this research is to investigate the role of other factors such as nocturnality and predation with a view toward quantifying their effect on eye size. Using eye diameter and body length as measures of size, Ritland (1982, p. 130) found correla-

tions between eye size and behavior for a large sample of birds, concluding that the relative length of the optical axis was inversely related to the width of the visual field necessary for a particular species's lifestyle, and that eye size in general reflected the relative importance of vision among birds. The same conclusion may well hold true for other classes of terrestrial vertebrates. For example, birds in general need to scan the environment over long distances during flight for food and predators and thus have large eyes, attesting to the importance of vision and the need for great resolving power in avian life. The high speeds at which some birds (especially raptors) fly also creates a need for high visual acuity (Walls, 1967, pp. 173-174). However, in this regard, Hall (2000) in an examination of Leuckart's law (which states that swifter moving animals have larger eyes) did not find convincing evidence for it in a study of a number of bird species.

On the other hand, rodents have highly developed senses of olfaction and hearing, senses which at times are better suited than vision to a nocturnal lifestyle. However, when vision remains important in nocturnal animals such as owls, larger eyes can maximize the amount of light reaching the retina. It may not be possible,

therefore to make generalized predictions about eye size based solely on the nocturnal or diurnal lifestyle of animal groups. Some nocturnal animals rely on senses other than vision, which is reflected in their small eye size. Others take the strategy of increasing eye size as much as possible to compensate for the low light conditions.

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Appendix A

Axial length and weight data. For all references, only the first author's name is given to save space. Notes and an explanation of the data quality rankings are given below.

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Reference for weight	Quality
Alytes obstetri- cans	Midwife toad	Amphibians	0.0100	4.000	Rochon- DuVigneaud (1943)	Note 10	Group 5
Bombinator pachypus	Yellow-bellied toad	Amphibians	0.0100	3.000	Rochon- DuVigneaud (1943)	Bellairs (1970), Note 3	Group 5
Bufo americanus	American toad	Amphibians	0.0113	1.480	Mathis (1988)	Note 1	Group 5
Bufo americanus	American toad	Amphibians	0.0164	6.083	Mathis (1988)	Note 1	Group 5
Bufo americanus	American toad	Amphibians	0.0104	0.982	Mathis (1988)	Note 1	Group 5
Rana catesbei- ana	N. American bull frog	Amphibians	0.5199	11.459	Note 30	Altman (1962)	Group 6
Rana temporaria	Common frog	Amphibians	0.5930	5.300	Note 30	Altman (1962)	Group 6
Accipiter nisus	Sparrow hawk	Birds	1.5600	13.500	Lord Jr. (1956)	Note 29	Group 5
Alle alle	Dovekie	Birds	0.1030	10.488	Note 30	Altman (1962)	Group 6
Amazilia tzacatl	Rufous-tailed hummingbird	Birds	0.0048	4.132	Note 30	Altman (1962)	Group 6
Anas acuta	Pintail	Birds	0.6700	9.986	Note 30	Altman (1962)	Group 6
Anas carolinen- sis	Green-winged teal	Birds	0.3050	8.792	Note 30	Altman (1962)	Group 6
Apteryx australis	Brown kiwi	Birds	2.2000	8.000	Sivak (1987b)	Perrins (1985)	Group 3
Apus apus	Common swift	Birds	0.0197	8.900	Rochon- DuVigneaud (1943)	Note 20	Group 5

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Refer- ence for weight	Quality
Aquila chrysae- tos	Golden eagle	Birds	4.3451	32.024	Hughes (1977)	Hughes (1977)	Group 3
Aquila rapax	Tawny eagle	Birds	2.5315	26.510	Note 30	Altman (1962)	Group 6
Athene noctua	Little owl	Birds	2.7800	12.500	Rochon- DuVigneaud (1943)	Note 24	Group 5
Balearica pavon- ina	Black crowned crane	Birds	4.4480	18.928	Note 30	Altman (1962)	Group 6
Bubo bubo	Eurasian eagle owl	Birds	1.8268	34.970	Hughes (1977)	Hughes (1977)	Group 3
Bubo virginianus	Great horned owl	Birds	3.5800	38.000	Murphy (1985)	Note 23	Group 5
Bucorvus cafer	Southern ground hornbill	Birds	3.2500	27.458	Note 30	Altman (1962)	Group 6
Buteo buteo	Buzzard	Birds	2.5500	23.000	Rochon- DuVigneaud (1943)	Perrins (1985)	Group 3
Buteo jamaicen- sis	Red-tail hawk	Birds	2.5500	26.000	Miller, Note 16	Perrins (1985)	Group 2
Cacatua galerita	Sulfur crested cockatoo	Birds	0.3115	13.260	Murphy, Note 14	Murphy, Note 14	Group 1
Cardinalis sinuatus	Pyrrhuloxia	Birds	0.0300	5.010	Rochon- DuVigneaud (1943)	Perrins (1985)	Group 3
Cathartes aura	Turkey vulture	Birds	10.4700	19.000	Note 30	Note 28	Group 7
Catharus guttatus	Hermit thrush	Birds	0.0947	9.071	Hughes (1977)	Hughes (1977)	Group 3
Choriotis kori	Bustard	Birds	7.7700	30.022	Note 30	Altman (1962)	Group 6
Ciconia ciconia	White stork	Birds	3.3500	21.664	Note 30	Altman (1962)	Group 6
Columba livia	Pigeon	Birds	0.3150	11.620	Martin (1991)	Terres (1980)	Group 3
Corvus brac- hyrhynchos	Crow	Birds	1.0005	15.157	Hughes (1977)	Hughes (1977)	Group 3
Corvus monedula	Jackdaw	Birds	0.7900	15.000	Rochon- DuVigneaud (1943)	Perrins (1985)	Group 3
Cygnus cygnus	Trumpeter swan	Birds	5.6000	13.650	Murphy, Note 14	Murphy, Note 14	Group 1
Delichon urbica	House martin	Birds	0.0325	7.200	Rochon- DuVigneaud (1943)	Perrins (1985)	Group 3
Dromaius novae- hollandiae	Emu	Birds	13.6100	26.970	Murphy, Note 14	Murphy, Note 14	Group 1
Dromaius novae- hollandiae	Emu	Birds	23.5900	30.650	Murphy, Note 14	Murphy, Note 14	Group 1
Eudyptes chrysocome	Rockhopper penguin	Birds	23.3400	22.700	Howland (1984)	Note 26	Group 5
Falco sparverius	American kestral	Birds	0.1120	12.454	Note 30	Altman (1962)	Group 6

Appendix A (continued)

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Reference for weight	Quality
Falco tinnuncu- lus	Kestrel	Birds	0.2033	14.936	Hughes (1977)	Hughes (1977)	Group 3
Fregata aquila	Ascension frigate- bird	Birds	1.4050	19.655	Note 30	Altman (1962)	Group 6
Callus domesti- cus	Chicken	Birds	0.6741	13.250	Note 30	Altman (1962)	Group 6
Gavia stellata	Red-throated loon	Birds	1.5490	14.471	Note 30	Altman (1962)	Group 6
Grus americana	Wild whooping crane	Birds	5.0000	16.510	Murphy, Note 14	Murphy, Note 14	Group 1
Grus canadensis	Sandhill crane	Birds	1.6510	18.579	Note 30	Altman (1962)	Group 6
Haliaeetus vocifer	African fish eagle	Birds	3.5000	23.523	Note 30	Altman (1962)	Group 6
Hirundo rustica	Barn swallow	Birds	0.0255	9.314	Hughes (1977)	Hughes (1977)	Group 3
Hydrobates pelagicus	Storm petrel	Birds	0.0465	6.750	Rochon- DuVigneaud (1943)	Perrins (1985)	Group 3
Lagopus lagopus	Willow ptarmigan	Birds	0.5410	11.604	Note 30	Altman (1962)	Group 6
Larus Philadel- phia	Bonaparte's gull	Birds	0.2050	12.249	Note 30	Altman (1962)	Group 6
Larus argentatus	Herring gull	Birds	0.5350	16.542	Note 30	Altman (1962)	Group 6
Larus delawar- ensis	Ring-billed gull	Birds	0.7200	17.225	Note 30	Altman (1962)	Group 6
Larus ridibundus	Black headed gull	Birds	1.0450	11.500	Rochon- DuVigneaud (1943)	Perrins (1985)	Group 3
Leptoptilus crumeniferus	Marabou stork	Birds	7.1300	25.350	Note 30	Altman (1962)	Group 6
Melopsittacus undulatus	Budgie	Birds	0.0077	6.000	Miller, Note 16	Note 22	Group 4
Mergus serrator	Red-breasted merganser	Birds	0.7700	11.734	Note 30	Altman (1962)	Group 6
Motacilla flava	Yellow wagtail	Birds	0.0327	9.314	Hughes (1977)	Hughes (1977)	Group 3
Nymphicus hollandicus	Cockatiel	Birds	9.1550	8.500	Miller, Note 16	Note 22	Group 4
Nyroca affnis	Lesser scaup	Birds	1.0410	11.929	Note 30	Altman (1962)	Group 6
Nyroca marila	Greater scaup	Birds	0.7870	10.102	Note 30	Altman (1962)	Group 6
Passer domesti- cus	House sparrow	Birds	0.0367	6.417	Hughes (1977)	Hughes (1977)	Group 3
Pelecanus occidentalis	Brown pelican	Birds	3.2900	19.523	Note 30	Altman (1962)	Group 6
Phalacrocorax carbo	Great cormorant	Birds	3.6300	15.000	Rochon- DuVigneaud (1943)	Terres (1980)	Group 3

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Refer- ence for weight	Quality
Phasianus colchicus	Ring-necked pheasant	Birds	0.6250	14.601	Note 30	Altman (1962)	Group 6
Phoeniconaias minor	Lesser flamingo	Birds	1.5405	12.572	Note 30	Altman (1962)	Group 6
Puffinus griseus	Sooty shearwater	Birds	0.2680	12.416	Note 30	Altman (1962)	Group 6
Puffinus puffinus	Manx shearwater	Birds	0.4420	11.820	Martin (1991)	Terres (1980)	Group 3
Quiscalus quiscula	Common grackle	Birds	0.2370	8.100	Rochon- DuVigneaud (1943)	Perrins (1985)	Group 3
Ramphastos toco	Toco toucan	Birds	0.6250	18.370	Murphy, Note 14	Murphy, Note 14	Group 1
Serinus canarius	Island canary	Birds	0.0162	5.496	Note 30	Altman (1962)	Group 6
Spheniscus humboldti	Humboldt pen- guin	Birds	25.0460	20.500	Sivak (1987b)	Note 27	Group 5
Spheniscus magellanicus	Magellanic penguin	Birds	25.2900	27.300	Howland (1984)	Note 25	Group 5
Strix aluco	Tawny owl	Birds	0.4145	22.854	Hughes (1977)	Hughes (1977)	Group 3
Strix nebulosa	Great gray owl	Birds	4.0000	14.000	Rochon- DuVigneaud (1943)	Perrins (1990)	Group 3
Struthio camelus	Ostrich	Birds	99.2008	44.220	Hughes (1977)	Hughes (1977)	Group 3
Sturnus vulgaris	European starling	Birds	0.0762	7.920	Martin (1991)	Terres (1980)	Group 3
Sylvia atricapilla	Blackcap	Birds	0.0070	7.750	Rochon- DuVigneaud (1943)	Terres (1980)	Group 3
Unknown	Owl	Birds	0.0900	10.817	Hughes (1977)	Hughes (1977)	Group 3
Unknown	Parrot	Birds	0.3605	15.157	Hughes (1977)	Hughes (1977)	Group 3
Acipenser ruthenus	Sterlet	Fishes	37.1900	6.000	Rochon- DuVigneaud (1943)	Note 13	Group 5
Acipenser ruthenus	Sterlet	Fishes	66.2700	6.000	Rochon- DuVigneaud (1943)	Wheeler (1985)	Group 3
Alosa alabamae	Alabama shad	Fishes	0.6150	10.381	Note 30	Altman (1962)	Group 6
Aplodinotus grunniens	Freshwater drum	Fishes	0.9370	15.906	Note 30	Altman (1962)	Group 6
Balistes capriscus	Grey triggerfish	Fishes	0.2950	12.529	Note 30	Altman (1962)	Group 6
Callionymus lyra	Dragonet	Fishes	0.5350	3.600	Rochon- DuVigneaud (1943)	Note 21	Group 5
Carangoides bartholomaei	Yellow jack	Fishes	4.8120	22.775	Note 30	Altman (1962)	Group 6

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Reference for weight	Quality
Caranx hippos	Crevallejack	Fishes	2.3050	26.878	Note 30	Altman (1962)	Group 6
Carassius auratus	Goldfish	Fishes	0.0108	3.456	Hughes (1977)	Hughes (1977)	Group 3
Carcharias littoralis	Sand shark	Fishes	35.6050	30.421	Note 30	Altman (1962)	Group 6
Coregonus clupeaformis	Lake whitefish	Fishes	0.7726	11.377	Note 30	Altman (1962)	Group 6
Coryphaena hippurus	Common dolphin-fish	Fishes	19.0400	33.427	Note 30	Altman (1962)	Group 6
Cyprinus carpio	Common carp	Fishes	1.0510	12.070	Note 30	Altman (1962)	Group 6
Dasyatis pastinaca	Common stingray	Fishes	1.8300	12.000	Rochon- DuVigneaud (1943)	Allyn (1947)	Group 3
Dasyatis sabina	Atlantic stingray	Fishes	17.5800	26.165	Note 30	Altman (1962)	Group 6
Epinephelus itajara	Itajara	Fishes	32.8900	26.972	Note 30	Altman (1962)	Group 6
Erpetoichthys calabaricus	Reedfish	Fishes	0.5680	2.250	Rochon- DuVigneaud (1943)	Note 21	Group 5
Esox lucius	Northern pike	Fishes	0.3630	14.204	Note 30	Altman (1962)	Group 6
Euthynnus alletteratus	Little tunny	Fishes	6.2910	27.025	Note 30	Altman (1962)	Group 6
Gadus ogac	Greenland cod	Fishes	2.5715	25.022	Note 30	Altman (1962)	Group 6
Galeocerdo cuvier	Tiger shark	Fishes	200.0000	37.227	Note 30	Altman (1962)	Group 6
Gymnothorax funebris	Green moray	Fishes	3.5100	9.338	Note 30	Altman (1962)	Group 6
Haemulon plumieri	Grunt	Fishes	0.3000	13.778	Note 30	Altman (1962)	Group 6
Haplochromis burtoni	African cichlid fish		0.3190	4.037	Kroger (1994)	Note 8	Group 5
Itiophorus albicans	Atlantic sailfish	Fishes	25.2000	40.785	Note 30	Altman (1962)	Group 6
Labrus melops	Corkwing wrasse	Fishes	0.3330	2.200	Rochon- DuVigneaud (1943)	Note 21	Group 5
Labrus mixtus	Cuckoo wrasse	Fishes	0.3330	8.500	Rochon- DuVigneaud (1943)	Nelson (1984)	Group 3
Lachnolaimus maximus	Hogfish	Fishes	0.4800	14.273	Note 30	Altman (1962)	Group 6
Leuciscus rutilus	Roach	Fishes	0.2640	3.500	Rochon- DuVigneaud (1943)	Note 21	Group 5
Lutjanus analis	Mutton snapper	Fishes	2.4900	22.367	Note 30	Altman (1962)	Group 6

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Reference for weight	Quality
Melanogrammus	Haddock	Fishes	3.2750	24.815	Note 30	Altman (1962)	Group 6
Mycteroperca bonaci	Black grouper	Fishes	2.7120	19.755	Note 30	Altman (1962)	Group 6
Myoxocephalus	Longhorn sculpin	Fishes	0.7820	10.000	Miller, Note 16	Note 21	Group 4
Negaprion brevi- rostris	Lemon shark	Fishes	92.9870	15.000	Hueter (1991)	Allyn (1947)	Group 3
Neogobius fluviatilis	Monkey goby	Fishes	0.3940	4.800	Rochon- DuVigneaud (1943)	Note 21	Group 5
Ocyurus chrysu- rus	Yellowtail snapper	Fishes	0.2550	13.495	Note 30	Altman (1962)	Group 6
Oncorhynchus mykiss	Rainbow trout	Fishes	2.7500	13.654	Note 30	Altman (1962)	Group 6
Oncorhynchus mykiss	Rainbow trout	Fishes	0.9000	6.400	Rochon- DuVigneaud (1943)	Note 9	Group 4
Perca flavescens	Yellow perch	Fishes	0.1795	8.805	Note 30	Altman (1962)	Group 6
Periophtalmus barbarus	Mudhopper	Fishes	0.1714	5.330	Rochon- DuVigneaud (1943)	Note 19	Group 5
Petromyzon marinus	Grand lamprey	Fishes	1.0490	6.000	Rochon- DuVigneaud (1943)	Car- lander (1969)	Group 3
Polypterus endlicheri	Bichir	Fishes	0.5680	6.000	Rochon- DuVigneaud (1943)	Note 21	Group 5
Porichthys notatus	Plainfin midship- man	Fishes	0.0101	3.750	Dissection, Note 6	Bass, Note 7	Group 1
Porichthys notatus	Plainfin midship- man	Fishes	0.0065	2.750	Dissection, Note 6	Bass, Note 7	Group 1
Porichthys notatus	Plainfin midship- man	Fishes	0.0056	3.375	Dissection, Note 6	Bass, Note 7	Group 1
Porichthys notatus	Plainfin midship- man	Fishes	0.0090	4.000	Dissection, Note 6	Bass, Note 7	Group 1
Porichthys notatus	Plainfin midship- man	Fishes	0.0034	2.863	Dissection, Note 6	Bass, Note 7	Group 1
Porichthys notatus	Plainfin midship- man	Fishes	0.0094	3.750	Dissection, Note 6	Bass, Note 7	Group 1
Porichthys notatus	Plainfin midship- man	Fishes	0.0050	3.000	Dissection, Note 6	Bass, Note 7	Group 1
Porichthys notatus	Plainfin midship- man	Fishes	0.0063	3.000	Dissection, Note 6	Bass, Note 7	Group 1
Porichthys notatus	Plainfin midship- man	Fishes	0.0039	2.875	Dissection, Note 6	Bass, Note 7	Group 1
Romboplites aurorubens	Vermilion snapper	Fishes	0.2020	11.414	Note 30	Altman (1962)	Group 6
Salmo salar	Atlantic salmon	Fishes	5.1415	16.674	Note 30	Altman (1962)	Group 6
Salmo trutta	Sea trout	Fishes	0.2920	11.027	Note 30	Altman (1962)	Group 6

Appendix A (continued)

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Reference for weight	Quality
Salvelinus fontinalus	Brook trout	Fishes	0.6150	4.750	Rochon- DuVigneaud (1943)	Bellairs (1970)	Group 3
Salvelinus namaycush	Lake trout	Fishes	2.8700	16.928	Note 30	Altman (1962)	Group 6
Scomberomorus	Spanish mackerel	Fishes	1.4570	16.662	Note 30	Altman (1962)	Group 6
Scyliorhinus stellaris	Cat shark	Fishes	102.2500	16.000	Rochon- DuVigneaud (1943)	Note 18	Group 5
Sinilabeo dero	Kalabans	Fishes	0.9186	3.000	Rochon- DuVigneaud (1943)	Note 21	Group 5
Sphyraena barracuda	Great barracuda	Fishes	8.7730	28.383	Note 30	Altman (1962)	Group 6
Tetrapturus albidus	Atlantic white marlin	Fishes	24.9400	46.371	Note 30	Altman (1962)	Group 6
Thunnus thynnis	Northern bluefin tuna	Fishes	5.2100	36.856	Note 30	Altman (1962)	Group 6
Torpedo torpedo	Common torpedo	Fishes	0.3450	9.132	Note 30	Altman (1962)	Group 6
Trachinotus ovatus	Derbio	Fishes	8.5040	35.875	Note 30	Altman (1962)	Group 6
Aepyceros melampus	Impala	Mammals	37.8600	29.506	Note 30	Altman (1962)	Group 6
Alcelaphus cokei		Mammals	134.0000	29.208	Note 30	Altman (1962)	Group 6
Artibeus cinereus	Gervais's fruit eating bat	Mammals	0.1035	4.400	Pettigrew (1988)	Grzimek (1990)	Group 3
Balaena mysticetus	Bowhead whale	Mammals	75000	45.571	Andersen (1971)	Grzimek (1990)	Group 3
Balaenoptera musculus	Blue whale	Mammals	105000	107.000	Altman (1962)	Grzimek (1990)	Group 3
Bos taurus	Beefalo	Mammals	816.4700	37.000	Miller, Note 16	(1973)	Group 2
Bos taurus	Brown Swiss	Mammals	680.4000	30.000	Miller, Note 16	Gay (1914)	Group 2
Bos taurus	Guernsey	Mammals	544.3200	29.000	Miller, Note 16	Gay (1914)	Group 2
Bos taurus	Hereford	Mammals	907.1900	30.000	Miller, Note 16	Rouse (1973)	Group 2
Bos taurus	Holstein	Mammals	759.7800	28.000	Miller, Note 16	Gay (1914)	Group 2
Bos taurus	Jersey Cow	Mammals	521.6400	37.000	Miller, Note 16	Gay (1914)	Group 2
Bos taurus	Red Angus	Mammals	691.7400	31.000	Miller, Note 16	Rouse (1973)	Group 2
Bos taurus	Red Holstein	Mammals	873.1700	30.000	Miller, Note 16	Rouse (1973)	Group 2

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Reference for weight	Quality
Bos taurus	Simmental	Mammals	918.5300	25.000	Miller, Note 16	Rouse (1973)	Group 2
Canis latrans	Coyote	Mammals	8.5100	18.658	Note 30	Altman (1962)	Group 6
Cam's lupus	Wolf	Mammals	47.5000	22.560	Andersen (1971)	Grzimek (1990)	Group 3
Canis lupus f. familiaris	Cocker spaniel	Mammals	9.0700	21.000	Miller, Note 16	Hutchinson (1935)	Group 2
Canis lupus f. familiaris	Collie	Mammals	23.8100	17.000	Miller, Note 16	Hutchinson (1935)	Group 2
Canis lupus f. familiaris	Doberman	Mammals	31.7500	16.000	Miller, Note 16	American Kennel Club (1938)	Group 2
Canis lupus f. familiaris	Dog	Mammals	13.0723	20.146	Hughes (1977)	Hughes (1977)	Group 3
Canis lupus f. familiaris	Golden retriever	Mammals	27.9000	22.500	Miller, Note 16	American Kennel Club (1938)	Group 2
Canis lupus f. familiaris	Pekingese	Mammals	3.4000	17.000	Miller, Note 16	Hutchinson (1935)	Group 2
Canis lupus f. familiaris	Pomeranian	Mammals	9.0700	20.000	Miller, Note 16	Hutchinson (1935)	Group 2
Canis lupus f. familiaris	Siberian huskie	Mammals	30.6200	22.000	Miller, Note 16	American Kennel Club (1938)	Group 2
Canis lupus f. familiaris	Basset hound	Mammals	20.4100	25.000	Miller, Note 16	Hutchinson (1935)	Group 1
Capra hircus	Dwarf goat	Mammals	27.6600	25.843	Note 30	Altman (1962)	Group 6
Capreolus capreolus	Roe deer	Mammals	17.5000	22.000	Rochon- DuVigneaud (1943)	Grzimek (1990)	Group 3
Castor canaden- sis	American beaver	Mammals	5.0050	9.578	Note 30	Altman (1962)	Group 6
Castor fiber	European beaver	Mammals	24.3500	11.280	Andersen (1971)	Grzimek (1990)	Group 3
Crocuta crocuta	Spotted hyena	Mammals	62.3700	28.684	Note 30	Altman (1962)	Group 6
Cystophora cristata	Hooded seal	Mammals	375.0000	55.000	Sivak (1987a)	Grzimek (1990)	Group 3
Delphinapterus leucas	Beluga whale	Mammals	375.1300	25.034	Note 30	Altman (1962)	Group 6

Appendix A (continued)

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Reference for weight	Quality
Delphinus delphis	Common dolphin	Mammals	51.2277	20.564	Hughes (1977)	Hughes (1977)	Group 3
Diceros bicornis	Black rhinoceros	Mammals	764.0000	23.621	Note 30	Altman (1962)	Group 6
Didelphis virginiana	Opossum	Mammals	4.0500	10.000	Martin (1991)	Whitaker (1980)	Group 3
Dugong dugon	Dugong	Mammals	143.2072	21.935	Hughes (1977)	Hughes (1977)	Group 3
Elephas asiaticus	Asian elephant	Mammals	4263.8100	30.456	Andersen (1971)	Grzimek (1990)	Group 3
Elephas asiaticus	Asian elephant	Mammals	4263.8100	40.000	Miller, Note 16	Grzimek (1990)	Group 2
Enhydra lutris	Sea otter	Mammals	27.0000	14.000	Murphy (1990)	Grzimek (1990)	Group 3
Equus burchelli	Zebra	Mammals	338.1256	50.018	Hughes (1977)	Hughes (1977)	Group 3
Equus burchelli	Zebra	Mammals	300.0000	35.000	Miller, Note 16	Grzimek (1990)	Group 2
Equus caballus	1/2 Arabian	Mammals	430.9200	41.000	Miller, Note 16	Patten (1960)	Group 3
Equus caballus	American saddle- breed	Mammals	476.2800	40.000	Miller, Note 16	Patten (1960)	Group 2
Equus caballus	Appaloosa	Mammals	504.6300	32.000	Miller, Note 16	Patten (1960)	Group 2
Equus caballus	Arabian	Mammals	430.9200	36.000	Miller, Note 16		Group 6
Equus caballus	Connemara	Mammals	351.5400	42.000	Miller, Note 16		Group 3
Equus caballus	Horse	Mammals	694.3845	41.962	Andersen (1971)	Hughes (1977)	Group 3
Equus caballus	Horse	Mammals	694.3845	40.733	Hughes (1977)	Hughes (1977)	Group 3
Equus caballus	Morgan	Mammals	476.2800	37.000	Miller, Note 16	Patten (1960)	Group 3
Equus caballus	Palomino	Mammals	476.2800	34.000	Miller, Note 16	Patten (1960)	Group 2
Equus caballus	Pinto	Mammals	453.6000	36.000	Miller, Note 16	Patten (1960)	Group 6
Equus caballus	Quarter Horse	Mammals	487.6200	38.000	Miller, Note 16		Group 3
Equus caballus	Shetland pony	Mammals	99.2008	39.324	Hughes (1977)	Hughes (1977)	Group 6
Equus caballus	Standard bred	Mammals	907.1900	42.000	Miller, Note 16		Group 3
Equus caballus	Thoroughbred	Mammals	476.2800	45.000	Miller, Note 16	Gay (1914)	Group 3
Equus caballus	Welsh Pony	Mammals	238.7400	35.000	Miller, Note 16		Group 3
Erignathus barbatus	Bearded seal	Mammals	281.0000	33.263	Note 30	Altman (1962)	Group 6
Felis capensis	Cape cat	Mammals	7.6870	20.211	Note 30	Altman (1962)	Group 6

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Reference for weight	Quality
Felis catus	Cat	Mammals	3.0544	21.935	Hughes (1977)	Hughes (1977)	Group 3
Felis lynx	Lynx	Mammals	8.7952	30.456	Andersen (1971)	Grzimek (1990)	Group 3
Felis lynx	Lynx	Mammals	8.7932	23.192	Hughes (1977)	Hughes (1977)	Group 3
Felis ocreata	Kaffir cat	Mammals	2.7000	15.535	Note 30	Altman (1962)	Group 6
Felis oreqonensis	Mountain lion	Mammals	28.7900	17.522	Note 30	Altman (1962)	Group 6
Gazella thomsoni	Thomson's gazelle	Mammals	24.3700	24.953	Note 30	Altman (1962)	Group 6
Genetta tigrina	Large spotted genet	Mammals	1.4135	12.796	Note 30	Altman (1962)	Group 6
Giraffa camelo- pardalis	Giraffe	Mammals	1468.5137	48.147	Hughes (1977)	Hughes (1977)	Group 3
Herpestes auropunctatus	Indian mongoose	Mammals	1.5000	9.000	Nellis (1989)	Grzimek (1990)	Group 3
Hippopotamus amphibius	Hippopotamus	Mammals	1351.0000	29.213	Note 30	Altman (1962)	Group 6
Hippotragus niger	Sable antelope	Mammals	225.0000	30.000	Miller, Note 16	Grzimek (1990)	Group 2
Ichneumia albicauda	White-tailed mongoose	Mammals	4.4000	13.278	Note 30	Altman (1962)	Group 6
Kogia breviceps	Pygmy Sperm Whale	Mammals	500.0000	18.000	Miller, Note 16	Grzimek (1990)	Group 2
Lama glama	Llama	Mammals	142.5000	35.000	Miller, Note 16	Grzimek (1990)	Group 2
Lama guanicoe	Guanaco	Mammals	100.0000	36.000	Miller, Note 16	Grzimek (1990)	Group 2
Lama Pacos	Alpaca	Mammals	60.0000	33.000	Miller, Note 16	Grzimek (1990)	Group 2
Lepus arcticus	Arctic hare	Mammals	2.2705	13.980	Note 30	Altman (1962)	Group 6
Loxodonta africana	African elephant	Mammals	4754.6439	51.206	Hughes (1977)	Hughes (1977)	Group 3
Lutra lutra	Otter	Mammals	8.1706	13.283	Hughes (1977)	Hughes (1977)	Group 3
Macroderma gigas	Ghost bat	Mammals	0.1100	7.000	Pettigrew (1988)	Grzimek (1990)	Group 2
Macropus giganteus	Eastern gray kan- garoo	Mammals	49.0000	24.816	Andersen (1971)	Grzimek (1990)	Group 3
Marmota monax	Woodchuck	Mammals	4.5750	11.000	Miller, Note 16	Grzimek (1990)	Group 2
Megaderma lyra	Asian false vam- pire bat	Mammals	0.1100	4.200	Pettigrew (1988)	Grzimek (1990)	Group 3
Megaptera nova- eangliae	Humpback whale	Mammals	43035	61.240	Hughes (1977)	Hughes (1977)	Group 3
Mesoplodon bidens	Sowerby's beaked whale	Mammals	1666.6700	24.000	Miller, Note 16	Grzimek (1990)	Group 2
Mustela arctica	Arctic weasel	Mammals	0.1452	4.258	Note 30	Altman (1962)	Group 6

Appendix A (continued)

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Reference for weight	Quality
Mustela putorius f. furo	Ferret	Mammals	0.6600	7.500	Murphy, Note 14	Murphy, Note 14	Group 1
Nasua narica	White-nosed coatimundi	Mammals	6.2500	11.091	Note 30	Altman (1962)	Group 6
Nyctophilus gouldi	Gould's long eared bat	Mammals	0.0270	1.900	Pettigrew (1988)	Grzimek (1990)	Group 3
Odobenus rosmarus	Walrus	Mammals	667.0000	24.963	Note 30	Altman (1962)	Group (
Odocoileus virginianus	Whitetail Deer	Mammals	77.5000	22.000	Miller, Note 16	Grzimek (1990)	Group 2
Ommatophoca rossi	Ross seal	Mammals	183.8193	29.326	Hughes (1977)	Hughes (1977)	Group 3
Ornithorhynchus anatinus	Duckbilled platy- pus	Mammals	1.4595	4.640	Duke-Elder (1963)	Grzimek (1990)	Group 3
Otocyon megalotis	Bat-eared fox	Mammals	3.3350	13.961	Note 30	Altman (1962)	Group (
Ovis aries	Sheep	Mammals	52.1000	26.113	Note 30	Altman (1962)	Group 6
Panthera leo	Lion	Mammals	185.0000	41.000	Miller, Note 16	Grzimek (1990)	Group 2
Panthera onca	Jaguar	Mammals	34.4700	21.614	Note 30	Altman (1962)	Group
Panthera tigris	Tiger	Mammals	197.5000	30.000	Miller, Note 16	Grzimek (1990)	Group
Panthera tigris tigris	White tiger	Mammals	197.5000	32.000	Miller, Note 16	Grzimek (1990)	Group
Phacochoerus aethiopicus	Warthog	Mammals	83.7853	30.200	Hughes (1977)	Hughes (1977)	Group ?
Phoca groenlan- dica	Harp seal	Mammals	150.0000	29.328	Andersen (1971)	Grzimek (1990)	Group 3
Phoca hispida	Ringed seal	Mammals	39.7200	34.727	Note 30	Altman (1962)	Group
Phoca richardii	Spotted seal	Mammals	107.3000	32.847	Note 30	Altman (1962)	Group
Phocoena phocoena	Harbor porpoise	Mammals	142.4300	32.198	Note 30	Altman (1962)	Group
Pĥocoena phocoena	Harbor porpoise	Mammals	65.0000	19.000	Rochon- DuVigneaud (1943)	Grzimek (1990)	Group 3
Phocoenoides dalli	Dall's porpoise	Mammals	135.0000	22.000	Miller, Note 16	Grzimek (1990)	Group 2
Physeter catodon	Sperm whale	Mammals	39009	55.286	Note 30	Altman (1962)	Group
Pipistrellus pipistrellus	Common pipist- relle	Mammals	0.0055	1.400	Rochon- DuVigneaud (1943)	Grzimek (1990)	Group 3
Plecotus auritus	Brown long-eared bat	Mammals	0.0085	2.707	Andersen (1971)	Grzimek (1990)	Group
Plecotus auritus	Brown long-eared bat	Mammals	0.0085	2.100	Rochon- DuVigneaud (1943)	Grzimek (1990)	Group

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Reference for weight	Quality
Potamochoerus porcus	Bush pig	Mammals	102.1577	23.192	Hughes (1977)	Hughes (1977)	Group 3
Potos flavus	Kinkajou	Mammals	2.6200	10.363	Note 30	Altman (1962)	Group 6
Pteropus giganteus	Flying fox	Mammals	1.5000	9.650	Neuweiler (1962)	Grzimek (1990)	Group 3
Rangifer tarandus	Reindeer	Mammals	189.0000	30.000	Miller, Note 16	Grzimek (1990)	Group 2
Raphicerus campestris	Steenbok	Mammals	8.6200	20.560	Note 30	Altman (1962)	Group 6
Redunca redunca	Bohor Reedbuck	Mammals	31.7000	26.918	Note 30	Altman (1962)	Group 6
Rhinoceros unicornis	Greater Indian rhinoceros	Mammals	3538.0600	23.000	Duke-Elder (1963)	Grzimek (1990)	Group 3
Rhinolophidae rouxi	Pennisular horse- shoe bat	Mammals	0.0220	1.800	Pettigrew (1988)	Grzimek (1990)	Group 6
Rupicapra rupicapra	Chamois	Mammals	38.0000	28.877	Andersen (1971)	Grzimek (1990)	Group 3
Sus scrofa	Wild boar	Mammals	182.0000	24.800	Altman (1962)	Grzimek (1990)	Group 3
Syncerus caffer	African buffalo	Mammals	759.0000	31.782	Note 30	Altman (1962)	Group 6
Tachyglossus aculeatus	Short-nosed echidna	Mammals	4.5000	8.000	Hughes (1977)	Grzimek (1990)	Group 3
Taphozous georgianus	Common sheath- tail bat	Mammals	0.0165	3.700	Pettigrew (1988)	Grzimek (1990)	Group 3
Tapirus bairdii	Baird's tapir	Mammals	58.0600	20.564	Note 30	Altman (1962)	Group 6
Tragelaphus scriptus	Bushbuck	Mammals	40.5300	28.710	Note 30	Altman (1962)	Group 6
Trichechus inunguis	Manatee	Mammals	400.0000	13.500	Rochon- DuVigneaud (1943)	Grzimek (1990)	Group 3
Trichechus manatus	West Indian manatee	Mammals	490.9600	32.525		Altman (1962)	Group 6
Unknown	Bat	Mammals	0.0238	1.967	Hughes (1977)	Hughes (1977)	Group 3
Urocyon cine- reoargenteus	Grey fox	Mammals	3.7590	13.300	Note 30	Altman (1962)	Group 6
Vulpes lagopus	Arctic fox	Mammals	3.3850	15.027	Note 30	Altman (1962)	Group 6
Vulpes vulpes	Red fox	Mammals	6.2500	21.000	Miller, Note 16	Grzimek (1990)	Group 2
Wallabia bicolor	Swamp wallaby	Mammals	13.8500	11.400	Duke-Elder (1963)	Grzimek (1990)	Group 3
Callitrix jacchus	Common marmo- set	Primates	0.3300	12.544	Troilo (1993)	Grzimek (1990)	Group 3
Cercopithecus aethiops	Vervet monkey	Primates	4.1850	17.278	Note 30	Altman (1962)	Group 6
Cercopithecus mitis	Blue monkey	Primates	2.9000	17.979	Note 30	Altman (1962)	Group 6

Appendix A (continued)

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Refer- ence for weight	Quality
Galago senegal- ensis	Northern Lesser Bushbaby	Primates	0.2000	12.938	Note 30	Altman (1962)	Group 6
Gorilla gorilla	Gorilla	Primates	167.5000	22.500	Altman (1962)	Grzimek (1990)	Group 3
Homo sapiens	Human	Primates	72.3416	24.521	Hughes (1977)	Hughes (1977)	Group 3
Macaca mulatta	Rhesus macaque	Primates	9.2500	17.599	Hughes (1979)	Grzimek (1990)	Group 3
Macaca sylvanus	Barbary macaque	Primates	6.0000	19.176	Andersen (1971)	Grzimek (1990)	Group 3
Pan troglodytes	Chimpanzee	Primates	51.5000	19.000	Rochon- DuVigneaud (1943)	Grzimek (1990)	Group 3
Papio cynoceph- alus	Yellow baboon	Primates	19.5100	19.750	Note 30	Altman (1962)	Group 6
Tupaia belangeri	Tree shrew	Primates	0.1150	8.070	Norton (1992)	Grzimek (1990)	Group 3
Alligator missis- sippiensis	Alligator	Reptiles	24.5000	15.000	Rochon- DuVigneaud (1943)	Bellairs (1970)	Group 6
Amblyrhynchus cristatus	Marine iguana	Reptiles	4.1900	8.532	Note 30	Altman (1962)	Group (
Ancistrodon piscivorus	Water moccasin	Reptiles	0.7280	7.098	Note 30	Altman (1962)	Group (
Boa c. imperator	Boa constrictor	Reptiles	1.8290	6.858	Note 30	Altman (1962)	Group 3
Chelonia mydas	Green sea turtle	Reptiles	17.4600	12.510	Northmore (1991)	Note 2	Group 4
Chelonia mydas	Green sea turtle	Reptiles	91.1700	29.425	Note 30	Altman (1962)	Group 6
Chelydra serpentina	Snapping turtle	Reptiles	5.1250	7.501	Note 30	Altman (1962)	Group 6
Clemmys guttata	Spotted turtle	Reptiles	2.1630	9.248	Note 30	Altman (1962)	Group 6
Coluber constrictor	Eastern racer	Reptiles	0.3948	4.830	Note 30	Altman (1962)	Group 6
Crocodylus spp.	Crocodiles	Reptiles	32.2100	21.000	Rochon- DuVigneaud (1943)	Bellairs (1970), Note 4	Group 3
Iguana iguana	Green iguana	Reptiles	0.7500	12.380	Murphy, Note 14	Murphy, Note 14	Group 1
Macrochelys lacertina	Alligator snapping turtle	Reptiles	1.8480	8.917	Note 30	Altman (1962)	Group 3
Natrix natrix	Grass snake	Reptiles	0.0230	4.000	Rochon- DuVigneaud (1943)	Note 11	Group 3
Phrynosoma cornutum	Texas horned lizard	Reptiles	0.0250	5.811	Note 30	Altman (1962)	Group 3
Pseudemys scripta	Red-eared slider	Reptiles	10.4500	7.720	Northmore (1991)	Note 2	Group 2

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Refer- ence for weight	Quality
Python molurus	Burmese python	Reptiles	116.4800	7.000	Rochon- DuVigneaud (1943)	Note 12	Group 6
Tarentola mauritanica	Wall gecko	Reptiles	0.0300	4.500	Rochon- DuVigneaud (1943)	Bellairs (1970), Note 5	Group 3
Thamnophis melanogaster	Mexican garter snake	Reptiles	0.0200	3.500	Schaeffel (Note 15)	Calculations (Note 17)	Group 3
Thamnophis sirtalis	Common garter snake	Reptiles	0.0184	3.130	Schaeffel, Note 15	Note 17	Group 3
Blarina brevicauda	Short-tailed shrew	Rodents	0.0106	1.368	Hughes (1977)	Hughes (1977)	Group 3
Citellus citellus	Active European ground	Rodents	0.1860	8.450	Murphy, Note 14	Murphy, Note 14	Group 1
Citellus citellus	European ground squirrel	Rodents	0.3159	8.939	Hughes (1977)	Hughes (1977)	Group 3
Citellus citellus	Hibernating Eur. ground	Rodents	0.0960	8.100	Murphy, Note 14	Murphy, Note 14	Group 1
Citellus citellus	Hibernating Eur. ground	Rodents	0.1410	8.150	Murphy, Note 14	Murphy, Note 14	Group 1
Citellus citellus	Hibernating Eur. ground	Rodents	0.1560	8.650	Murphy, Note 14	Murphy, Note 14	Group 1
Citellus parryi	Arctic ground squirrel	Rodents	0.9180	10.083	Note 30	Altman (1962)	Group 6
Cricetus cricetus	Common hamster	Rodents	0.1075	4.992	Note 30	Altman (1962)	Group 6
Dicrostonyx rubricatus	Bering collared lemming	Rodents	0.0521	4.400	Note 30	Altman (1962)	Group 6
Erethizon dorsatum	North American porcupine	Rodents	2.8000	11.791	Note 30	Altman (1962)	Group 6
Graphiurus murinus	African dormouse	Rodents	0.0177	3.127	Note 30	Altman (1962)	Group 6
Hystrix cristata	N. African crested porcupine	Rodents	17.5000	11.280	Andersen (1971)	Grzimek (1990)	Group 3
Lemmus trimucronatus	Brown lemming	Rodents	0.0386	2.403	Note 30	Altman (1962)	Group 6
Marmota caligata	Hoary marmot	Rodents	5.4558	12.899	Hughes (1977)	Hughes (1977)	Group 3
Marmota marmota	Alpine marmot	Rodents	4.7100	14.664	Andersen (1971)	Grzimek (1990)	Group 3
Mastomys coucha	Multimammate mouse	Rodents	0.2180	3.532	Note 30	Altman (1962)	Group 6
Meles meles	Eurasian badger	Rodents	10.1842	10.052	Hughes (1977)	Hughes (1977)	Group 3
Microtus drummondi	Meadow mouse	Rodents	0.0233	2.408	Note 30	Altman (1962)	Group 6
Microtus pennsylvanicus	Meadow vole	Rodents	0.0458	2.765	Hughes (1977)	Hughes (1977)	Group 3
Microtus pennsylvanicus	Meadow vole	Rodents	0.0266	2.487	Note 30	Altman (1962)	Group 6

Scientific name	Common name	Group	Wt in kg	Axial (mm)	Reference for axial length	Refer- ence for weight	Quality
Mus musculus	House mouse	Rodents	0.0331	5.281	Note 30	Altman (1962)	Group 6
Ondatra zibethicus	Muskrat	Rodents	0.9000	10.326	Note 30	Altman (1962)	Group 6
Oryctolagus cuniculus	European rabbit	Rodents	2.7158	18.074	Hughes (1977)	Hughes (1977)	Group 3
Procyon lotor	Raccoon	Rodents	11.9000	12.634	Andersen (1971)	Grzimek (1990)	Group 3
Procyon lotor	Raccoon	Rodents	11.9000	7.500	Miller, Note 16	Grzimek (1990)	Group 2
Rattus norvegicus	Norway rat	Rodents	0.2780	5.579	Note 30	Altman (1962)	Group 6
Sciurus carolinensis	Easetern grey squirrel	Rodents	0.0656	8.809	Hughes (1977)	Hughes (1977)	Group 3
Sorex palustris	Water shrew	Rodents	0.0204	1.489	Hughes (1977)	Hughes (1977)	Group 3
Tamias striatus	Eastern chipmunk	Rodents	0.0750	6.883	Note 30	Altman (1962)	Group 6
Unknown	Rat	Rodents	0.3579	6.417	Hughes (1977)	Hughes (1977)	Group 3
Zapus hudsonicus	Meadow jumping mouse	Rodents	0.0173	2.498	Note 30	Altman (1962)	Group 6

Notes

- 1. We used the weight and interocular distance of a spade-foot toad to determine the weight of the American toad, using the ratio $W_2 = (W_1^3 L_2/L_1)^{1/3}$ (Eq. (3)).
- 2. We found the length and weight of a radiated tortoise and used Eq. (3) to calculate the weights of the red-eared slider and green sea turtle.
- 3. We calculated the weight of the yellow-bellied toad using the weight and length of the tree frog given in Bellairs (1970), the length of the yellow-bellied toad given in Halliday and Adler (1986), and Eq. (3).
- 4. We calculated the weight of a crocodile from the weight and length of an alligator given in Bellairs (1970) and Eq. (3).
- 5. We calculated the weight of a gecko using the average length of the gecko given in Halliday and Adler (1986), the weight and length of the smallest member of Sphaerodactyla given in Bellairs (1970), and Eq. (3).
- 6. Dissection of fish preserved in 10% formalin to remove eyes. Axial length was measured with calipers.
- 7. We obtained the fixed weight of the fish and added 5% to estimate live weight. Specimens courtesy of Dr. Andrew Bass, Section of Neurobiology and Behavior, Cornell University.

- 8. We calculated the weight of an African cichlid using the length given by Wheeler (1985), the average length and weight of *Salmo fontinalis*, and Eq. (3).
- 9. We calculated the weight of *Salmo irideus* using the average length and weight for that species given by Wheeler (1985).
- The midwife toad is related to the yellow-bellied toad, and they have similar lengths and weights. Refer to Note 3.
- 11. We obtained the weight and length of a copperhead snake from Bellairs (1970), the average length of a grass snake given by Halliday and Adler (1986), and Eq. (3).
- 12. We obtained the length and weight of a large python from Bellairs (1970) and the average length of a python from Halliday and Adler (1986), and we used Eq. (3) to calculate the weight of an average python.
- 13. The average length of the sturlet was given in Carlander (1969), and the average weight was calculated using Eq. (3) and the average length and weight of an Atlantic sturgeon.
- 14. Data courtesy of Dr. Christopher Murphy.
- 15. Data courtesy of Dr. Frank Schaeffel.
- 16. Measured from prepared slides of cross sections of eyes provided by Mary Lou Miller, Dept. of Comparative Ophthalmology, Cornell University School of Veterinary Medicine.

- 17. Calculated from Eq. (3) using python weight and length.
- 18. Cat shark weight was calculated from its length as well as the weight and length of the porbeagle shark given by Allyn (1947) and Eq. (3).
- 19. Mudhopper weight was calculated using its length and the rockskipper length and weight from Allyn (1947) and Eq. (3).
- 20. Common swift length and both the length and the weight of Vaux's swift were obtained from Terres (1980) and Eq. (3).
- 21. Weight was calculated using Eq. (3), the length given by Nelson (1984), and the length and weight of the brook trout from the same source.
- 22. Budgie and cockatiel weights were calculated using the length and weight of the blue-grey gnatcatcher given by Terres (1980) and Eq. (3). Lengths of the budgie and cockatiel were given by Christie (1985).
- 23. The great horned owl weight was calculated by applying Eq. (3) to the length and weight of the great grey owl given by Perrins and Middleton (1985) and the length of the great horned owl from Perrins (1990).
- 24. We calculated the weight of the little owl using great grey owl data (see Note 23) and little owl length from Perrins (1990).
- 25. Magellanic penguin weight was calculated using emperor penguin weight and length given in Perrins and Middleton (1985) and Eq. (3). The length of the magellanic penguin was given in Perrins (1990).
- 26. We calculated the weight of the rockhopper penguin using emperor penguin data (see Note 25) and the rockhopper penguin length given in Perrins (1990).
- 27. We calculated the weight of the Humboldt penguin using emperor penguin data (see Note 25) and the Humboldt penguin length given in Perrins (1990).
- 28. We calculated the turkey vulture weight by applying Eq. (3) to the weight and length of the Andean condor as well as the turkey vulture length given in Perrins (1990).
- 29. The sparrow hawk weight was calculated using the weight and length of the northern goshawk given by Perrins and Middleton (1985), the length of a sparrow hawk given by Perrins (1990), and Eq. (3).
- 30. Altman and Dittmer (1962) listed the weight of the eye in grams as well as body weight in kilograms. By regressing log axial length vs. log eye weight for the animals listed by Altman and Dittmer (1962) whose axial lengths we knew, we derived a formula to calculate axial lengths for animals for which we had only eye weights.

Data quality legend

The data were ranked according to the accuracy, with direct measurements of weight and axial lengths (Group

- 1) being the most accurate and derivations of both (Group 7) being the least accurate:
- Group 1: Axial length and weight measured directly.
- Group 2: Axial length measured directly; weight read from text.
- Group 3: Both axial length and weight read from text.
- Group 4: Axial length measured directly; weight derived through calculations using animal length.
- Group 5: Axial length read from text; weight derived through calculations using animal length.
- Group 6: Axial length derived from calculations; weight read from text.
- Group 7: Both axial length and weight derived through calculations.

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