Journal of Mammalogy, 86(5):1042–1049, 2005

MAMMALIAN POSTNATAL GROWTH ESTIMATES: THE INFLUENCE OF WEANING ON THE CHOICE OF A COMPARATIVE METRIC

AMANDA D. MELIN, PHILIP J. BERGMANN,* AND ANTHONY P. RUSSELL

Department of Biological Sciences, University of Calgary, Calgary, Alberta T2N 1N4, Canada (ADM, PJB, APR)
Present address of ADM: Department of Anthropology, University of Calgary, Calgary, Alberta T2N 1N4, Canada
Present address of PJB: Department of Ecology and Evolutionary Biology, Tulane University,
New Orleans, LA 70118, USA

In an investigation of the postnatal growth of the vertebral column of the Norway rat (*Rattus norvegicus*), we recorded hind-foot length as a standard metric, along with skull, tail, femur, and tibia lengths, against which to compare the growth of axial components. We confirmed a nonlinear relationship of head–body length against hind-foot length, tail length, and tibia length across the time course from neonate to adult and also discovered a nonlinear relationship between both skull and femur length to head–body length. Differences in growth rate are directly related to preweaning and postweaning periods. The pattern of differential growth was distinctly least pronounced for femoral length. We therefore advocate the latter as the most appropriate to use as an easily measured proxy for growth across the entire neonate to adult growth period. This study reveals implications for the choice of optimal variables used as size proxies and also suggests functional implications of shifts in form–function relationships from unweaned to weaned individuals. However, variation in body form across mammals and altricial versus precocial modes of natal expression will continue to complicate the search for appropriate comparative metrics in the study of the development and evolution of body form.

Key words: body size, comparative metrics, growth, mammals, morphometrics, *Rattus norvegicus*, reduced major-axis regression, Rodentia, standard measures, weaning

Understanding patterns of relative scaling during ontogeny is of interest for many reasons. It is an essential prerequisite for the comprehension of vertebrate population dynamics and life histories (Lu 2003; Moscarella and Aguilera 1999; Sadleir 1969), reproductive biology and ecology of species (Hoying and Kunz 1998), functional morphology (Lu 2003), and the processes of evolution and speciation (Gaillard et al. 1997). Growth, most simply described as an increase in size over time, is an inherent process in the development of all vertebrates and, indeed, most living organisms. Many studies of growth have been conducted (Garde and Escala 1996; Gibson et al. 2000; Green and Fekete 1934; Lammers et al. 2001; Lu 2003; Moss and Baer 1956; Reik et al. 2001), and a focal consideration of many such studies has been the recognition of morphological features that can be used as accurate proxies of overall corporeal growth. Even with the advent of multivariate approaches to the study of growth (Anderson 1963; Bookstein 1997), single variable proxies for body size remain useful because of difficulties of interpreting multivariate proxies (Beuttell and Losos 1999; Jungers and German 1981).

In the study of mammalian growth, a number of measurements are frequently recorded, including body mass, head–body or crown–rump length, hind-foot length, tail length, and ear length (Garde and Escala 1996; Green and Fekete 1934; Lammers et al. 2001; Lu 2003). These are standard measures and are suggested as routine data to collect when mammalian specimens are being documented (e.g., DeBlase and Martin 1974). Such measures are considered here as potential proxies for general body size.

Head–body length is the most frequently employed metric for body size because it includes most of the body, is minimally affected by the nutritional state of the specimen, contains, and is contributed to by axial bony elements (skull and vertebrae), and generally subsumes other variables such as the skull and vertebral column. However, this measure is not useful for assessing growth of components making up the sagittal axis because such measurements are a component part of the whole and thus lack independence. Body mass is a further, highly inclusive, metric for body size, but is often difficult to collect from museum specimens and is subject to the vagaries of

---

* *Correspondent: pbergman@tulane.edu*

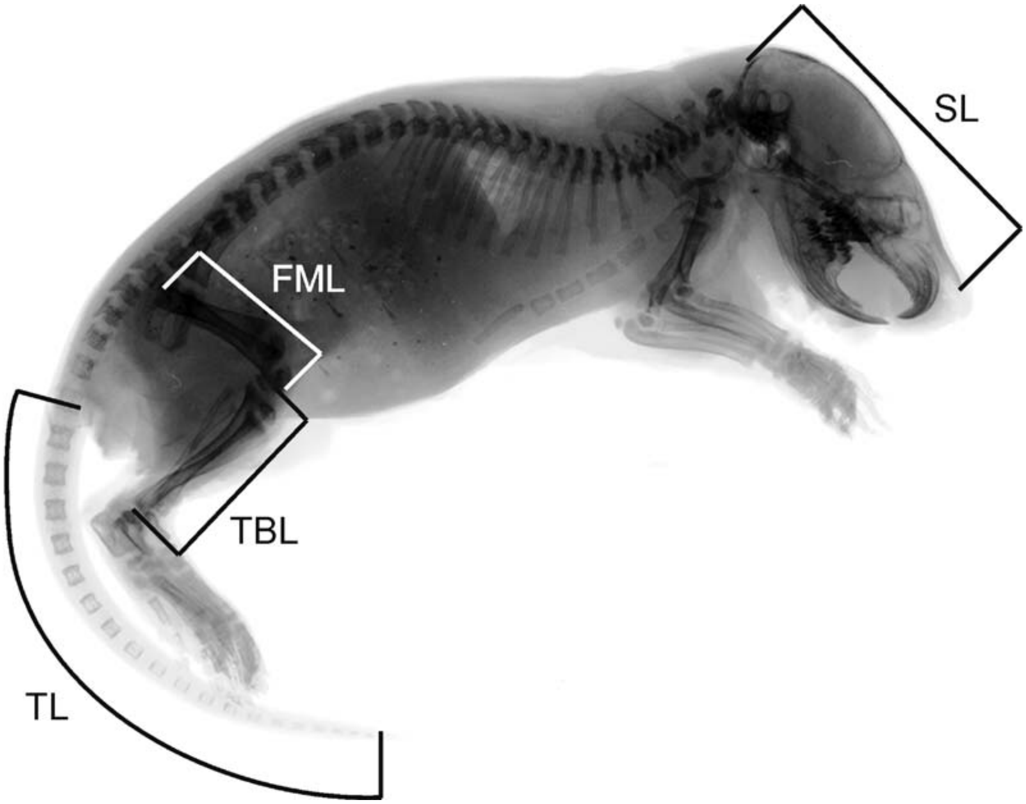

Fig. 1.—Radiograph of an 18-day-old specimen of *Rattus norvegicus* depicting morphometric variables examined in this study. Abbreviations: FML, femur length; SL, skull length; TBL, tibia length; TL, tail length. Head–body length is encompassed by the distance between the anterior extremity of SL and the anterior extremity of TL.

differential metabolic rates (Reiss 1991) and nutritional condition of specimens (Bauer et al. 1989).

In conducting a study of growth of the postnatal growth of the vertebral column in the Norway rat (*Rattus norvegicus*), we assessed various dimensions as the standard measure against which to scale aspects of vertebral growth. This was necessitated because of the variability in growth rates of skeletal dimensions noted by Green and Fekete (1934). We required a measure that included skeletal elements and that was independent of the vertebral column. In their study of growth in the mouse, Green and Fekete (1934) indicated that the femur grows relatively constantly throughout the postnatal period, whereas the tibia and hind foot do not. We undertook to test these findings, to investigate the relative deviance from linearity of these measures, and to explore their implications.

Materials and Methods

Specimens.—Cross-sectional data were collected from 105 Sprague–Dawley–strain Norway rats, ranging in age from 0 to 84 days (neonate to adult). Study specimens were raised under standard laboratory conditions and euthanized via carbon dioxide asphyxiation after University of Calgary Animal Care approval and by following guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). Specimens were stored frozen at −20°C, and thawed at 4°C to allow manipulation, at which time external measurements and radiographs were taken.

A cross-sectional ontogenetic series of individuals of known age, equally sampled at all sizes, was assembled, in a fashion similar to that of Green and Fekete (1934). Although there are limitations associated with elevated levels of variance present in cross-sectional data sets (German 2004), we deemed this approach preferable because of the ease of working with and availability of such data, and also because our goal was to make this study highly applicable to other researchers who use museum specimens. Five rats from each sampled postnatal age were included, which in most instances consisted of both males and females. Individuals were sampled on every other day from birth to 22 days of age (day 0, 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, and 22), and on every 7th day thereafter (day 28, 35, 42, 49, 56, 63, 70, 77, and 84). Six other adult rats, older than 84 days, were examined to confirm that the 84-day-old rats had attained adult size. Furthermore, radiographs of 84-day-old rats indicated that femoral epiphyseal plates were fused.

Measurements.—Measurements of head–body length and tail length were taken with a straight-edge ruler to the nearest millimeter. Right hind-foot length was measured with Mitutoyo digital calipers (Aurora, Illinois) to the nearest 0.01 mm. Each measurement was taken 3 times, and the average was used in all subsequent analyses. Body weight was measured to the nearest 0.1 g with either an Ohaus 2,610-g-capacity triple-beam balance (Pine Brook, New Jersey) or a Fisher/Ainsworth M-300 DR electronic balance (Pittsburgh, Pennsylvania). Radiographs were taken with a Hewlett-Packard Faxitron model 43805N radiology unit (Palo Alto, California) and Polaroid Type 55 black and white positive/negative film (Waltham, Massacusetts). During radiography, rat specimens were positioned on their right side and in direct contact with the film, yielding a 1:1 object to image size ratio (Fig. 1; Bergmann and Russell 2001; Myers 1998).

Table 1.—Sexual dimorphism in variable means (male and female) of log-transformed variables (lengths and mass) for *Rattus norvegicus*, evaluated with χ^2 approximations for Mann–Whitney *U*-tests. Tests were done on the entire ontogenetic series (males: $n = 48$; females: $n = 57$), and on adult individuals ($n = 5$ for each sex). For all cases, $d.f. = 1$.

	All individuals				Adults			
Variable	Males	Females	χ^2	*P*	Males	Females	χ^2	*P*
Head–body length	2.1309	2.0845	1.4162	0.2340	2.3916	2.3456	6.8181	0.0090
Mass	1.8731	1.7136	1.6222	0.2028	2.6843	2.4538	6.8181	0.0090
Tail length	1.9378	1.8920	0.8110	0.3678	2.3545	2.3162	6.8181	0.0090
Hind-foot length	1.4222	1.3904	1.4469	0.2290	1.6562	1.6193	6.8181	0.0090
Skull length	1.5173	1.4919	1.0199	0.3125	1.6878	1.6585	6.8181	0.0090
Tibia length	1.2134	1.1807	0.4693	0.4933	1.5888	1.5547	4.8109	0.0283
Femur length	1.0908	1.0593	0.2145	0.6433	1.4932	1.4540	2.4545	0.1172

Table 2.—Statistics for evaluating sexual dimorphism in reduced major-axis residuals from regressions including all individuals for *Rattus norvegicus*. Statistics from *t*-test (*t*) and Mann–Whitney *U*-test (*U*) are presented. Females have higher residual values in all variables.

Variable (lengths)	Test	*d.f.*	t/χ^2	*P*
Tail	*t*	102	4.9321	1.4×10^{-6}
Hind foot	*U*	1	3.3811	0.0659
Skull	*U*	1	3.7000	0.0544
Tibia	*t*	102	4.5587	1.4×10^{-5}
Femur	*U*	1	14.8504	0.0001

Subsequent to radiography, all radiographs were scanned, saved as digital images (in JPEG format), and imported into Image J 1.29 software (Rasband 2002; http://rsb.info.nih.gov/ij/). The diameter of a 1-cent coin (19 mm), measured to the nearest 0.01 mm with Mitutoyo digital calipers, was used to calibrate Image J by using the "set scale . . ." function. Image J was then used to measure skull, tibia, and femur lengths (Fig. 1) to the nearest 0.01 mm.

Statistical analysis.—All data were log transformed by using Excel XP software (Microsoft, Redmond, Washington), and statistical analyses were conducted with SYSTAT 10.2 (Wilkinson 2002). Log transformation of growth data linearizes them and is justified because log transformation of Huxley's (1932) power formula for growth also is linearized (Jolicoeur 1963). Hence, log transformation allows for the modeling of exponential growth by using linear methods, such as regression. Sexual dimorphism of pertinent parameters was evaluated before analysis. Log-transformed head–body, tail, hind-foot, skull, tibia, and femur lengths were compared between sexes by using 2-sample *t*-tests, or, when the assumptions of these tests were violated, by using Mann–Whitney *U*-tests. To evaluate sexual size dimorphism at maximum size, the same tests were conducted on these measurements, comparing the 5 largest individuals of each sex. Residuals from reduced major-axis regressions (see below) also were compared by using 2-sample *t*-tests or Mann–Whitney *U*-tests, as well as plotted to visualize sexual differences. Finally, slopes of reduced major-axis regressions were assessed on males and females separately and were compared by using Clarke's (1980) T_{12} statistic. Log-transformed data and reduced major-axis residuals were tested for normality by using Kolmogorov–Smirnov tests, and for homoscedasticity between sexes by using $F_{\max}$-tests. If either normality or homoscedasticity were not supported, the Mann–Whitney *U*-test was employed.

Linearity of each size-proxy candidate was tested by running reduced major-axis regressions against head–body length and against body mass, and plotting the residuals. The same analyses were run on untransformed measures. A scaling relationship was deemed linear if residuals formed a visually random scatter with no apparent patterns. If a point of inflection was found (that is, the size-proxy candidate did not scale linearly with head–body length), then 2 reduced major-axis regressions were calculated on age subsets of the data set delimited by the point of inflection. To test for the objective definition of the point of inflection, data were divided into 2 subsets, with the boundary between those subsets being changed (13, 17, 21, 30, and 50 days). The division that yielded the greatest and most significant difference in slopes was deemed the position of the inflection. Although this approach for identifying the point of inflection does not elucidate how sudden the inflection is and is limited in resolution by the frequency of age sampling, it does indicate at what head–body length the subset data sets differ most, and so indicates the closest approximation of the position of inflection. Clarke's (1980) T_{12} statistic was used to determine whether slopes of reduced major-axis regressions differed significantly for subsets of data. We used all of these approaches to evaluate the relative performance of each variable in representing body size, as envisioned by head–body length and body mass.

Results

Sexual dimorphism.—Mean values of head–body, tail, hind-foot, skull, tibia, and femoral lengths, as well as body mass, do not differ between the sexes (Mann–Whitney *U*-tests; Table 1). These results indicate a general comparability in the ontogenetic series for the sexes, but this is an artifact of comparing means of an ontogenetic series between sexes. However, for the 5 oldest individuals of each sex, males are larger than females in all measures, except femoral length (Table 1).

Significant sexual differences in reduced major-axis residuals were observed for tail, tibia, and femur length, but not for hind-foot and skull length, where differences approached significance (Table 2). In all situations, females had slightly larger relative magnitudes of the measures, indicating that they are relatively, if not absolutely, larger. Subsequent analyses were conducted separately for each sex because both relative and size dimorphism were documented. Nevertheless, general qualitative patterns exhibited by rats and revealed here were consistent between the sexes (Figs. 2 and 3). Specifically, points of inflection and extent of linearity of relationship are comparable for both sexes.

Evaluating linearity of measurements.—Linear scaling of tail, hind-foot, skull, tibia, and femur length relative to head–body length was initially evaluated by including individuals comprising the entire ontogenetic series and by using reduced major-axis regression. Slopes and intercepts, their standard errors, and r^2 values for each regression for each sex are presented in Table 3. Examination of these slopes and their standard errors indicates that none of the variables examined

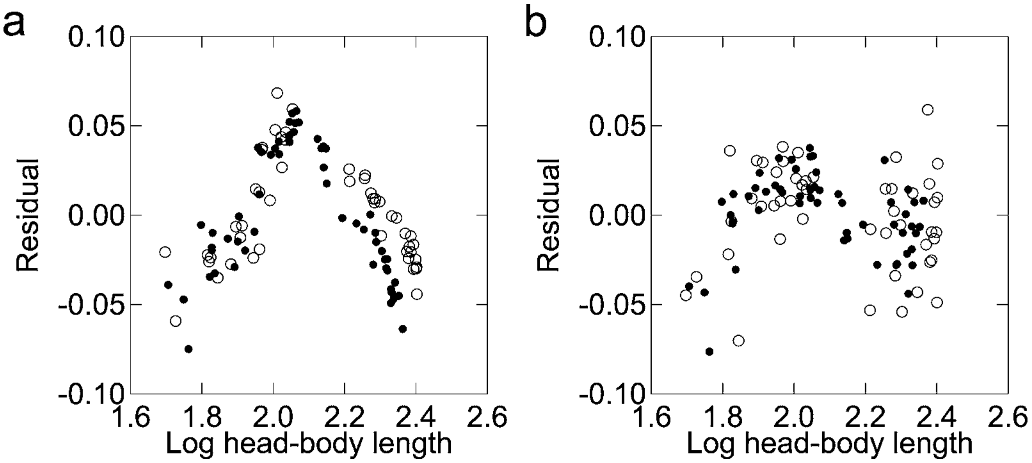

Fig. 2.—Reduced major-axis residuals of a) hind-foot length and b) femoral length plotted against log-transformed head–body length for *Rattus norvegicus*. Residuals on each graph arise from separate regressions for the sexes. Open circles, males; closed circles, females.

grow isometrically relative to head–body length. Skull length grows negatively allometrically, whereas the other dimensions exhibit positive allometry (Table 3).

Examination of residuals for each of these regressions, particularly that for hind-foot length, revealed that residuals are not randomly distributed on the plot, and show a distinct inverted V-shaped trend (Fig. 2a). Such a pattern indicates that hind-foot length data do not scale in a linear manner relative to head–body length. There is a point of inflection at the apex of the V. This same trend is evident, but far less pronounced, for

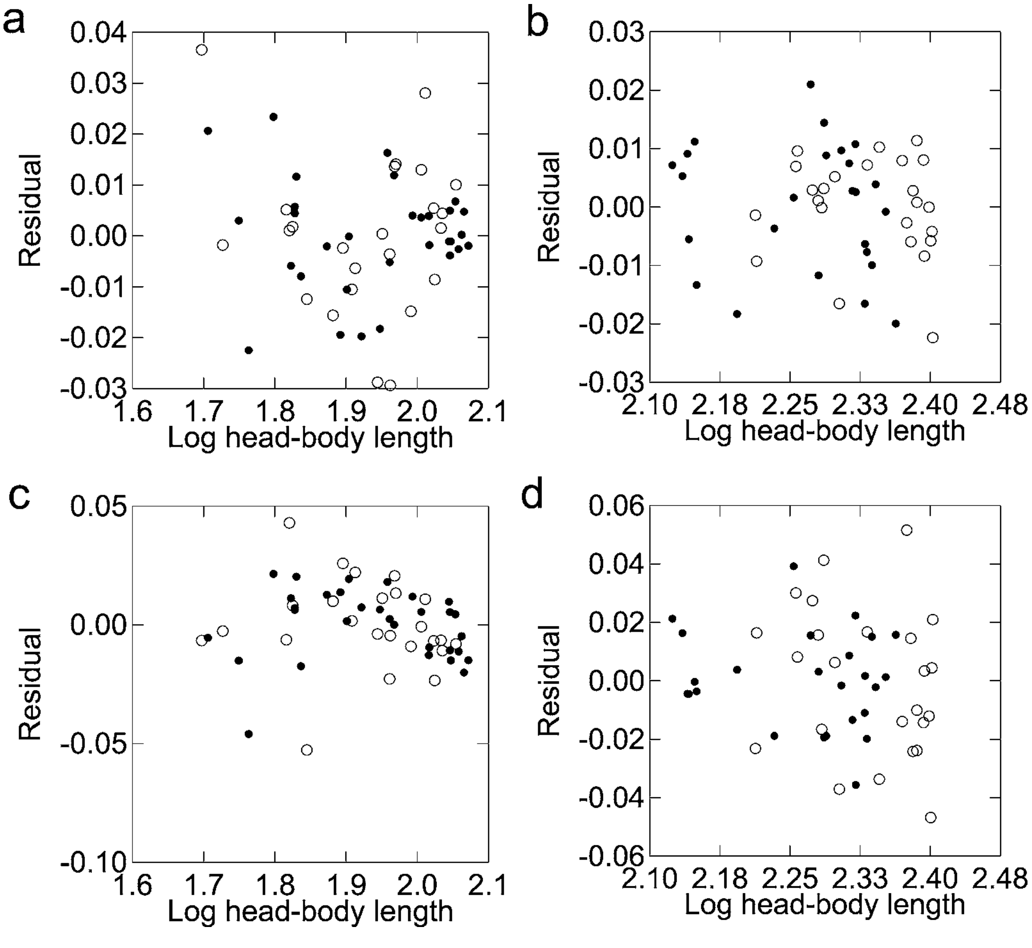

Fig. 3.—Reduced major-axis residuals of a) and b) hind-foot length and c) and d) femoral length plotted against log-transformed head–body length for a) and c) individuals less than 21 days of age and b) and d) more than 21 days of age for *Rattus norvegicus*. Residuals on each graph arise from separate regressions for the sexes. Open circles, males; closed circles, females.

TABLE 3.—Linear scaling of variables to head and body length for *Rattus norvegicus*, showing r^2 values, slopes, intercepts, and standard errors associated with slopes and intercepts (reduced major-axis regression analysis). Regressions include all individuals ($n = 105$).

Variable (lengths)	Sex	r^2	Slope	*SE* slope	Intercept	*SE* intercept
Tail	Male	0.9914	1.7002	0.0227	−1.6852	0.0233
Tail	Female	0.9901	1.7676	0.0234	−1.7925	0.0218
Hind foot	Male	0.9680	1.0570	0.0273	−0.8302	0.0280
Hind foot	Female	0.9379	1.1533	0.0384	−1.0136	0.0357
Skull	Male	0.9732	0.6630	0.0157	0.1044	0.0161
Skull	Female	0.9356	0.7380	0.0251	−0.0465	0.0233
Tibia	Male	0.9849	1.4956	0.0265	−1.9735	0.0272
Tibia	Female	0.9811	1.5836	0.0291	−2.1204	0.0271
Femur	Male	0.9753	1.4045	0.0318	−1.9021	0.0327
Femur	Female	0.9800	1.5535	0.0293	−2.1789	0.0272

TABLE 4.—Linear scaling of variables to head and body length for *Rattus norvegicus*, including only young (<21 days old) or old (>21 days old) individuals, and showing r^2 values, slopes, and intercepts (reduced major-axis regression analysis). Also presented are comparisons between regressions including young and old individuals, using T_{12} statistics, degrees of freedom (*d.f.*), and *P* values (males: young $n = 24$, old $n = 24$; females: young $n = 31$, old $n = 26$).

Variable (lengths)	Sex	Young		Old				
		r^2	Slope	r^2	Slope	T_{12}	*d.f.*	*P*
Tail	Male	0.9605	1.8104	0.9403	1.2987	5.1665	25.56	1.14×10^{-5}
Tail	Female	0.9811	1.9566	0.9664	1.5353	5.5561	27.52	3.22×10^{-6}
Hind foot	Male	0.9649	1.4916	0.9415	0.6332	13.7194	25.34	1.56×10^{-13}
Hind foot	Female	0.9862	1.6403	0.9353	0.5868	18.9705	23.53	9.99×10^{-16}
Skull	Male	0.9769	0.9242	0.8910	0.6511	4.7209	22.28	5.04×10^{-5}
Skull	Female	0.9781	1.0203	0.7842	0.6965	4.0236	22.56	2.74×10^{-4}
Tibia	Male	0.9596	1.8292	0.9219	1.1799	6.2414	24.97	7.91×10^{-7}
Tibia	Female	0.9879	1.9692	0.9801	1.3316	11.5260	27.85	2.05×10^{-12}
Femur	Male	0.9499	1.6879	0.7936	1.5075	1.0935	23.09	1.43×10^{-1}
Femur	Female	0.9762	1.8578	0.9422	1.5222	3.6434	26.12	5.85×10^{-4}

femur length (Fig. 2b), with the point of inflection at the same head–body length as for hind-foot length. Tail, skull, and tibia lengths also exhibit the same pattern with an identically located point of inflection (graphs not shown), but the clarity of the trend is intermediate to that of hind-foot length, where it is extreme, and femur length, where it is moderate. Regression of these variables against log-transformed body mass resulted in identical patterns to those presented above (Fig. 2). Regression against untransformed head–body length resulted in similar patterns, with the residuals forming an inverted V with an inflection point, but more variation was apparent, which obscured this pattern. Use of untransformed body mass also resulted in an nonlinear pattern, but the inverted V transformed into an inverted U, with a beveled inflection. This resulted from the data reaching an asymptote at high body masses and the use of untransformed data, which is not expected to approximate linearity under Huxley's (1932) model. Because of the conservatism of the observed patterns, only results from log-transformed analyses with head–body length as size proxy are presented in detail. These results show patterns most clearly, and are justified given the exponential growth equation and its transformation into a linear equation (Huxley 1932; Ricker 1984).

Performing reduced major-axis regressions on differently delimited subsets of the data resulted in varying differences between the resultant slopes. For example, for hind-foot length, the difference in slopes was lowest when the data were divided into 2 groups at 13 days of age (difference in slope = 0.74) and increased steadily until the point of division was 21 days (a difference of 0.89 for 17 days and 0.96 at 21 days). This difference then decreased again as the point of division continued to increase (0.81 at 30 days and 0.50 at 50 days). The probabilities associated with these differences in slope were always highly significant, peaking at $P = 9.99 \times 10^{-16}$ for the 21-day division. To summarize, the inflection point is best defined and most absolute for hind-foot length. For the other metrics examined, determination of the exact position of the inflection is supported, but less strongly.

When regressions were conducted on subsets of the data, separated by the determined inflection point (120 mm, age ~21 days), plots of residuals against head–body length for pairs of regressions examining hind-foot length (Figs. 3a and 3b), femur length (Figs. 3c and 3d), and all other collected measures (not shown) indicate the desired random scattering. This suggests that subset data sets do scale linearly with head–body length (Sokal and Rohlf 1995). Examination of residuals for males and females (Fig. 3) again shows similar trends between sexes.

Significant differences between each pair of lines (Table 4) are indicated for each sex by comparison of regression slopes between younger and older individuals (separated by the point of inflection). Hence, there is a statistically identifiable inflection point for all of tail, hind-foot, skull, and tibia lengths for both sexes. There is also an inflection for femoral length for females. Only in femoral length for males is there no significant difference between slopes and, therefore, no inflection point (Table 4). Given that none of the measurements studied is an ideal proxy for head-body length for both sexes, examination of probability values associated with each T_{12} statistic allowed us to rank the different variables in order of their suitability for this purpose. The most suitable is femur length (it is ideal for males but somewhat inflected for females), followed by skull, tibia, tail, and finally hind-foot length (Table 4). If probability is used as a measure of suitability in this analysis, then it is important to note that even skull length in females is the only other measure that performs comparably to femur length in the same sex. All other candidates are far worse than this. Tibia and tail length are 4–8 orders of magnitude worse, and hind-foot length, a widely collected standard measure for mammals, is 12 orders of magnitude less representative of head–body length than is femur length across the entire growth trajectory for both sexes.

DISCUSSION

Comparative metrics.—The overall utility of standard measures, and other linear measurements, collected from mammalian specimens was ostensibly questioned by Green and Fekete (1934) in their study of relative growth in mice. Their conclusions are potentially important for studies of mammalian growth, but because most such studies do not incorporate measurements from across the entire postnatal growth period (largely omitting the preweaning period, see below), their implications have not been further assessed or reinvestigated.

We examined several standard measures and candidates for size proxies in *R. norvegicus*, and found that none scale linearly with head–body length or body mass, which are the most comprehensive simple measures of body size. Instead, we found that there is a point of inflection in growth rates for all examined measures (as found by Green and Fekete 1934) that corresponds to the time of weaning (this study). This is especially marked for hind-foot length, and least pronounced for femoral length (where it is absent in males).

As predicted by Green and Fekete (1934), of the 5 measures evaluated, hind-foot length was the worst proxy for body size and femur length was by far the best. Femur length is not subsumed in the measure of head–body length, allowing independent study of vertebrae and other axial structures. It also scaled most linearly with head–body length over the complete ontogenetic series evaluated and so is the best choice for a single measure that can be employed across the size range from neonate to adult. Furthermore, inflection in growth rate at the time of weaning is the least substantial of all evaluated measures, and is absent for males. However, even femur length must be used with caution over the entire postnatal ontogenetic series because there is a statistically significant difference in growth rates (slopes) of the variable between weaned and unweaned individuals in female rats.

Functional correlates of non-linear growth.—The location of the point of inflection relative to size and age of the specimen was similar for all variables evaluated, and correlates with a head–body length of approximately 120 mm and an age of approximately 21 days, the time at which juvenile *R. norvegicus* are weaned (Farris 1949; Fortman et al. 2005; Reichling and German 2000). Although Green and Fekete (1934) noted inflection points in their study of the growth of the mouse, such points of inflection were not all aligned in terms of body size or days of development. Furthermore, Green and Fekete (1934) did not correlate changes in growth trajectories with any biological event, but instead appealed to a somewhat enigmatic mammalian ‘‘metamorphosis.’’ The shift in growth is apparently functionally correlated.

All mammals pass through a transitional weaning period during which they acquire independence from maternal milk as their primary nutritional resource and replace this with alternate food sources (Fortman et al. 2005; Sadleir 1969). Weaning is a major period of transition for young mammals and involves a wide range of behavioral and physiological changes in both the mother and offspring (Martin and Bateson 1988). Changes in growth rate may occur at the time of weaning (Deag et al. 1988) and major changes in biomechanics occur through the weaning period (Jarvis 1991). Norway rats are born blind and hairless, and have closed ears, undeveloped limbs, and a short tail. The eyes do not open until 14–17 days after birth. The 1st molar tooth erupts at 19 days and the 2nd at 21 days (Farris 1949). Thus, over a relatively brief period of about 4–7 days, rat pups make the transition to fully mobile individuals capable of masticating solid foods. The growth period up to the time of weaning thus entails establishing body proportions and structure associated with processing solid foods, as reflected in skull growth parameters, and supporting the body during foraging and other locomotor bouts, as reflected in growth patterns of the limb elements. The functional demands of adult-type locomotor and feeding patterns are accommodated by growth patterns established in the early postnatal and weaning periods, after which growth patterns and rates associated with attaining adult body proportions are established.

Before weaning, growth is mediated through maternal resource partitioning, and may be very rapid (Small 1971), whereas other environmental factors limit growth in weaned individuals (Bergallo and Cerqueira 1994; Reik et al. 2001). Once weaned, mammals forage independently (van Jaarsveld et al. 1988), which increases the energy expenditure devoted to obtaining food, exposes them to higher predation risks, and puts them at higher risk of starvation or dehydration (Cerqueira and Lara 1991; Lu 2003). As a result, relatively less energy is available to devote to growth relative to maintenance in individuals after weaning, and a decrease in growth rates relative to head–body length are expected, and documented herein, in response to differential allocation of available energy (Gaillard et al. 1997). For example, a well-developed appendicular skeleton is a requirement for an independently foraging individual (Levenson 1979; van Jaarsveld et al. 1988) and, as such, resource allocation to the appendicular skeleton is likely preferentially higher before weaning, correlating with the trends seen in growth rate of tibia, hind foot, and femur.

Although weaning is a gradual process, taking 4–7 days (Farris 1949), we observed a very fast transition in growth rate at final weaning (21 days), at least in some measures (especially hind-foot length). Such a phenomenon is at least partially inconsistent with a gradual change in diet and function, but nevertheless correlates very well with final weaning. This suggests that other factors, such as genetic controls, may also be involved in the rapid transition in growth trajectory.

CONCLUSION

We confirm herein that not all potential variables available as comparative metrics for growth perform equally well. Especially noteworthy is the observation that hind-foot length is a particularly poor estimator for the Norway rat, yet is the one skeletally based metric routinely suggested to be taken for mammalian specimens, presumably because of its ease of acquisition. Although we cannot be sure that it performs equally poorly for other mammalian taxa across the entire growth trajectory, we suggest that it be tested further before being applied as a comparative metric. Femur length performed best as a proxy for head–body length and body mass because it scaled the most linearly with those measures over the entire ontogenetic series. However, even femur length is not without systematic bias at least in females, although Green and Fekete

(1934) reported that in the mouse, there is only a single growth phase for this element. When using any of the variables examined in this study as measures of mammalian growth, analyses of pre- and postweaning individuals should be carried out separately. Further, investigations should be conducted to determine whether the phenomena discovered here are widespread among the Mammalia, and should evaluate other potential metrics. Rats are altricial mammals and have a period of time in the nest during which mobility and coordination develop gradually. In this species, and in mice, the observed switch in growth rates coincides with weaning and the rapid assumption of an independent existence. In precocial mammals, however, weaning and the attainment of independent, coordinated locomotion are decoupled, so differential growth rates, if they exist at all, may be expressed quite differently. For example, in precocial mammals, such as the giraffe and other ungulates, free mobility is established essentially at birth, and supplementing the diet with solid foods begins as early as 1 month after birth, although suckling may continue for up to 2 years (Dagg and Foster 1976). Among rodents, many hystricomorphs can consume solid foods within 1 or 2 days of birth and can survive away from the mother after 2 weeks, although they are normally suckled for much longer periods (Kleiman 1974). Thus, like young ungulates, such rodents are precocial, and are fully furred and have their eyes open at birth (Weir 1974). Some species require only 5 days of lactation before they are able to survive independently (Weir 1974). The period when offspring are relatively dependent (Caro 1994) thus varies widely among mammals, and such variance is likely to have major effects on relative growth rates, prenatally and postnatally, of skeletal components that must assume the demands of a free-living existence at relatively different points along their developmental trajectory.

ACKNOWLEDGMENTS

We acknowledge the Natural Sciences and Engineering Research Council of Canada for provision of funds that enabled this research. We thank Mr. D. Apel for help with radiography and recording of measurements, and S. Delannoy and H. Jamniczky for their input and advice. This manuscript was greatly improved by the comments of an anonymous reviewer and, especially, Rebecca German, who kindly made available unpublished data that helped in our interpretations.

LITERATURE CITED

ANDERSON, T. W. 1963. Asymptotic theory of principal component analysis. Annals of Mathematics and Statistics 34:122–148.

ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

BAUER, A. M., A. P. RUSSELL, AND B. D. EDGAR. 1989. Utilization of the termite *Hodotermes mossambicus* (Hagen) by gekkonid lizards near Keetmanshoop, South West Africa. South African Journal of Zoology 24:239–243.

BERGALLO, H. G., AND R. CERQUEIRA. 1994. Reproduction and growth of the opossum *Monodelphis domestica* (Mammalia: Didelphidae) in northeastern Brazil. Journal of Zoology (London) 232:551–563.

BERGMANN, P. J., AND A. P. RUSSELL. 2001. Growth of the original tail in *Anolis grahami*: isometry of the whole is a product of regional differences. Journal of Herpetology 35:232–238.

BEUTTELL, K., AND J. B. LOSOS. 1999. Ecological morphology of Caribbean anoles. Herpetological Monographs 13:1–28.

BOOKSTEIN, F. L. 1997. Morphometric tools for landmark data: geometry and biology. Cambridge University Press, Cambridge, United Kingdom.

CARO, T. M. 1994. Cheetahs of the Serengeti Plains: group living in an asocial species. The University of Chicago Press, Chicago, Illinois.

CERQUEIRA, R., AND M. LARA. 1991. Rainfall and reproduction of cricetid rodents in northeastern Brazil. Pp. 545–549 in Global trends in wildlife management (K. Bobek, K. Perzanowaki, and W. L. Regelin, eds.). Swiat Press, Cracow, Poland.

CLARKE, M. R. B. 1980. The reduced major axis of a bivariate sample. Biometrica 67:441–446.

DAGG, A. I., AND J. B. FOSTER. 1976. The giraffe: its biology, behaviour, and ecology. Van Nostrand Reinhold Company, New York.

DEAG, J. M., A. MANNING, AND C. E. LAWRENCE. 1988. Factors influencing the mother–kitten relationship. Pp. 23–39 in The domestic cat: the biology of its behaviour (D. C. Turner and P. Bateson, eds.). Cambridge University Press, Cambridge, United Kingdom.

DEBLASE, A. F., AND R. E. MARTIN. 1974. A manual of mammalogy with keys to families of the World. Wm. C. Brown Company, Dubuque, Iowa.

FARRIS, E. J. 1949. Breeding of the rat. Pp. 1–18 in The rat in laboratory investigation (E. J. Farris and J. Q. Griffith, eds.). Hafner Publishing Company, New York.

FORTMAN, J. K., II, T. REICHLING, AND R. Z. GERMAN. 2005. The impact of maternal protein malnutrition on pre-weaning skeletal and visceral organ growth in neonatal offspring of *Rattus norvegicus*. Growth, Development and Aging 69:47–60.

GAILLARD, J.-M., D. PONTIER, D. ALLAINE, A. LOISON, J.-C. HERVE, AND A. HEIZMANN. 1997. Variation in growth form and precocity at birth in eutherian mammals. Proceedings of the Royal Society of London, B. Biological Sciences 264:859–868.

GARDE, J. M., AND T. M. ESCALA. 1996. Morphometric characteristics and relative growth of the water vole, *Arvicola sapidus* (Rodentia, Arvicolidae). Folia Zoologica 45:227–236.

GERMAN, R. Z. 2004. The ontogeny of sexual dimorphism: the implications of longitudinal vs. cross-sectional data for studying heterochrony in mammals. Pp. 11–23 in Shaping primate evolution (F. Anapol, R. Z. German, and N. G. Jablonski, eds.). Cambridge University Press, Cambridge, United Kingdom.

GIBSON, A. T., S. CARNEY, E. CAVAZZONI, AND J. K. H. WALES. 2000. Neonatal and post-natal growth. Hormone Research 53:42–49.

GREEN, C. V., AND E. FEKETE. 1934. Differential growth in the mouse. Journal of Experimental Zoology 66:351–370.

HOYING, K., AND T. H. KUNZ. 1998. Variation in size at birth and post-natal growth in the insectivorous bat *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). Journal of Zoology (London) 245:15–27.

HUXLEY, J. W. 1932. Problems in relative growth. Cambridge University Press, London, United Kingdom.

JARVIS, J. U. M. 1991. Reproduction of naked mole-rats. Pp. 384–425 in The biology of the naked mole-rat (P. W. Sherman, J. U. M. Jarvis, and R. D. Alexander, eds.). Princeton University Press, Princeton, New Jersey.

JOLICOEUR, P. 1963. The multivariate generalization of the allometry equation. Biometrics 19:497–499.

JUNGERS, W. L., AND R. Z. GERMAN. 1981. Ontogenetic and interspecific skeletal allometry in nonhuman primates: bivariate versus multivariate analysis. American Journal of Physical Anthropology 55:195–202.

Kleiman, D. G. 1974. Patterns of behaviour in hystricomorph rodents. Pp. 171–209 in The biology of hystricomorph rodents (I. W. Rowlands and B. J. Weir, eds.). Symposia of the Zoological Society of London 34:1–576.

Lammers, A. R., H. A. Dziech, and R. Z. German. 2001. Ontogeny of sexual dimorphism in *Chinchilla lanigera* (Rodentia: Chinchillidae). Journal of Mammalogy 82:179–189.

Levenson, H. 1979. Sciurid growth rates: some correlations and additions. Journal of Mammalogy 60:232–235.

Lu, X. 2003. Postnatal growth of skull linear measurements of Cape hare *Lepus capensis* in northern China: an analysis in an adaptive context. Biological Journal of the Linnean Society 78:343–353.

Martin, P., and P. Bateson. 1988. Behavioural development in the cat. Pp. 9–22 in The domestic cat: the biology of its behaviour (D. C. Turner and P. Bateson, eds.). Cambridge University Press, Cambridge, United Kingdom.

Moscarella, R. A., and M. Aguilera. 1999. Growth and reproduction of *Oryzomys albigularis* (Rodentia: Sigmodontinae) under laboratory conditions. Mammalia 63:349–362.

Moss, M. L., and M. J. Baer. 1956. Differential growth of the rat skull. Growth 20:107–120.

Myers, M. F. 1998. Morphometry of the limb skeleton of *Anolis garmani*: practical and theoretical implications. M.S. thesis, University of Calgary, Calgary, Alberta, Canada.

Rasband, W. 2002. Image J version 1.29. National Institutes of Health, Bethesda, Maryland.

Reichling, T. D., and R. Z. German. 2000. Bones, muscles and visceral organs of protein-malnourished rats (*Rattus norvegicus*) grow more slowly but for longer durations to reach normal final size. Journal of Nutrition 130:2326–2332.

Reik, W., K. Davies, W. Dean, G. Kelsey, and M. Constancia. 2001. Imprinted genes and the coordination of fetal and postnatal growth in mammals. Novartis Foundation Symposium, Wiley, Chichester, United Kingdom 237:19–35.

Reiss, M. J. 1991. The allometry of growth and reproduction. Cambridge University Press, Cambridge, United Kingdom.

Ricker, W. E. 1984. Computation and uses of central trend lines. Canadian Journal of Zoology 62:1897–1905.

Sadleir, R. M. F. S. 1969. The ecology of reproduction in wild and domestic mammals. Methuen, London, United Kingdom.

Small, G. L. 1971. The blue whale. Columbia University Press, New York.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. 3rd ed. W. H. Freeman and Company, New York.

van Jaarsveld, A. S., J. D. Skinner, and M. Lindeque. 1988. Growth, development and parental investment in the spotted hyaena, *Crocuta crocuta*. Journal of Zoology (London) 216:45–53.

Weir, B. J. 1974. Reproductive characteristics of hystricomorph rodents. Pp. 265–301 in The biology of hystricomorph rodents (I. W. Rowlands and B. J. Weir, eds.). Symposia of the Zoological Society of London 34:1–576.

Wilkinson, L. 2002. SYSTAT: the system for statistics. SYSTAT Inc., Chicago, Illinois.

Submitted 11 August 2004. Accepted 9 March 2005.

Associate Editor was Enrique P. Lessa.