

## Skull dimensions in relation to body size in nonhuman mammals: The causal bases for acoustic allometry

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### Summary

Although the type of information conveyed by animal vocalizations has been a focus of theoretical interest for many years, little attention has been paid to the ways in which the evolution of signals may be constrained by basic acoustics combined with functional morphology. It has been shown recently that correlations between body size and vocal tract length, combined with the causal relationship of vocal tract length to vocal tract resonances or “formants”, lead to accurate acoustic correlates of body size in some mammals. In this paper, an analysis of the relationship between body size (both weight and length) and vocal tract length (measured from museum skulls) in a variety of mammalian species shows that these relationships are typical of a much wider variety of species. Strong allometric relationships between these variables are documented, both intra- and inter-specifically. An analysis of regression coefficients indicates that inter- and intra-specific relationships can be significantly different, with interspecific correlations corresponding closely to the 3.0 slope predicted by geometric isometry, but intraspecific relationships deviating significantly from it. The data suggest that the acoustic correlates of vocal tract length, formant frequencies, could provide a cue to body size in a wide variety of mammals.

### Introduction

A fundamental question in the evolution of communication is the degree to which signals convey information to observers, and if so, what sorts of information are conveyed. Despite considerable theoretical debate over this issue (Morton 1977, 1982; Dawkins & Krebs 1978; Hinde 1981; Krebs & Dawkins 1984; Zahavi 1993; see Hauser 1996 for a review), little attention has been paid to the ways in

which functional morphology and physical laws might constrain the evolution of signals (though see Ryan 1986; Ryan and Drewes 1990). In this paper, I investigate “acoustic allometry”: the relationship between an organism’s body size and acoustic characteristics of its vocalizations. I conclude that, due to ubiquitous, strong correlations between vocal tract dimensions and body size (either mass or length), vocal tract resonance frequencies (“formants”) could provide accurate information about a vocalizer’s size in many mammals. Such acoustic cues to body size result from anatomical correlations combined with basic acoustic principles, and should be persistent and widespread in lieu of active selection against them. Thus, information about body size will be conveyed “by default” in many mammalian vocalizations, and there is no need to invoke selection for “honest” information transfer to account for this fact. Given the importance of body size in social behavior, we might expect strong selection on receivers to perceive these cues.

### Acoustic Allometry

Body size plays a pivotal role in many aspects of animal anatomy, physiology, ecology and social behavior. For example, an animal’s body size relative to competitors often plays a crucial role in territorial or mating success (e.g., Davies & Halliday 1978; Ryan 1980; Kawata 1988; Modig 1996), and scaling relationships between body mass and animal shape have been posited to play a major role in morphological evolution (Gould 1966, 1975; Thompson 1948) and physiological functioning (Schmidt-Nielsen 1984). The multiple ramifications and influences of body size make it an extremely important

factor in understanding both differences between species and the relative success of individuals within a species (see Gould 1966; Calder 1984; Peters 1983 for reviews).

The sounds that vertebrates produce are strongly influenced by the size of the individual components of their vocal production systems (lungs, larynx and vocal tract). For example, the length and mass of the vocal folds ("vocal cords") are crucial determinants of voice pitch, while the length of the vocal tract determines the overall spacing between vocal tract resonance frequencies or "formants" (Lieberman & Blumstein 1988; Titze 1994; Fitch & Hauser 1995; Fitch 1997). If the size of these components of the vocal production apparatus scales with overall body mass, as might be reasonably surmised, the corresponding acoustic parameters could serve as reliable indicators of a vocalizer's size. Thus, relationships between body size and acoustic parameters might play a significant role in the evolution of acoustic communication. Acoustic allometry is the study of such relationships. Note that while body size (usually body mass) is a nuisance variable to be "regressed away" in many morphological studies, in acoustic allometry it is the variable of interest: we wish to determine how well body size (mass or length) can be predicted based on some acoustic variable.

One proposed example of an acoustic cue to body size is an inverse relationship between body mass and voice fundamental frequency or "pitch". Although the pitch/mass relationship is often treated as an inevitable fact (e.g., Morton 1977; Alcock 1989 p. 239), a careful consideration of its causal basis suggests otherwise. The lowest fundamental frequency an animal can produce when phonating is related to the length of its vocal folds (Titze 1994). If (and only if) there is a significant positive correlation between body size and vocal fold length, low-pitched voices would provide a reliable indication of large size. Such a correlation exists in some frogs and toads (Davies & Halliday 1978; Ryan 1988) though not in other anurans (Asquith & Altig 1990; Sullivan 1984). In humans and some other mammal species (McComb 1991; Lass & Brown 1978; Künzel 1989; van Dommellen 1993), voice pitch does not reliably correlate with body size, because there is no correlation between body mass and vocal fold length (Sawashima et al. 1983). This is likely due to the fact that the larynx, floating at the top of the trachea and tethered loosely to the skull base, is not tightly constrained by the size of neighboring structures or overall body size, and thus can grow completely out of proportion to other body parts. This happens under the influence of testosterone at puberty in human males (Beckford et al. 1985; Tuohimaa et al. 1981), and is carried to an extreme in howler monkeys (*Alouatta* spp.) where the

male larynx can rival the skull in size (Schön-Ybarra 1988), or in the hammerhead bat *Hypsignathus monstrosus*, in which the male's larynx fills most of its thoracic cavity (Kingdon 1974; Schneider et al. 1967). The relative lack of constraint on larynx size in mammals suggests that selection for deep voices (e.g., due to mate choice based on voice pitch; Ryan 1980) could easily obliterate any primitive relationship between body size and voice pitch (Fitch 1994, 1997; Fitch & Hauser 1995, *contra* Morton 1977). Thus, the voice pitch/body size relationship is unlikely to be as ubiquitous a feature of animal communication systems as is often presumed.

Another possible example of acoustic allometry is the correlation between body size and vocal tract resonance frequencies or formants (Fitch & Hauser 1995; Fitch 1997). In terrestrial vertebrates, sound generated by a source within the animal (typically the larynx) must pass through the oral and/or nasal passages before exiting to the environment. These passages (the supralaryngeal vocal tract, or simply "vocal tract"), contain air which, like any column of air, has certain natural modes or resonances which enhance sound transmission at certain frequencies. The vocal tract thus acts as a filter which amplifies certain frequencies and attenuates others. The resonances of the vocal tract are called "formants" (from the Latin *formare* "to shape"), and play a crucial role in human speech production and perception (Chiba & Kajiyama 1941; Fant 1960; Lieberman & Blumstein 1988; Titze 1994). Formants have also been demonstrated to be produced and/or perceived by a wide variety of birds and mammals (Dooling & Brown 1990; Heinz & Brady 1988; Heinz et al. 1981; Owren 1990; Owren et al. 1997; Sommers et al. 1992; Fitch 1997). It is important to note that formants are completely independent of the fundamental frequency or harmonics (the correlates of perceived pitch); although there is no word for the perceptual correlate of formants, low frequency formants lead to a deeper, more baritone, timbre.

The most important determinant of formant frequencies is the length of the vocal tract: the distance between the larynx and the lips or nostrils (Fant 1960; Peterson & Barney 1952; Lieberman & Blumstein 1988). In mammals, the larynx is typically located at the back of the oral cavity, either within or directly below the opening into the nasopharynx. Thus, vocal tract length in most mammals is essentially determined by the length of the snout (Negus 1949). If snout length is in turn related to overall skull length and to body size we would accordingly expect formants to provide a reliable cue to a vocalizer's body size. Fitch (1997) investigated this prediction in rhesus macaques (*Macaca mulatta*). Using computer graphic techniques to measure vocal tract length from lateral radiographs, he found a significant positive correlation between body size

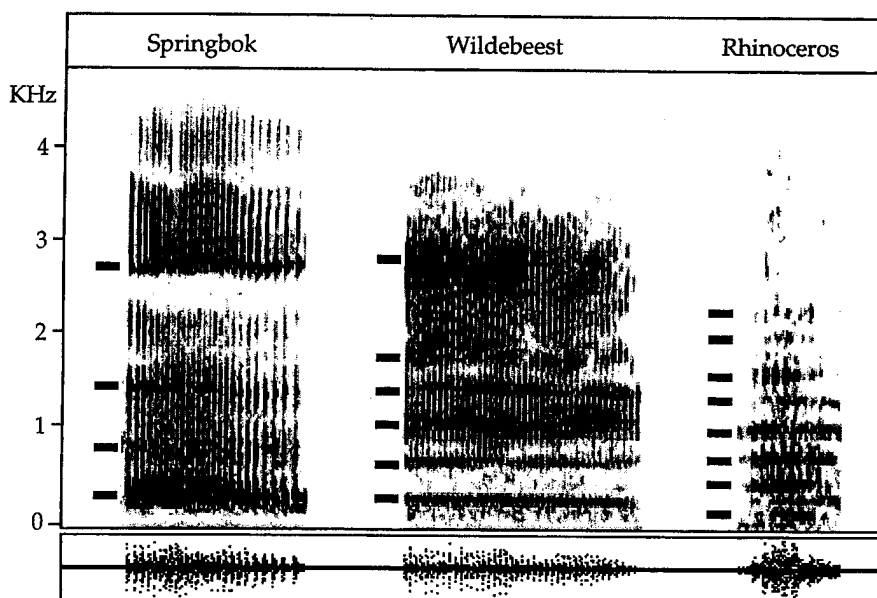
(either length or mass), skull length and vocal tract length. Then, he investigated the acoustic consequences of these correlations, using linear prediction (a digital signal processing algorithm for spectral analysis) to measure formant frequencies in the same macaques' threat vocalizations. The average frequency difference between successive formants, termed "formant dispersion", was inversely correlated with vocal tract length and hence with body size. The same techniques have since been applied to dogs *Canis familiaris* (Riede & Fitch 1999) demonstrating similarly strong negative correlations between body size and formant dispersion in dog growls. Finally, Fitch & Giedd (1999) have used magnetic resonance imaging (MRI) to document a strong positive relationship between vocal tract length and body weight or length in humans. Thus, in all of the mammal species that have been examined thus far, formant frequencies can provide a relatively accurate indication of a vocalizing individual's body size.

The morphological considerations above suggest that the relationship between vocal tract length and body size first documented for macaques by Fitch (1997) might be widespread among mammals. The primary purpose of the current paper is to determine whether the vocal tract/body size relationship holds true for mammals other than the three species mentioned above. In other words, can a typical mammal estimate a conspecific's body size based on acoustic cues to the vocalizer's vocal tract length?

A graphic illustration of formants is given in Figure 1, which is a spectrographic view of low-pitched vocalizations from three mammal species of different body masses. The vertical striations each represent an individual glottal pulse (closing of the vocal

folds). The sequence of pulses, which together make up the source signal from the larynx, excite the vocal tract resonances or formants. The formants are visible as horizontal stripes (paralleled with dark bars, added for clarity). As can be seen in the figure, the spacing between the formants decreases with increasing body mass across different species. This raises the possibility of formant dispersion as a cue to body size in *inter*-specific vocal interactions as well (despite large differences in vocal tract length and hence formant dispersion). A perceptual mechanism which utilized formants to gauge the body size of conspecifics might also prove useful in estimating the body size of other species as well (e.g. in interactions with predators or with prey). How well would cues to vocal tract length predict body size between different species?

Many authors have noted that a statistically significant regression analysis does not always indicate a linear scaling relationship. For example, sexual dimorphism in males and females could result in a "dimorphism artifact", where a statistically significant regression in fact results from categorical differences between two groups, rather than a *bona fide* scaling with body size. Such a dimorphism artifact (or two-point regression) is present in voice pitch in humans. Due to enlargement of the larynx at puberty, men have longer vocal cords, and thus lower voices, than women. Because men are also on average some 20% heavier than women, a regression analysis of voice pitch vs. body size is significant if it includes both sexes (perhaps contributing to the widespread intuition that low pitch signals large size). However, if the analysis is restricted to within a sex, there is no significant correlation: attempts to rank men's (or women's) body sizes by voice are at chance levels (Cohen et al. 1980;



**Fig. 1.** Spectrogram (time vs. frequency representation) of calls from three mammals of different sizes, illustrating the decrease in formant frequency spacing with increasing size. Springbok *Antidorcas marsupialis* (45 kg); Wildebeest *Connochaetes taurinus* (240 kg); White rhinoceros *Ceratotherium simum* (2800 kg). Sounds were taken from the commercially available CD "Animal Calls of Africa", Gillard, Parklands, South Africa. The sampling rate is 11.025 kHz, spectrograms made with Hamming window and 512 pt FFT. The black bars provide a time scale (representing 250 ms), and indicate the location of the formant frequencies for each call.

Künzel 1989; van Dommellen 1993) because there is no correlation between vocal fold length and body size within a sex (Sawashima et al. 1983). A similar artifact could result from categorical developmental differences between juveniles and adults. To guard against such artifacts, I perform separate analyses of adult males and females, and of juveniles and adults, whenever intraspecific sample sizes were adequate.

An ancillary goal of the present work is to begin assessing the underlying causal basis of the morphological relationships described in acoustic allometry. Traditionally, allometric methods have largely been used to derive empirical relationships, rather than to test hypotheses concerning their causation (Gould 1966; Wolpoff 1985). An exception is the recent debate concerning the causal basis for thoroughly-documented allometric relationships between body mass, basal metabolism and home range size (Economos 1982; Koslowski & Wiener 1997; West et al. 1997; Cates & Gittleman 1997; Witting 1997). At issue is the degree to which selection within a species drives the patterns observed between species, rendering interspecific allometries epiphenomenal (Koslowski & Wiener 1997), or whether both derive from the same underlying physiological relationships or biomechanical constraints (West et al. 1997; Cates & Gittleman 1997). These papers have highlighted the need for comparisons of inter- and intra-specific allometry. Indeed, "empirical intraspecific allometries are hardly available" (Koslowski & Wiener 1997, p. 353). The data presented below, comparing inter- and intra-specific allometric curves in mammals, provide such empirical data.

In summary, the primary goal of the current study is to analyze the relationship between body mass, skull size and vocal tract length in a variety of mammal species, both within and between species, testing the prediction that both skull and vocal tract length correlate with body size. The null hypothesis is that there is no relationship between these variables, as is the case for the larynx/body size relationship described earlier. Any statistically significant correlation suffices to reject this null hypothesis, indicating that organisms could potentially garner information about body size from the acoustic correlates of vocal tract length. Second, a number of comparisons between different subgroups in the intraspecific data will be performed to guard against possible artifactual or spurious "correlations" that result simply from categorical differences between males and females, or adults and young. Finally, given significant non-artifactual correlations, I will compare the form of the skull size/body size allometric relationship between and within species, to determine whether both sets of relationships share the same causal basis. Here, the null hypotheses

are 1) equivalence of intra- and inter-specific slopes, and 2) the "geometric null" hypothesis of a slope of 3.0 that is predicted with isometric preservation of shape with size (see Discussion).

## Materials and methods

### Specimens

The collections of the Museum of Comparative Zoology (MCZ) at Harvard University and the U.S. National Museum (USNM) at the Smithsonian Institution provided the skulls measured in this study. Systematic nomenclature follows Nowak (1991), except that pinnipeds are treated as a suborder of the Carnivora (following Simpson 1945; Wozencroft 1989; Wayne et al. 1989); traditional Linnaean taxonomic subdivisions are used for descriptive and organizational convenience.

More than half of the specimens measured in this study came from three primate species (*Macaca fascicularis*, *Nasalis larvatus* and *Hylobates lar*) collected by the Harvard Primate Expedition to Southeast Asia in 1937, in which all specimens were weighed and measured immediately after death (Coolidge 1940 gives a detailed report). In contrast, the weights obtained for other specimens often were from animals differing widely in physical condition and season of collection. This is expected to decrease correlations with body weight, especially for carnivores which vary seasonally in fatness. For example, museum tags for individual foxes (*Vulpes vulpes*) reported physical conditions varying from "emaciated" to "fat".

### Intraspecific comparisons

It is unusual to find museum specimens from animals weighed shortly after death, or indeed with any weight information whatsoever. Thus, my choice of species for the intraspecific comparisons was limited by availability. My aim was to collect data from several species from within the same order to allow an intraordinal comparison; I measured adequate numbers of four primate species and four carnivore species (considered here to include pinnipeds). A more detailed intraspecific study of rodents is in preparation. For each species measured, all specimens with intact skulls and weights from intact animals were measured (329 in total): no other selection of specimens was performed. Subadults (sexual maturity determined from museum tags) were present for each species, and for the primates represented a substantial proportion of the data. This allowed a comparison of allometry during the growth period with static allometry among adults, which could be different (Shea 1981), and both of which may be important in body size estimation via acoustic cues.

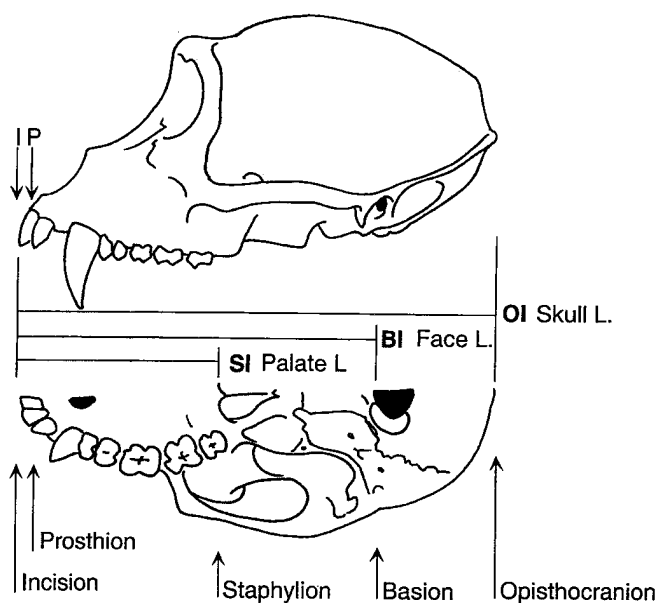
### Interspecific comparisons

Species were selected by the availability of body weight data in the literature and intact adult (defined as skulls with all molars fully erupted) skulls at the MCZ (139 in total). Body weights were taken as species or sex averages from Silva & Downing (1995) and Nowak (1991); species for which the range of weight values given in

these sources was unusually large were not used (e.g., *Mirounga laeonina*, 1000–10,000 kg in Silva & Downing (1995); 350–5000 kg in Nowak (1991)). In cases where sexes vary significantly in size and skulls of both sexes were available (e.g., *Ursus*, *Gorilla*, *Castor*), only the male was measured. Species in which skull or vocal tract morphology is known to be deviant from the typical mammalian pattern were excluded from analysis. For example, in humans the larynx has “descended” away from the typical mammalian pattern giving humans a longer tract than would be expected given their short palate (Lieberman 1984; Crelin 1987). Similarly, I excluded mammals with hypertrophied tympanic bullae inflated posteriorly past the occiput (e.g., rodents such as *Ctenomys* spp. or *Dipodomys* spp.) as this significantly distorts the skull shape relative to that of other mammals. Species and data are given in Appendix I.

## Measurements

Skulls were measured using skull calipers (Hermann, Zurich) for large skulls (accurate to 1.0 mm) and digital calipers (accurate to 0.1 mm; Forestry Suppliers #59598, Jackson, MS) for all measurements under 16 cm. Measurement accuracy was assessed by remeasuring 98 values from 33 skulls one month later, blind to the original measures. I used standard craniometric landmarks and measuring techniques relative to the Frankfort horizontal plane (Bass 1971; von den Driesch 1976). These landmarks are illustrated in Figure 2 and defined briefly here. “Opisthocranion” (O) is the most posterior point on the cranium. “Basion” (B) is the midpoint of the anterior margin of the foramen magnum, and in some species coin-



**Fig. 2.** Craniometric landmarks and linear measurements performed in this study, using a *Macaca fascicularis* skull as an example. Incision was used as the default anterior landmark; Prosthion was used only if upper incisors do not exist (e.g., artiodactyls) or were posterior to prosthion (rodents and seals). Details given in Table 1 and the appendix.

cides with opisthocranion. “Staphylion” (S) is the point where a straight line joining the deepest notches of the posterior margin of the palate cuts the mid-sagittal plane. “Prosthion” (P) is the point on the maxilla between the incisor roots. Finally, “Incision” (I), is the anterior-most point on most skulls, at the incisal level of the upper central incisors. Linear measures are named by the initials of the points they span (e.g., “OI” is from opisthocranion to incision). At least two midsagittal measures were made of each skull: “total skull length” (from anterior-most point (AMP) to posterior-most point (PMP)), and “palate length” (staphylion to AMP). In some cases, where basion was distant from opisthocranion, an additional measure from basion to AMP was made, which gives a measure of “face length”. Because of significant differences in skull form between species, it was necessary to use different craniometric landmarks for different species to obtain these measures; details are given in Table 1 and the Appendix. I always measured to the anterior-most point on the skull which was typically incision, except in artiodactyls, certain rodents, and *Phoca*, where the AMP was prosthion. Where incision was used, only specimens with intact incisors were measured.

To assess the accuracy of measurements, I re-measured 98 values from 33 skulls (OI, BI, SI from the *Nasalis larvatus* sample), and examined the absolute errors. Error magnitude ranged from 0.0 to 1.3 mm, the mean absolute error was 0.32 mm. Relative errors (mean absolute error/mean value) for the three measures were OI: 0.2%, BI: 0.3%, SI 1.5%. This was insignificant relative to the large amount of variability between individuals: coefficients of variation were OI: 19%, BI 28%, SI 29% (see Results).

Different anatomical landmarks were used to delimit the anterior and posterior points of the skull in different species, to compensate for interspecific differences in morphology. To rule out an effect of these differences on interspecific comparisons, I performed measurements using all of these landmarks for 82 *Macaca fascicularis* skulls. Correlation coefficients between these variant measures were: OI vs. OP: 0.995, OI vs. BI: 0.992, BP vs. BI: 0.996. Therefore it is extremely unlikely that the choice of one measure over another would have any significant impact on the magnitude of the correlations discussed below, or would bias the interspecific comparisons.

In non-human mammals, the larynx lies in the caudal-most portion of the oral and/or nasal cavities, apposed to the velum (soft palate) (Negus 1949). Thus, using canonical craniometric landmarks, palate length as defined above provides the best skeletal proxy of true vocal tract length. A better measure in some species would be the linear distance from prosthion to the hamulus (the caudal extension of the pterygoid process, which supports the back edge of the soft palate, and thus is typically very close to the location of the larynx). Unfortunately, the delicate hamulus was broken in many specimens and too poorly defined for accurate measurement in several species, making this potentially useful cranial metric inadequate for the comparative purposes of this study. Because the larynx is a mobile structure, no skeletal measurement can provide a perfect estimate of true vocal tract length, which can only be measured via radiographic or other imaging techniques, preferably on vocalizing animals. The two studies which have measured actual vocal tract lengths have demonstrated very high correla-

tions ( $r = 0.95\text{--}0.96$ ) between skeletal measures and soft-tissue vocal tract length (Fitch 1997; Riede & Fitch 1999). Thus, while the skeletal proxy of vocal tract length used here (palate length) is adequate for the purposes of this study, these values should not be misinterpreted as exact soft-tissue vocal tract length, which would typically be some 10–20% longer.

### Statistical Analysis

There has been considerable debate about the appropriate statistics to use in examining scaling equations (see LaBarbera 1989 for a review and discussion). In general, Model II regression, which uses a major axis or reduced major axis (RMA) metric to fit the regression line, is preferable for most scaling studies. The widely-used Model I regression, typically referred to simply as “regression”, uses an ordinary least squares (OLS) metric and consistently underestimates regression slopes if correlation coefficients are low. OLS regression is the more appropriate choice, however, if the primary purpose of the analysis is to use one variable to predict another (Lande 1985; LaBarbera 1989). Because the primary question of this study is how well can one predict body size from vocal tract length, the correct statistical analyses is thus

Model I OLS regression with log body mass as the dependent variable. This analysis inverts the axes of the graphs and slopes from the traditional scheme in allometry, where body size is typically the independent (x) variable (this could be confusing unless clearly noted). In cases where the general structural (rather than predictive) relationship between x and y is of interest, I also report RMA statistics. Importantly, the different methods produce nearly identical results if correlation coefficients are high, as is typically the case in the current study (Seim & Sæther 1983).

## Results

### Intraspecific Scaling

The eight species ( $N = 329$  individuals) for whom adequate amounts of data were collected are listed in Table 1 along with descriptive data, and shown graphically in Figure 3 (carnivores) and Figure 4 (primates). For 295 of these individuals, both body mass and palate length data were available. All correlations were positive and highly significant ( $p < 0.001$ ).

**Table 1.** Overview of Intraspecific Allometry: Summary data and regression analysis for intraspecific analysis. Lengths in mm, weight is body mass (kg). Column 3 gives the craniometric landmarks used for each species (see Methods). Regression results use  $\log_{10}$  body mass as the dependent variable,  $\log_{10}$  SI, OI, etc. as the independent. Slope values from both Model I OLS regression and Model II RMA regression are given, and confidence limits (“95% conf. lims.”) are from OLS regression.

Species			Mean	SD	Min	Max	R	slope		95% conf. lims.		
								OLS	RMA	lower	upper	Intcpt
<b>Hylobates lar</b> N = 66, 26 juveniles	Palate:	SI	37.4	6.4	21.2	45.9	0.969	3.3	3.4	3.1	3.5	−4.6
	Skull:	OI	100.4	9.4	73.8	111.1	0.970	6.5	6.7	6.1	6.9	−12.4
	Weight:		4.4	1.9	0.5	7.3						
<b>Pongo pygmaeus</b> N = 29, 9 juveniles	Palate:	SI	85.0	17.0	37.0	108.8	0.971	3.2	3.3	2.9	3.5	−4.6
	Skull:	OI	207.0	33.2	127.3	265.0	0.965	4.4	4.6	3.9	4.9	−8.7
	Weight:		42.0	24.6	2.7	90.7						
<b>Nasalis larvatus</b> N = 33, 13 juveniles	Palate:	SI	45.4	10.1	18.3	52.8	0.987	3.3	3.3	3.1	3.5	−4.2
	Skull:	OI	106.6	19.8	74.0	143.0	0.987	5.3	5.4	5.0	5.7	−10.0
	Weight:		9.3	6.7	0.7	23.6						
<b>Macaca fascicularis</b> N = 72, 30 juveniles	Palate:	SI	39.8	8.4	16.1	55.5	0.953	2.2	2.3	2.0	2.3	−3.1
	Skull:	OI	110.9	13.5	60.5	125.0	0.962	3.7	3.8	3.4	3.9	−6.9
	Weight:		2.9	1.2	0.9	5.9						
<b>Vulpes vulpes</b> N = 25, 2 juveniles	Palate:	SI	65.5	8.0	44.5	75.9	0.869	2.7	3.2	2.1	3.4	−4.4
	Skull:	BI	122.0	14.9	82.1	142.1	0.913	3.0	3.3	2.4	3.7	−5.8
	Weight:		3.7	1.1	1.5	5.7						
<b>Ursus americanus</b> N = 21, 1 juvenile	Palate:	SI	134.3	11.4	109.8	161.1	0.843	5.2	6.2	3.6	6.9	−9.2
	Skull:	OI	272.4	29.7	204.0	323.0	0.862	4.4	5.1	3.1	5.6	−8.7
	Weight:		96.8	46.5	63.3	204.1						
<b>Enhydra lutris</b> N = 14, 1 juvenile	Palate:	SI	58.9	7.5	36.3	65.5	0.921	3.4	3.7	2.5	4.3	−4.9
	Skull:	OI	129.6	13.2	91.0	144.3	0.940	4.6	4.9	3.5	5.6	−8.6
	Weight:		15.1	6.6	3.2	26.8						
<b>Phoca vitulina</b> N = 35, 3 juveniles	Palate:	SP	78.2	14.2	59.1	105.3	0.921	4.2	4.6	3.6	4.9	−6.5
	Skull:	BP	163.8	26.1	126.8	209.0	0.922	4.6	5.0	3.9	5.4	−8.8
	Weight:		34.8	29.0	7.0	110.2						

## Intraspecific Scaling in Young and Adults

In order to test the hypothesis that the pattern of scaling differs between adults and young, growing animals (Cock 1966; Lande 1985; Martin & Harvey 1985), I performed a regression analysis (log palate length vs. log body size) separately for young animals and adults. Only for the four primate species

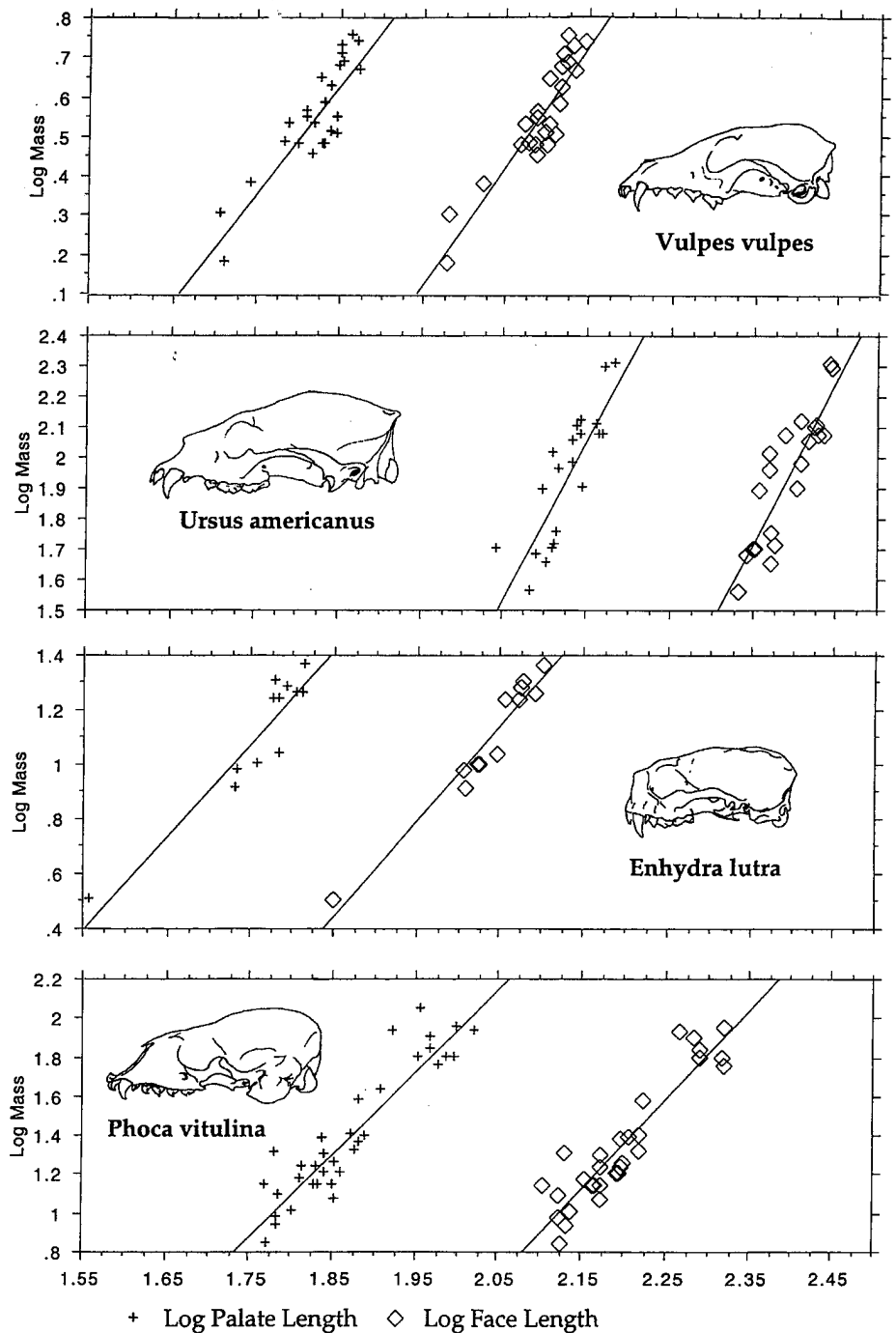
were samples of juveniles adequate to allow this analysis (see Table 1). Results are given in Table 2. For all species except *H. lar*, the values are quite similar, and 95% confidence intervals overlap for the juvenile vs. adult distributions. The difference between slopes in *H. lar* is great enough that the 95% confidence limits do not overlap. This appears to result from the low correlation coefficient for the

**Table 2.** Analysis for Maturational Artifact: Results of intraspecific regression analysis of  $\log_{10}$  palate length vs.  $\log_{10}$  body mass for adults considered separately from juveniles and infants. Labels as in Table 1.

Species	N	r	95% conf. lims.				
			OLS slope	low	high	RMA slope	intercept
<i>Hylobates lar</i>							
Adults:	40	0.580	1.70	0.92	2.49	2.94	-2.01
Juveniles:	26	0.967	3.29	2.92	3.66	3.40	-4.59
<i>Pongo pygmaeus</i>							
Adults:	20	0.870	3.39	2.44	4.34	3.89	-4.99
Juveniles:	9	0.989	2.96	2.57	3.35	2.99	-4.19
<i>Nasalis larvatus</i>							
Adults:	20	0.928	2.79	2.23	3.34	3.00	-3.42
Juveniles:	13	0.970	3.50	2.92	4.09	3.61	-4.53
<i>Macaca fascicularis</i>							
Adults:	42	0.885	1.73	1.44	2.02	1.95	-2.29
Juveniles:	30	0.944	1.84	1.59	2.09	1.95	-2.56

**Table 3.** Analysis for Sexual Dimorphism Artifact: Regression analysis of  $\log_{10}$  palate length vs.  $\log_{10}$  body mass for males and females separately, either for all ages (first two rows) or for adults only (last two rows). Labels as in Tables 1 and 2.

Species	N	r	slope		95% conf. lims		intercept	p
			OLS	RMA	lower	upper		
<i>Hylobates lar</i>								
F:	33	0.978	3.36	3.43	3.10	3.62	-4.68	0.0001
M:	33	0.952	3.30	3.46	2.91	3.69	-4.59	0.0001
Adult F:	17	0.700	2.60	3.72	1.14	4.07	-3.46	0.0018
Adult M:	29	0.329	0.89	2.70	-0.27	2.04	-0.67	NS
<i>Pongo pygmaeus</i>								
F:	15	0.932	2.76	2.96	2.11	3.40	-3.78	0.0001
M:	14	0.980	3.27	3.33	2.85	3.69	-4.75	0.0001
Adult F:	11	0.332	0.64	1.93	-0.73	2.02	0.33	NS
Adult M:	9	0.861	3.67	4.26	1.73	5.61	-5.54	0.0029
<i>Nasalis larvatus</i>								
F:	22	0.987	3.33	3.38	3.08	3.59	-4.29	0.0001
M:	11	0.984	3.26	3.31	2.81	3.71	-4.23	0.0001
Adult F:	13	0.289	0.86	2.97	-1.03	2.74	-0.36	NS
Adult M:	7	0.761	2.47	3.24	0.05	4.88	-2.86	0.0470
<i>Macaca fascicularis</i>								
F:	38	0.919	2.35	2.55	2.01	2.69	-3.31	0.0001
M:	34	0.972	2.22	2.29	2.03	2.42	-3.14	0.0001
Adult F:	22	0.563	1.57	2.78	0.49	2.64	-2.03	0.0064
Adult M:	20	0.748	1.69	2.26	0.95	2.43	-2.22	0.0001



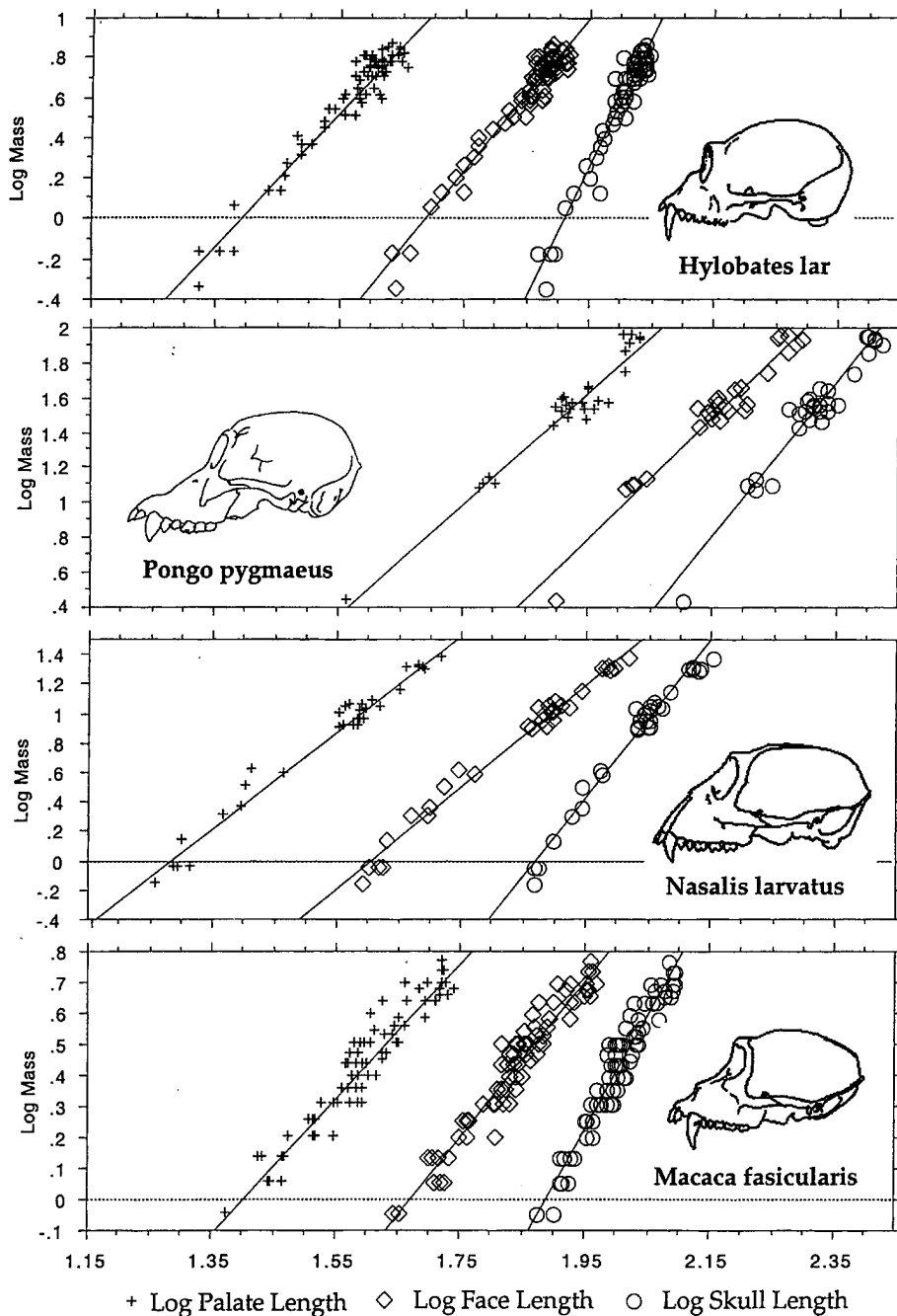
**Fig. 3.** Intraspecific analysis for carnivores. Log Palate length cm (+) and Skull length cm (◇) vs. log body mass (kg).

adult data (0.58). Because OLS regression systematically underestimates the slope when  $r$  is low (LaBarbera 1989), I also calculated the slope using RMA regression. With the RMA values, the difference in slopes for adult and juvenile *H. lar* is statistically insignificant.

The regression data for *N. larvatus* (Fig. 3) provide a visual impression of an inflection in the scaling curve between the smaller animals (with an apparently lower slope) and larger animals (with higher slope). However, this inflection does not coincide with maturity, since some of the ani-

mals in the "larger" group were not sexually mature or full grown, both as revealed by the anatomical inspection performed by the original collector (Adolph H. Schultz) shortly after the animals' death, or by independent dental criteria (the larger animals listed as "juveniles" all had unerupted molars). Thus, even if the apparent inflection is real it does not coincide with attainment of maturity. In summary, these data provide no support for the hypothesis that patterns of adult primate scaling differ from those for young, growing animals.





**Fig. 4.** Intraspecific analysis for primates. Log Palate length cm (+); Face length cm (◇) and Skull length cm (○) vs. log body mass (kg).

### Intraspecific Scaling in Females and Males

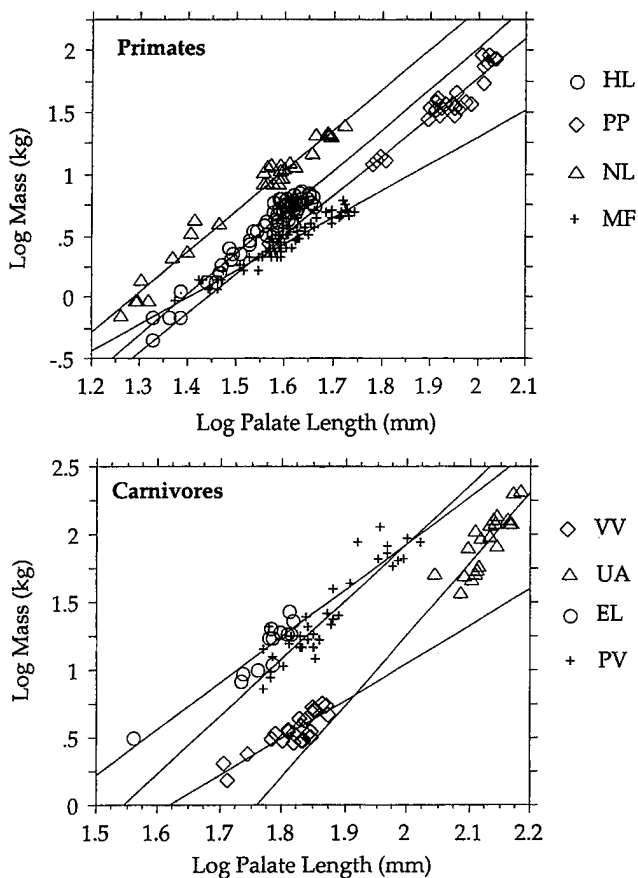
Male and female data were analyzed separately in order to determine if growth and scaling patterns might differ between the sexes (Leutenegger & Cheverud 1985; Cochard 1985). Results are given in Table 3. Again, only the primates had adequate sample sizes for this comparison. When individuals of all ages were included in the analysis, there were no significant differences between male and female patterns of scaling. I also ran these analyses on adults only, to determine if adult correlations result-

ed simply from size differences between males and females (sexual dimorphism). Although sample sizes were reduced by this restriction, five of eight single-sex analyses remained statistically significant. For the macaque skulls, both male and female adult regressions were significant and strong, and nearly identical in slope and intercept. A similar result was reported for a different species of macaque by Cochard (1985). Thus, these data provide no support for the hypothesis that males and females differ significantly in ontogenetic or adult scaling pattern in any of the four primate species mea-

sured, or that the allometric patterns observed are artifacts of sexual dimorphism in size.

### Intraordinal Comparison of Intraspecific Scaling

Figure 5 overlays the intraspecific graphs for palate length vs. body mass for primates and carnivores. It is clear that the intraspecific curves vary considerably between species, especially among the carnivores, suggesting that the causal factors that underlie these intraspecific correlations vary between species. Since the four primate species are closely related (two families within the same Catarrhine infra-order), while each carnivore species is traditionally considered a member of a different family (indeed some would consider *P. vitulina* as being from a separate order), it is not surprising that the carnivores appear to vary more than the primates. In the primate data, where correlation coefficients are high enough to warrant more detailed discussion, both slope and intercept differences can be observed. The decrease in slope observed for macaques results from a disproportionate increase in facial skeleton size, relative to over-



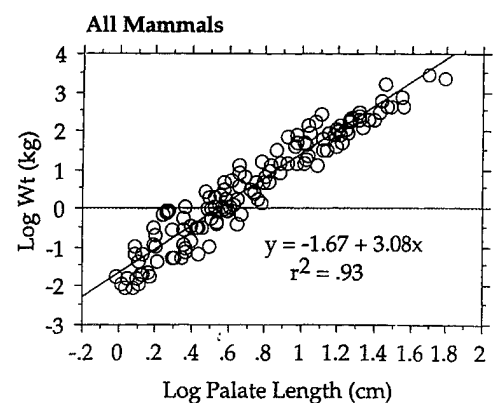
**Fig. 5.** Comparative Intraspecific analysis: Palate length vs. body mass (kg) for Carnivores and Primates. Species initials are those given in Table 1, in the same sequence.

all skull size, observed in many ground-dwelling catarrhines (Washburn 1942). In contrast, *Nasalis larvatus*, the proboscis monkey, shows a deflected intercept relative to the other primates, which follows from the significant increase in gut weight seen in this and other colobine species as an adaptation to leaf-eating (Washburn 1942; Martin et al. 1985).

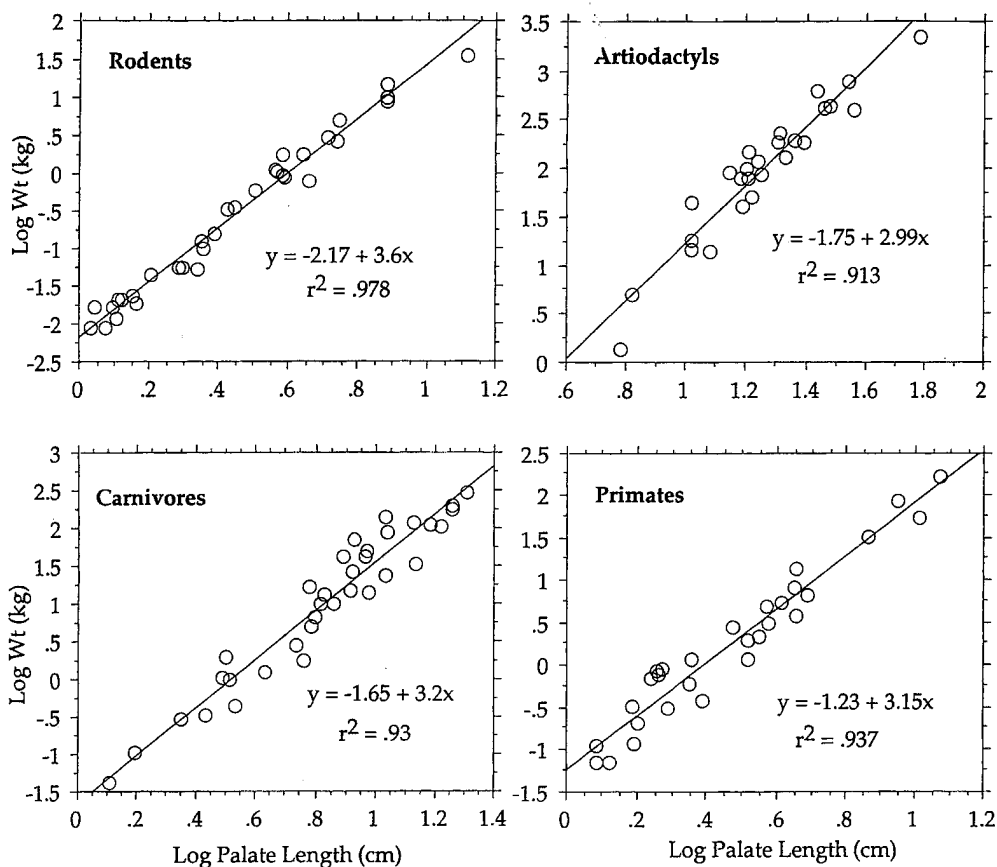
### Interspecific Scaling

For these analyses I measured one skull from each of 139 different mammal species and compared the measurements with species-average body weights gleaned from the literature (min. 9 g *Mus musculus*, max. 2800 kg *Loxodonta africana*). Raw data are provided in the Appendix. The regression was highly significant ( $r^2 = 0.92$ ,  $p < 0.0001$ ), and the slope of the least square regression line relating log palate length to log body size almost exactly that predicted by geometric isometry (OLS slope = 3.08, 95% confidence limits 2.9–3.2, RMA slope = 3.21). Figure 6 presents the data for all species combined. It should be noted that the scatter around the regression line is almost an order of magnitude, indicating that predictions of body mass based on vocal tract length are quite rough at this broad taxonomic level.

For four orders, sufficient specimens were available to do an interspecific comparison by traditional order: primates ( $N = 29$ ), carnivores ( $N = 34$ ), rodents ( $N = 33$ ), and artiodactyls ( $N = 26$ ). All of these analyses were again highly significant ( $p < 0.0001$ ). The results (and regression values) are shown in Figure 7. Thus, there are strong relationships between body mass, skull length and vocal tract length between mammalian species as well as within them. However, comparison among Figures 6 and 7 with the previous figures for intraspecific data illustrates the fact that interspecific



**Fig. 6.** Interspecific Scaling: Palate length vs. body mass (kg) for 130 mammalian species.



**Fig. 7.** Interspecific Scaling: Palate length vs. body mass (kg) for individual species in four traditional Linnaean orders.

data would be extremely misleading if they were used as a guide to within-species scaling. When intraspecific allometric relationships are examined, slopes vary widely from 2 to 5. When each species is used as a single data point, a line with nearly 3.0 slope results in all cases.

## Discussion

In general the intraspecific correlation coefficients are quite high ( $>0.84$ ), though carnivore coefficients are lower than those for primates (Table 1). This is unlikely to reflect any real difference between the two taxa, but instead the lack of consistency in body mass data for the carnivore skulls, as noted in the Methods section, and perhaps the smaller sample of juveniles for the carnivores. Note that although some of the correlations exhibit the slope of 3.0 expected from basic geometric scaling, others deviate significantly from this value. Deviations are either higher (e.g., OI for *N. larvatus* has a slope of more than five) or lower (SI for *M. fascicularis* is around two) than the geometrical prediction. This is true even though the correlation coefficients for these species are very high ( $>0.95$ ). For all species, the slope of the skull length vs. body size curve is greater than 3.0, indicating that body size

increases faster than the cube of skull length. This is expected, because young mammals have large heads relative to adults (body size increases faster than head size). In contrast, the relationship between palate length and body size is more variable, with some species falling above and some below the 3.0 slope of isometry. Thus, for instance, the palate grows disproportionately quickly in *Macaca* relative to the rest of the skull, or to the body (Washburn 1942), while the palate of *Ursus* grows disproportionately slowly. Therefore, the differences in skull proportions visible clearly visible in the adult skulls (Figs. 3 and 4) are paralleled by more subtle ontogenetic differences in these species.

## Acoustic Allometry: VTL as a pan-mammalian cue to body size

These data reveal strong correlations between body mass, skull size and palate length (the skeletal proxy for vocal tract length) in a variety of mammalian species. Together with acoustic analyses for several species (Fitch 1997; Riede & Fitch 1999; Fitch & Giedd 1999), they suggest that vocal tract length could provide a reliable cue to body size in a wide variety of mammals if the proper perceptual mechanisms (particularly the ability to perceive and discriminate formant frequencies) are available. A

number of experimental studies suggest that such perceptual abilities exist in both mammals and birds (Dooling 1990; Heinz & Brady 1988; Heinz et al. 1981; Owren 1990; Sommers et al. 1992). Furthermore, the finding of strong interspecific correlations indicates that a perceptual mechanism which originally evolved to estimate the size of conspecifics (i.e., for evaluating potential opponents or mates, or for use in individual recognition) might also provide information about size in other mammal species (e.g. predators or prey).

The morphology of the skull is under multiple functional constraints: in addition to any role it plays in sound-production, it must successfully support respiration, food capture, processing and intake, support and protection of brain and sense organs, etc. As a result, skull size may be difficult to decouple from body size based solely on selection for acoustics (e.g., via selection on male vocalizations via female mate choice). Thus, the correlation between vocal tract length, skull size and body size appears to be a rather general and perhaps pan-mammalian phenomenon, providing the structural basis for a new type of acoustic allometry. In contrast, the correlation between voice pitch and body size discussed by Morton (1977), Hauser (1993) and others appears to be quite labile and unreliable probably due to the lack of constraint on laryngeal size relative to the rest of the body. Besides producing voiced sounds, the larynx must only perform its relatively unchallenging gating function of guarding the respiratory tract. Thus, when selection on vocal communication is strong (e.g. in lekking hammerhead bats *Hypsignathus monstrosus*, females appear to choose males on the basis of their calls and the most successful 6% of males receives 79% of matings, Bradbury 1977) the larynx increases in size beyond all proportion, filling the entire ribcage in hammerhead bats.

Thus, the greatly enlarged larynx of howler monkeys and hammerhead bats may represent a breakdown of a primitive larynx size/body size correlation, possible functioning to exaggerate body size. Is it possible that the constraints which enforce the vocal tract length/body size correlation can be evaded under the influence of selection? Although oral vocal tract length appears to generally be closely tied to the length of the skull (Negus 1949; Fitch 1997; Riede & Fitch 1999), nasal vocal tract length can be decoupled from skull size via elongation of the cartilaginous portion of the nose into a proboscis. For example, the nasal vocal tract of the elephant includes the proboscis, which is obviously much longer than its oral vocal tract. Although it seems unlikely that proboscises arose to increase the impression of size conveyed by a vocalizing animal (nasal elongation seems more likely a feeding/olfactory adaptation), nasal elongation could

have this effect secondarily, and size exaggeration could perhaps be its primary function in species (e.g., proboscis monkeys) in which nasal elongation is sexually dimorphic, and the elongated nose appears to serve no other purpose. Such cases, combined with nasally-emitted vocalization, might lead to a breakdown of the typical correlation between vocal tract length and body size. However, much more needs to be known about both the production and perception of communication sounds in such species before this possibility can be evaluated.

A second way to decouple vocal tract length from body size is to lower the larynx, as occurs in humans both during infancy (Sasaki et al. 1977) and puberty (Fant 1975, Fitch & Giedd 1999). If the larynx is not confined to the posterior oral cavity, the correlation between skull size and vocal tract length might begin to break down. However, the MRI study of Fitch & Giedd (1999), which examined vocal tract length in 129 humans aged 3–25, found strong correlations between body weight or height and vocal tract length in our own species. These correlations were comparable both in strength and form to those seen in other mammals. This was true despite a slight additional decensus of the larynx in post-pubertal males, which may function to lower formants and thus serve to exaggerate the impression of size conveyed by the adult male voice. Thus, a basic cue to body size based on formants and vocal tract length may survive such putative size-exaggerating morphological changes.

### The Causal Basis of Morphological Scaling Relations

An ongoing debate concerns the degree to which selection within a species drives the patterns observed between species, rendering interspecific allometries epiphenomenal (Koslowsky & Wiener 1997), or whether both derive from the same underlying physiological relationships or biomechanical constraints (West et al. 1997; Cates & Gittleman 1997). This debate highlights the need for comparisons of inter- and intra-specific allometry to test among these hypotheses. The current data reveal significant differences between intraspecific allometric curves in closely related species, as well as significant differences between intra- and interspecific curves. This suggests that the causal basis for the relationships under study differs between species, and across different taxonomic levels.

What are the causal bases of these allometric relationships? One important factor in allometric scaling is simple geometry. Even supposing it were genetically and developmentally possible, it would be biomechanically impossible for a mouse-sized body to have a horse-sized head or vice-versa. There are presumably constraints on how small or large the

head can be relative to the body simply in terms of effective locomotion, food intake, respiration, etc. If shape is constant, volume increases as the cube of length  $L$ , and because volume is directly proportional to mass  $M$ ,

$$M = aL^3,$$

where  $a$  is a constant relating head size to body size. Under logarithmic transformation (the standard methodology in allometric studies), this power function is linearized, and the predicted slope of the resulting regression line is 3:

$$\log_{10} M = 3 \log_{10} L + \log_{10} a.$$

Thus, simple geometric considerations with shape conservation predict a log-log regression slope of 3.0 between skull length and body mass. To the extent that preservation of geometric similarity ("isometry") fully explains skull/body scaling, a slope of 3.0 will be ubiquitous both within and between species. Given this result we could tentatively conclude that the correlations result from a universal, physically-based constraint common to all vertebrates. Significant deviation from a slope of 3.0 would indicate that other factors shaping the relationship of skull form to body size are at work. These potential "other factors" are quite diverse and complex, and the subject of a large literature (Emerson & Bramble 1993 offers a good introduction). Most prominently, they include biomechanical or other physical/functional factors, combined with phylogenetic constraints resulting from genetic and developmental factors. A further delineation of non-geometric factors in acoustic allometry is beyond the scope of the present work, which has only the modest goal of comparing inter- and intra-specific scaling constants to each other and to the geometric prediction of isometry. The data presented here can only reject the null hypothesis of equivalence of between- and within-species along with the "geometric null" (*sensu* Emerson & Bramble 1993) of isometric scaling. Of course, there may be "nested constraints", in that simple geometry provides a relatively coarse constraint on skull size (e.g. at the interspecific level), while other factors are operative within the much narrower size range of a single species. In this case, a comparison of intra- and inter-specific allometries may provide an indication of the range over which such nested constraints operate.

Addressing the interspecific relations first, it seems that they result from a simple geometric scaling relationship, which predicts a log-log regression slope of 3. This prediction is met by some of the intraspecific regressions, and all of the interspecific analyses described above, including the overall

"mouse to elephant" analysis and the analyses restricted to traditional Linnaean orders. The causal basis for this geometric scaling appears straightforward: even given rather lax constraints on the relative proportions of head and body, a strong correlation between head and body size is inevitable for a group with as broad a size range as terrestrial mammals. Thus basic biomechanical and physiological factors, shared by all mammals, are enough to account for strong correlations between head and body size in a comparison where body size varies over many orders of magnitude. At such a broad scale of analysis, this rough isometry gives a correlation very close to the 3.0 slope predicted by simple geometry.

However, despite high correlation coefficients, most of the intraspecific slopes deviate significantly from this cubic relation (see Tab. 1), illustrating that additional, taxon-specific factors underlie these relationships (see Martin & Harvey 1985; Shea 1981 for further discussion of this issue). Although the current study was not designed to examine these factors specifically, the current data do permit us to exclude certain hypotheses. There is no evidence that adult curves differ from those of young, growing animals in the current sample. Instead, these comparisons are consistent with the idea that adult scaling simply reflects a particular individual's stopping point along a shared ontogenetic trajectory. In determinate-growth species like those considered here, there is no significant growth of the skeleton or skull after sexual maturity, and the differences in skeletal size among adults probably reflects just the different sizes reached by individuals at puberty. There is also no evidence that the adult curves are artifactual byproducts of sexual dimorphism in size, or indications that different developmental programs operate in males and females. Despite low sample sizes, intraspecific correlations were often significant even when restricted to adults of one sex. Neither these curves, nor the ontogenetic curves, differed significantly between the sexes. However, the reduced sample sizes, weaker correlations and consequently reduced statistical power render this last conclusion provisional.

A parsimonious interpretation of the current data suggests at a minimum two distinct causal factors underlying the patterns of scaling observed. The intraspecific correlations could all result from allometric scaling during growth, which is the same for all members of a species but can differ substantially between species. Myriad factors might underlie this scaling (e.g. biomechanical factors relating to bite force, physiological constraints on brain size, or developmental constraints such as "pleiotropic" effects of circulating growth hormones which affect the entire body, not just the skull or torso). The current data provide little aid in evaluating such hypothe-

ses. Fortunately, this decade has seen fundamental breakthroughs in our understanding of both craniofacial biomechanics and cranial development (e.g., Hanken & Thorogood 1993; Hanken & Hall 1993), and we can expect rapid progress towards the goal of understanding the details of these scaling patterns in the coming years.

In contrast to the intraspecific data, the interspecific data are clearly compatible with the hypothesis that the strong correlations observed result from constraints due to simple geometric factors which are the same for all vertebrates. This appears to be an example of a broad limitation on the physical forms that are possible over a large range of body sizes. This geometric limitation may however have little relevance over the much smaller range of body sizes that typify individuals of a given species. In the context of the current debate about the "epiphenomenality" (Koslowski & Wiener 1997) of intra- or inter-specific allometry, the current data suggest that:

- 1) Intra- and inter-specific scaling relations may derive from different causes, neither one more "real" than the other, and thus can differ significantly from one another; and
- 2) Using interspecific curves to analyze, predict or understand intraspecific phenomena (or *vice versa*) could give extremely misleading results.

These results suggest that comparisons of intra- and inter-specific scaling, preferably by the same researcher using the same methods, can provide useful data for exploring the causal bases of empirically-observed morphological correlations.

## Conclusion

The data presented above reveal ubiquitous, strong correlations between vocal tract dimensions, skull size and body size. Combined with basic acoustic theory (Lieberman & Blumstein 1988; Titze 1994; Fitch & Hauser 1995) as well as empirical data (Fitch 1997; Riede & Fitch 1999), this suggests that vocal tract resonance frequencies ("formants") could provide accurate information about a vocalizer's body size in many mammals. Such acoustic cues to body size result from anatomical correlations combined with basic acoustic principles, and should be persistent and widespread in lieu of active selection against them. Thus, information about body size could be conveyed "by default" in many mammalian vocalizations, and there is no need to invoke selection for "honest" information transfer to account for this fact. The current data support the notion that functional morphology and physical laws might provide significant constraints on the evolution of acoustic signaling in mammals (Ryan 1986,

1988; Ryan & Drewes 1990) and that the study of such constraints will play a major role in advancing our understanding of the evolution of signaling (Hauser 1996; Bradbury & Vehrencamp 1998, p. 554–570).

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## Appendix: Interspecific Data

The following table provides species, common name, family and order for each skull measured for the interspecific dataset. The final column, "Inc?" tells whether the anterior most point on the skull was incision (Y) or prosthion (N). Measures given are SL: total skull length (OI or OP); FL: face length (BI or BP); and PL: palate length (SI or SP). Weights are taken from Silva & Downing (1995) and Nowak (1991). The "•" symbol indicates missing data (due to damaged skulls).

Sex	Species	Common Name	Family	Order	Wt1 (kg)	SL (cm)	FL (cm)	PL (cm)	Inc?
1 M	<i>Macropus rufus</i>	Red Kangaroo	Macro.	Marsupalia	66	20	18	12.98	Y
2 M	<i>Tapirus terrestris</i>	SA Tapir	Tapir.	Perisso.	225	37.3	35	18.4	N
3 F	<i>Equus burchelli</i>	Burchell's zebra	Equ.	Perisso.	302	54.5	48.7	26.2	Y
4 ?	<i>Rhinoceros unicornis</i>	Indian Rhino	Rhino.	Perisso.	1700	60.2	60.2	28.2	Y
5 M	<i>Bison bison</i>	Bison	Bov.	Artiodact.	628	49.7	44.3	27.2	N
6 ?	<i>Syncerus caffer</i>	African Buffalo	Bov.	Artiodact.	450	53.3	49.8	30.2	N
7 M	<i>Kobus elipsiprymnus</i>	Waterbuck	Bov.	Artiodact.	190	39	35.7	20.2	N



Appendix. (Continued).

Sex	Species	Common Name	Family	Order	Wt1 (kg)	SL (cm)	FL (cm)	PL (cm)	Inc?
8 M	<i>Neotragus moschatus</i>	Dwarf antelope	Bov.	Artiodact.	5	11.5	10.24	6.61	N
9 M	<i>Sylvicapra grimmia</i>	Common duiker	Bov.	Artiodact.	18.7	20.6	18.1	10.41	N
10 ?	<i>Boselaphus tragocamelus</i>	Nilgai (bluebuck)	Bov.	Artiodact.	191	42.8	38.7	24.6	N
11 ?	<i>Connochaetes taurinus</i>	Blue Wildebeest	Bov.	Artiodact.	195	44.5	39.7	22.8	N
12 F	<i>Damaliscus tiang</i>	Sassaby	Bov.	Artiodact.	130	39	35.7	21.4	N
13 F	<i>Bubalus quarlesi</i>	Anoa	Bov.	Artiodact.	150	26.5	24.2	15.98	N
14 F	<i>Kobus (Onotragus) leche</i>	Lechwe	Bov.	Artiodact.	78.7	27.6	24.9	15.06	N
15 M	<i>Redunca arundinum</i>	Reedbuck	Bov.	Artiodact.	80.5	28.4	25.6	16.04	N
16 M	<i>Oryx gazella</i>	Oryx	Bov.	Artiodact.	236	37.9	35.1	20.3	N
17 M	<i>Oreamnos americanus</i>	Mountain Goat	Bov.	Artiodact.	102.1	28.4	25.1	15.7	N
18 M	<i>Capricornis sumatrensis</i>	Serow	Bov.	Artiodact.	120	3	027.4	17.2	N
19 M	<i>Hydropotes inermis</i>	Chinese Water Deer	Cerv.	Artiodact.	14.5	17.1	15.23	10.38	N
20 ?	<i>Muntiacus mutjak</i>	Muntjac	Cerv.	Artiodact.	14	20.4	17.6	12.03	N
21 M	<i>Alces alces</i>	Moose	Cerv.	Artiodact.	412	62	54.5	36	N
22 M	<i>Odocoileus virginianus</i>	White-tailed deer	Cerv.	Artiodact.	86.2	29.2	26.3	17.6	N
23 M	<i>Tragulid javanicus</i>	Chevrotain	Cerv.	Artiodact.	1.37	9.63	8.19	6	N
24 ?	<i>Lama glama</i>	Llama	Camel.	Artiodact.	90	27.7	25.2	13.9	N
25 F	<i>Vicugna vicugna</i>	Vicuña	Camel.	Artiodact.	45	22.9	19.6	10.46	N
26 ?	<i>Camelus dromedarius</i>	Camel	Camel.	Artiodact.	415	52.1	47.2	28.6	N
27 M	<i>Antilocapra americana</i>	Pronghorn	Antilo.	Artiodact.	51.5	28.6	25.6	16.5	N
28 ?	<i>Giraffa camelopardis</i>	Giraffe	Giraff.	Artiodact.	800	62.8	57.3	34.7	N
29 ?	<i>Hippotamus amphibius</i>	Hippo	Hippo.	Artiodact.	2250	82	76	61	Y
30 F	<i>Loxodonta africana</i>	African Elephant	Elephant.	Probos.	2800	•	•	49	N
31 M	<i>Canis lupus</i>	Gray Wolf	Can.	Carnivora	33	27.8	24.2	13.6	Y
32 F	<i>Canis latrans</i>	Coyote	Can.	Carnivora	14.5	19.7	17.1	9.47	Y
33 F	<i>Vulpes chama</i>	Cape fox	Can.	Carnivora	2.9	11.39	10.6	5.4	Y
34 M	<i>Vulpes macrotis arripus</i>	Kit fox	Can.	Carnivora	1.82	11.39	10.55	5.78	Y
35 F	<i>Speothos venaticus</i>	Bush dog	Can.	Carnivora	5	12.71	12.13	6.12	Y
36 M	<i>Fennecus zerda</i>	Fennec fox	Can.	Carnivora	1.25	8.86	8.48	4.25	Y
37 M	<i>Chrysocyon brahyurus</i>	Maned wolf	Can.	Carnivora	23.8	22.7	19.8	10.78	Y
38 ?	<i>Ursus (Helarctos) malayanus</i>	Sun bear	Urs.	Carnivora	41	19.4	16.7	9.2	Y
39 ?	<i>Tremarctos ornatus</i>	Spectable bear	Urs.	Carnivora	140	24	20.6	10.76	Y
40 M	<i>Ursus arctos horribilis</i>	Grizzly bear	Urs.	Carnivora	306	41.1	35.9	20.3	Y
41 F	<i>Ursus maritimus</i>	Polar bear	Urs.	Carnivora	200	35.7	32.7	18.1	Y
42 M	<i>Gulo gulo</i>	Wolverine	Mustel.	Carnivora	15	16.7	14.08	8.24	Y
43 M	<i>Panthera leo</i>	Lion	Fel.	Carnivora	175	37.4	31.7	18.1	Y
44 M	<i>Panthera tigris</i>	Tiger	Fel.	Carnivora	113	32.7	27.6	15.2	Y
45 M	<i>Panthera pardus</i>	Leopard	Fel.	Carnivora	50.3	22.6	18.7	9.41	Y
46 M	<i>Panthera onca</i>	Jaguar	Fel.	Carnivora	89	26.2	21.6	10.98	Y
47 M	<i>Felis concolor</i>	Cougar	Fel.	Carnivora	70.9	21.3	17.8	8.4	Y
48 M	<i>Mustela nivalis pygmaeus</i>	Least weasel	Mustel.	Carnivora	0.043	•	3.03	1.27	Y
49 ?	<i>Mustela frenata</i>	Long-tailed weasel	Mustel.	Carnivora	0.294	•	4.84	2.23	Y
50 ?	<i>Mustela nigripes</i>	Black-footed ferret	Mustel.	Carnivora	1.021	•	6.38	3.22	Y
51 M	<i>Poecilogale albinucha</i>	African striped weasel	Mustel.	Carnivora	0.332	•	5.52	2.7	Y
52 F	<i>Mellivora capensis</i>	Honey badger	Mustel.	Carnivora	10	•	12.53	6.53	Y
53 M	<i>Mustela vison</i>	Mink	Mustel.	Carnivora	1.042	•	6.26	3.04	Y
54 M	<i>Mustela erminea</i>	Ermine	Mustel.	Carnivora	0.105	•	3.62	1.57	Y
55 ?	<i>Meles meles</i>	Badger	Mustel.	Carnivora	13	12.56	11.2	6.73	Y
56 ?	<i>Melogale everetti</i>	Ferrett badger	Mustel.	Carnivora	2	7.12	6.21	3.14	Y
57 M	<i>Martes pennanti</i>	Fisher	Mustel.	Carnivora	6.8	13.06	11.12	6.29	Y
58 F	<i>Martes americana</i>	Pine marten	Mustel.	Carnivora	0.45	7.08	6.4	3.39	Y
59 F	<i>Enhydra lutris</i>	Sea otter	Mustel.	Carnivora	17.24	13.2	11.5	6	Y
60 M	<i>Hydrurga leptonyx</i>	Leopard seal	Phoc.	Carnivora	270	28.6	28.6	12.6	Y
61 M	<i>Phoca vitulina</i>	Harbot seal	Phoc.	Carnivora	79.4	•	19.2	9.31	Y
62 M	<i>Gorilla gorilla</i>	Gorilla	Pong.	Primates	170	30.8	20.6	11.82	Y
63 M	<i>Papio hamadryas</i>	Baboon	Cerco.	Primates	32.5	16.7	12.1	7.31	Y
64 ?	<i>Lemur catta</i>	Ring-tailed lemur	Lemur.	Primates	2.9	7.45	5.95	3	Y

Appendix. (Continued).

Sex	Species	Common Name	Family	Order	Wt1 (kg)	SL (cm)	FL (cm)	PL (cm)	Inc?
65 ?	<i>Pteropus fulvus</i>	Brown lemur	Lemur.	Primates	3.2	9.22	7.86	3.77	Y
66 M	<i>Lepilemur mustellinus</i>	Sportive lemur	Megalap.	Primates	0.7	4.94	4.05	1.73	Y
67 F	<i>Microcebus murinus</i>	Mouse lemur	Chiero.	Primates	0.07	3.18	2.59	1.22	Y
68 M	<i>Microcebus rufus</i>	Mouse lemur	Cheiro.	Primates	0.07	3.19	2.59	1.33	Y
69 M	<i>Cheirogaleus major</i>	Dwarf lemur	Cheiro.	Primates	0.389	5.68	4.83	2.44	Y
70 ?	<i>Indri indri</i>	Indri	Indri.	Primates	8.5	10.86	9.51	4.49	Y
71 M	<i>Avahi laniger</i>	Avahi	Indri.	Primates	0.9	5.44	4.44	1.5	Y
72 ?	<i>Propithecus diadema</i>	Sifaka	Indri.	Primates	5	9.45	7.88	3.71	Y
73 ?	<i>Daubentonia madagascariensis</i>	Aye-aye	Dauben.	Primates	2	9.13	7.07	3.3	Y
74 M	<i>Perodictus potto</i>	Potto	Loris.	Primates	1.2	6.36	5.45	2.25	Y
75 M	<i>Euoticus elegantulus</i>	Needleclawed bushbaby	Loris.	Primates	0.315	5	3.91	1.54	Y
76 M	<i>Galago senegalensis</i>	Bush-baby	Loris-	Primates	0.21	4.45	3.34	1.59	Y
77 F	<i>Tarsius syrichta</i>	Tarsier	Tarsi.	Primates	0.12	3.87	2.67	1.55	Y
78 F	<i>Callicebus moloch</i>	Titi	Ceb.	Primates	0.62	6.72	5.04	2.26	Y
79 ?	<i>Aotus trivirgatus</i>	Owl monkey	Ceb.	Primates	0.8	6.1	4.39	1.82	Y
80 M	<i>Cebus apella</i>	Capuchin	Ceb.	Primates	2.2	9.8	6.98	3.55	Y
81 ?	<i>Saimiri sciureus</i>	Squirrel monkey	Ceb.	Primates	0.925	6.73	4.14	1.86	Y
82 M	<i>Pithecia monachus</i>	Monk saki	Ceb.	Primates	1.2	8.95	6.9	3.3	Y
83 M	<i>Alouatta caraya</i>	Black howler	Ceb.	Primates	6.7	12.88	11.12	4.89	Y
84 ?	<i>Callithrix jacchus</i>	Marmoset	Calli.	Primates	0.34	4.63	3.31	1.54	Y
85 F	<i>Cebuella pygmaea</i>	Pygmy marmoset	Calli.	Primates	0.112	3.65	2.61	1.21	Y
86 M	<i>Macaca fascicularis</i>	Macaque	Cerco.	Primates	3.82	10.9	7.83	4.53	Y
87 M	<i>Nasalis larvatus</i>	Proboscis monkey	Cerco.	Primates	14	12.16	8.77	4.54	Y
88 ?	<i>Hylobates lar</i>	White-handed gibbon	Hylobat.	Primates	5.67	10.47	7.71	4.1	Y
89 M	<i>Pongo pygmaeus</i>	Orangutan	Pong.	Primates	54.4	23.95	17.4	10.3	Y
90 M	<i>Hydrochoeris hydrochoeris</i>	Capybara	Hydro.	Rodentia	36	21.6	18.4	13.06	Y
91 M	<i>Castor canadensis</i>	Beaver	Castor.	Rodentia	15	12.47	11.42	7.65	Y
92 F	<i>Tamiasciurus hudsonicus</i>	Red squirrel	Sciur.	Rodentia	0.1592	4.3	3.98	2.46	N
93 F	<i>Marmota monax</i>	Woodchuck	Sciur.	Rodentia	2.6	8.69	8.69	5.45	Y
94 M	<i>Spermophilus spilosoma</i>	Ground squirrel	Sciur.	Rodentia	0.126	3.86	3.54	2.26	N
95 F	<i>Aplodontia rufa</i>	Mountain beaver	Aplodont.	Rodentia	0.774	6.43	6.43	4.59	N
96 M	<i>Tamias striatus</i>	E. chipmunk	Sciur.	Rodentia	0.0975	3.88	3.64	2.27	N
97 F	<i>Eutamias dorsalis</i>	W. chipmunk	Sciur.	Rodentia	0.056	3.57	3.23	1.99	N
98 ?	<i>Cynomys leucurus</i>	Prairie dog	Sciur.	Rodentia	1.05	5.68	5.68	3.71	N
99 M	<i>Glaucomys volans</i>	Flying squirrel	Sciur	Rodentia	0.055	3.45	3.16	1.95	N
100 F	<i>Petaurista petaurista</i>	Giant flying squirrel	Sciur.	Rodentia	1.75	8.07	7.37	4.43	N
101 •	<i>Myosciurus pumilio</i>	Pygmy squirrel	Sciur.	Rodentia	0.0165	2.25	1.89	1.1	N
102 M	<i>Ratufa bicolor</i>	Giant squirrel	Sciur	Rodentia	1.75	7.37	6.85	3.84	N
103 M	<i>Sciurus carolinensis</i>	Grey squirrel	Sciur.	Rodentia	0.583	•	5.24	3.2	N
104 M	<i>Lagidium peruanum</i>	Mountain viscacha	Chinchill.	Rodentia	1.134	7.48	6.35	3.66	N
105 M	<i>Proechimys trinitatus</i>	Spiny rat	Echimy.	Rodentia	0.34	5.39	4.78	2.66	N
106 M	<i>Agouti paca</i>	Paca	Dasy.	Rodentia	9.15	13.88	12.1	7.65	N
107 F	<i>Erithizon dorsatum</i>	Porcupine	Erith.	Rodentia	5	10.97	9.59	5.57	N
108 F	<i>Zapus hudsonicus</i>	Jumping mouse	Zapod.	Rodentia	0.0117	2.32	2.11	1.28	N
109 F	<i>Napeozapus insignis</i>	Woodland jumping mouse	Zapod.	Rodentia	0.017	2.28	2.02	1.25	N
110 M	<i>Apodemus sylvaticus</i>	Field mouse	Mur.	Rodentia	0.019	2.56	2.33	1.46	N
111 F	<i>Cricetomys gambianus</i>	Giant pouched rat	Mur.	Rodentia	0.9	6.37	6.08	3.9	N
112 M	<i>Mus musculus</i>	Mouse	Mur.	Rodentia	0.009	1.98	1.75	1.08	N
113 M	<i>Mus cooki</i>	Siamese mouse	Mur.	Rodentia	0.0209	2.33	2.11	1.3	N
114 F	<i>Rattus norvegicus</i>	Rat	Mur.	Rodentia	0.345	4.73	4.41	2.8	N
115 F	<i>Rhizomys sumatrensis</i>	Bamboo rat	Mur.	Rodentia	3	8.12	7.94	5.16	N
116 F	<i>Microtus breveri</i>	Vole	Mur.	Rodentia	0.0233	2.57	2.42	1.42	N
117 M	<i>Clethrionomys gapperi</i>	Bank vole	Mur.	Rodentia	0.021	2.52	2.37	1.33	N
118 M	<i>Ondatra zibethicus</i>	Muskrat	Mur.	Rodentia	0.938	6.25	5.94	3.84	N
119 M	<i>Peromyscus leucopus</i>	White-footed mouse	Mur.	Rodentia	0.009	2.22	1.95	1.19	N
120 M	<i>Onychomys leucogaster</i>	Grasshopper mouse	Mur.	Rodentia	0.045	2.86	2.68	1.61	N

**Appendix.** (Continued).

Sex	Species	Common Name	Family	Order	Wt1 (kg)	SL (cm)	FL (cm)	PL (cm)	Inc?
121 ?	<i>Pteropus giganteus</i>	Flying fox	Ptero.	Chiroptera	1.2	7.14	6.71	4.07	Y
122 M	<i>Hypsignathus monstrosus</i>	Hammerheaded bat	Ptero.	Chiroptera	0.42	7.21	6.86	4.37	Y
123 ?	<i>Epomops franqueti</i>	Epauled bat	Ptero.	Chiroptera	0.11	5.26	4.93	3.1	Y
124 F	<i>Epomophorus wahlbergi</i>	Epauled fruit bat	Ptero.	Chiroptera	0.07	4.56	4.25	2.7	Y
125 M	<i>Rousettus leachi</i>	Fruit bat	Ptero.	Chiroptera	0.078	4.2	3.74	2.29	Y
126 M	<i>Dobsonia moluccensis</i>	Bareback fruit bat	Ptero.	Chiroptera	0.44	6.2	5.66	3.51	Y
127 M	<i>Syncomycteris australis</i>	Blossom bat	Ptero.	Chiroptera	0.02	2.71	2.39	1.31	Y
128 F	<i>Triaenops persicus</i>	Triple leafnosed bat	Hippos.	Chiroptera	0.012	1.87	1.49	1.04	Y
129 M	<i>Eptesicus fuscus</i>	Big brown bat	Vesper.	Chiroptera	0.0175	1.93	1.64	0.97	Y

**Key to Appendix:**

Family names are the abbreviation given in the Table + "-idae", except for "Hippo." = Hippopotamidae, "Antilo." = Antilocapridae, "Macro." = Macropodidae, "Rhino" = Rhinocerotidae, "Cerro." = Cercopithecidae, "Cheiro." = Cheirogaleidae, "Dauben." = Daubentoniidae, "Calli." = Callitrichidae, "Hydro." = Hydrochaeridae, "Dasy." = Dasyproctidae, "Erith." = Erithizonidae, "Ptero." = Pteropodidae, "Hippos." = Hipposideridae, and "Vesper." = Vespertilionidae. Orders are as given except for "Artiodact." = Artiodactyla, "Probos." = Proboscidea and "Perisso." = Perissodactyla.

• signifies missing data.