

Growth of Skeletal Components in the Young Squirrel Monkey (*Saimiri sciureus boliviensis*): A Longitudinal Experiment

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ABSTRACT A functional skeletal criterion, as an extension of the van der Klaauw's cranial theory, was adopted in the present study. The null hypothesis tested was: "The major skeletal components of the platyrrhine body grow linearly, regardless of their functional dependence to different demands." The acceptance of the hypothesis will imply that all *Saimiri* skeletal growth may be satisfactorily explained by independent variables in a single equation. The rejection will suggest that such skeletal growth patterns have to be explained by variables in several different equations, and perhaps these equations may vary with the effect of sex and undernutrition. Control and undernourished squirrel monkeys were radiographed monthly for 2 years; they were also measured; and their volumetric and morphometric neurocranial, facial, and pelvic indices were calculated. The curves that best described each of the 24-point sequences were obtained. Three main growth patterns were observed: 1) *Simple linear* (femur length for all groups, and pelvic index for control and undernourished females), for which the simple regression equation explained more than 95% of the variation; 2) *Complex linear* (pelvic index for control and undernourished males, and neurocranial and facial indices for all of the groups), for which more than 95% of the variation was explained by one of the four four-function type equations; and 3) *Noncorrelated with age* (neurofacial index for undernourished males, and pelvifemoral index for control females and undernourished males and females), which showed nonsignificant correlations with respect to age. The food intake and the oscillations of the environmental temperature might help to explain the undulating growth trajectory observed in the complex linear components. *Am J Phys Anthropol* 112:57-68, 2000. © 2000 Wiley-Liss, Inc.

Longitudinal studies are a useful way to understand how humans and other mammals grow from birth to adulthood. However, due to their high cost in money and time, such studies are not frequently employed in comparative and experimental auxology. Rather, they are replaced by the faster, easier, and less expensive cross-

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tional studies. The cross-sectional information, however, is far from being sufficiently accurate. The main problem with cross-sectional data is that the comparisons are between the means from *different* individuals at *different* age stages. The main advantage of the longitudinal method is that a given individual may act as his own control at different growth stages. We agree with Tanner (1988) that, although longitudinal studies have to be accompanied by cross-sectional surveys and animal experimentation not to become sterile, longitudinal methods are indispensable in growth research. The "purely longitudinal" method is the best variant of longitudinal growth studies, because this approach requires all individuals to share the same birthday, and thus they are all measured simultaneously. This is feasible in experimental animals, in which, apart from age, all independent variables can be kept equally controlled throughout the analysis.

Morphologists can start researching on craniology from two opposite paradigms. The typological one considers the skeleton from a merely descriptive point of view. The other paradigm is not static and holds some independence in the growth behavior of skeletal components due to the functional demands imposed by a related organ, tissue, and/or cavity. The latter is the basic conception of the functional cranial theory postulated by Klaauw (1948–1952) in mammals and developed by Moss and Young (1960) and Moss (1973, 1979) for human and nonhuman primates. The skull can be considered as composed of many functional components, which display relative independence among each other. The variation of a functional cranial component (FCC) reflects the demands imposed by the growth of different related structures of the head. Each FCC is composed of a functional matrix (FM) and a skeletogen unity (SKU). The FM includes all the elements (organs, tissues, nerves, functional spaces, etc.) necessary to perform a function. The SKU supports and protects biomechanically its specific FM (Moss, 1973, 1979), and should be the object of measurement when osteologists go beyond a mere descriptive study. This conception is specially useful for study-

ing cranial structures (Moss and Young, 1960; Pucciarelli et al., 1990), though there is no reason for not extending it to the remaining parts of the skeleton. A good example is the recent cross-sectional study made by Humphrey (1998) on growth in humans.

According to Tanner (1988), fitting curves in growing individuals may be an actual muddle. Stature, for example, is composed of several different osseous individualities measured by height, foot, leg, thigh, pelvis, vertebrae, and skull height. Each of these has its own modality of growth. Fitting curves may indeed be impossible if one has a classical conception of the skeleton, but it is feasible when the functional criterion is extended to the skeletal frame. If specific curves are adjusted to each growing component, we will explain each functional behavior by its best fitted curve. Each functional component may be measured by specific variables and indices which assure a degree of homogeneity in growth behavior (Pucciarelli et al., 1990; Pucciarelli and Neves, 1992; Dressino and Pucciarelli, 1997). In the present study, the *Saimiri* skeleton was studied from this functional point of view. The growth of the neurocranium, face, and pelvis was measured by functional indices, together with indicators of linear (femur length) and three-dimensional (body weight) growth modalities.

The nearer to humans the taxonomic distance of the experimental animals, the more useful the experiment to understand human growth processes. In this respect, the squirrel monkey (*Saimiri sciureus*) is specially useful in experimental studies, since, according to several authors (Ameghino, 1909; Biegert, 1963; Petit-Maire, 1971; Petit-Maire et al., 1974), many morphological resemblances between *Saimiri* and *Homo* genera permit generalizing our findings to humans more than would findings in other New World monkeys. Several mixed-longitudinal (Leigh, 1996), longitudinal (Hamano et al., 1990; Garber and Leigh, 1997), and purely longitudinal (Dressino, 1991; Dressino and Pucciarelli, 1997) studies on growth in *Saimiri* species were made during the past few years.

The present purely longitudinal study was designed to test the null hypothesis:

"All major skeletal components of the platyrrhine body grow linearly, regardless of the functional dependence on different demands." If the null hypothesis is accepted, femur length and the three functional components studied here have to be explained by a single equation. If true, the conclusion would be that the platyrrhine skeleton is genetically hardwired and growth changes due to the environment affect it linearly. If the hypothesis is rejected, the conclusion will point out that different growth patterns in the skeletal frame do exist and the environment will act differentially on them. This study sets the three following objectives as its goals: 1) to find the equations that best describe the growth of the different functional skeletal components in *Saimiri* of both sexes; 2) to establish whether the equations that fit best in controls are the same as in undernourished animals; and 3) to infer if there is a relationship between *Saimiri* growth trends and environmental conditions of the tropical forest.

MATERIALS AND METHODS

Ten male and ten female platyrrhine monkeys (*Saimiri sciureus boliviensis*) were born and grown in captivity at the Centro Argentino de Primates (CAPRIM). After weaning the males weighed, on average, 463.2 ± 24.1 g and the females 412.7 ± 35.7 g. The animals were transferred to the Centro de Investigaciones en Genética Básica y Aplicada (CIGEB), and placed in individual cages measuring $60 \times 60 \times 60$ cm. They were fed ad libitum on a 20% protein semisynthetic diet. Each animal received a daily supplement of 40 g of fresh orange, and 5 ml of a 50% glucose fat-free milk water solution. This supply lasted until the end of the adaption period (1 year of age). The animals were periodically tested and prevented from developing parasitism and other illnesses. When the animals were 12 months old, they were rearranged in four groups of five: a) *control males* and b) *control females* received the 20% protein semisynthetic diet ad libitum, while c) *undernourished males* and d) *undernourished females* received a low-protein (10%) semi-

synthetic diet ad libitum (see Dressino and Pucciarelli, 1997, for details).

Two radiographs, one in strict later-lateral view and the other in strict dorsi-ventral view, were taken per animal/month, from the 13th to the 36th month of age. For this purpose, a Siemens Heliophos 4 from the Servicio de Diagnóstico por Imágenes, with 240 mA and 125 Kv of power, was employed. Shoots were regulated at 100 mA; 0.02 seg; 40–50 Kv (according to the age of the animal). A 110cm focus-film (AGFA 18×24 cm) distance was used to reduce the magnification effect, calculated as: $MgC = B_x/A_x$; where MgC = magnification coefficient, A_x = variable measured on the 24th month radiograph; and B_x = the same variable measured on the skull (Dressino and Pucciarelli, 1997). Data from the present study were multiplied by a $MgC = 0.94$ to get the actual value.

In the later-lateral view, the following measurements were made: neurocranial length (Nl), from nasion to opisthocranium; neurocranial height (Nh), from basion to bregma; face length (Fl), from prosthion to posterior nasal spine; face height (Fh), from nasion to gnathion; pelvic length (Pl), the maximum anterior-posterior distance measured perpendicularly to the vertebral column; pelvic height (Ph), from the highest point of the iliac crest to the lowest point of the pubis, and femur length (Fel), maximum length of the femur (parallel to the caliper). In the dorsi-ventral view, the following measurements were made: neurocranial width (Nw), bi-aurion distance; face width (Fw), bi-zygomatic distance; and pelvis width (Pw), maximum distance between the iliac crests. The following functional indices were calculated:

Neurocranial index (Ni)

$$= 100 \sqrt[3]{N} * Nw * Nh$$

Facial index (Fi) = $100 \sqrt[3]{F} * Fw * Fh$

Pelvic index (Pi) = $100 \sqrt[3]{P} * Pw * Ph$

Neurofacial index (NFi) = $100 * Ni/Fi$

Pelviofemoral index (PFi) = $100 * Pi/Fel$

TABLE 1. One-sample Kolmogorov-Smirnov (K-S) statistics for testing normality of the frequency distributions¹

	Control				Undernourished			
	Male		Female		Male		Female	
	DN	P	DN	P	DN	P	DN	P
Body weight	0.148	0.617	0.148	0.669	0.135	0.776	0.118	0.895
Femur length	0.127	0.791	0.163	0.544	0.128	0.114	0.198	0.305
Neurocranial length	0.138	0.699	0.138	0.699	0.092	0.975	0.099	0.956
Neurocranial width	0.163	0.494	0.161	0.512	0.221	0.166	0.188	0.321
Neurocranial height	0.219	0.174	0.219	0.174	0.102	0.944	0.119	0.846
Facial length	0.127	0.791	0.127	0.791	0.154	0.567	0.153	0.575
Facial width	0.142	0.670	0.142	0.670	0.146	0.633	0.142	0.668
Facial height	0.103	0.938	0.103	0.938	0.132	0.748	0.138	0.698
Pelvic length	0.119	0.843	0.119	0.843	0.195	0.283	0.150	0.596
Pelvic width	0.152	0.582	0.152	0.582	0.171	0.433	0.154	0.571
Pelvic height	0.114	0.882	0.114	0.882	0.160	0.519	0.085	0.990
Neurocranial index	0.133	0.787	0.233	0.146	0.177	0.443	0.111	0.927
Facial index	0.100	0.972	0.156	0.601	0.198	0.306	0.126	0.839
Pelvic index	0.232	0.147	0.101	0.979	0.176	0.447	0.112	0.925

¹ DN, result of K-S test; P, statistical probability. $P > 0.05$ means that the frequency distribution is symmetric.

The femur length was used as an indicator of growth in stature. The first three indices are called volumetric, since they detect size plus shape changes (Pucciarelli et al., 1990); they were expressed as the cubic root in order to compare the three-dimensionally measured components with chronological age. The same procedure was followed for body weight. The last two indices are called morphometric, since they detect only shape changes in terms of linear shift (Pucciarelli et al., 1990): the neurofacial index measures growth linearity between the neurocranium and the face, while the pelviofemoral index does so between the pelvis and the femur.

Food intake and water consumption were estimated per animal/day. The monthly average values for maximum, medium, and minimum temperature of the animal room were also calculated. Humidity was assured with a $1.0 \times 0.5 \times 0.5$ m metallic reservoir permanently filled with water. In this way the environment was wetter when the temperature increased and vice-versa. These values, together with body weight, were employed as independent variables in the multiple regression analyses.

Differences in body weight at the beginning of the experiment fluctuated between 425 g and 490 g in males, and 380 g and 455 g in females, i.e., by no more than 15% and 20%, respectively. The frequency distributions were tested by the one sample Kolmogorov-Smirnov (K-S) test. Results ranged from DN = 0.085 in pelvic height of under-

nourished females to DN = 0.233 for neurocranial index of control females. These results showed that the variables were normally distributed (Table 1).

Correlation tests, and simple and multiple regressions, were performed with the Systat 7.0 statistical program. Curve fitting procedures were carried out by the Table-Curve 2D program (Jandel, 1994).

RESULTS

The monthly mean and standard deviation values for body weight and femur length in male and female control and malnourished animals are shown in Tables 2 and 3, respectively.

Simple linear equation fitting

The constant values for adjusting each component to the simple linear $y = a + bx$ equation are shown in Table 4. In four comparisons (neurofacial index in undernourished males and pelviofemoral index in all except control males), there were nonsignificant F_m values. Consequently, the simple regression model was invalidated in those cases, and residual values were not registered. The determination coefficient (r^2) explained more than 95% of the variation in femur length for all the groups, and in the pelvic index for control and undernourished females (Fig. 1). The neurocranial and facial indices in the four samples, the pelvic index in males, the neurofacial index in control males and control and undernourished fe-

TABLE 2. Descriptive statistics for body weight and femur length in male and female controls¹

Age (months)	Males				Females			
	Body weight (g)		Femur length (mm)		Body weight (g)		Femur length (mm)	
	X	SD	X	SD	X	SD	X	SD
13	504.4	22.1	66.2	2.8	509.7	37.4	67.3	2.9
14	516.3	24.1	67.1	2.9	515.4	38.7	68.1	2.8
15	527.7	24.0	67.8	2.8	520.8	38.5	68.7	3.1
16	538.5	21.9	68.6	2.8	525.9	38.8	69.4	2.9
17	548.9	20.3	69.4	2.8	530.7	38.9	70.0	3.0
18	558.9	22.2	70.0	2.9	535.3	38.6	70.5	3.2
19	568.5	22.6	70.7	2.9	539.6	38.4	71.2	3.1
20	577.8	25.5	71.4	2.9	543.8	39.0	71.7	3.1
21	586.8	25.2	72.0	3.0	547.8	38.5	72.2	3.0
22	595.5	26.0	72.6	3.0	551.7	39.2	72.7	3.0
23	603.9	28.4	73.1	3.0	555.4	39.3	73.0	3.3
24	612.0	28.8	73.6	3.0	558.9	39.7	73.7	3.2
25	620.0	29.3	74.2	3.0	562.4	39.9	74.2	3.2
26	627.7	28.9	74.5	3.1	565.7	40.4	74.6	3.4
27	635.2	29.4	75.2	3.2	568.9	41.6	75.1	3.7
28	642.5	29.2	75.7	3.2	572.0	42.7	75.3	3.0
29	649.7	26.3	76.2	3.2	575.1	43.1	75.8	3.6
30	656.7	30.7	76.6	3.2	578.0	43.0	76.3	3.3
31	663.5	28.4	77.2	3.2	580.9	43.1	76.6	3.2
32	670.2	29.3	77.5	3.2	583.7	42.0	76.9	3.3
33	676.3	31.2	77.8	3.3	586.4	42.9	77.3	3.7
34	683.1	27.4	78.3	3.3	589.0	42.4	77.6	3.1
35	689.4	27.9	78.7	3.3	591.5	43.2	77.9	3.3
36	695.6	27.2	79.1	3.3	594.1	44.4	78.0	3.4

¹ X, mean values; SD, standard deviations.TABLE 3. Descriptive statistics for body weight and femur length in male and female undernourished animals¹

Age (months)	Males				Females			
	Body weight (g)		Femur length (mm)		Body weight (g)		Femur length (mm)	
	X	SD	X	SD	X	SD	X	SD
13	492.4	29.2	65.9	3.5	397.5	31.8	63.5	2.7
14	489.2	33.9	66.4	3.4	399.9	33.3	64.1	2.7
15	486.3	31.2	66.7	3.6	402.4	35.1	64.6	2.8
16	483.7	27.7	67.0	3.5	404.6	34.9	65.1	2.8
17	481.1	27.4	67.7	3.6	406.8	35.5	65.6	2.8
18	478.8	26.1	68.0	3.5	408.9	36.8	66.1	2.9
19	476.6	23.6	68.3	3.6	410.8	36.3	66.4	2.8
20	474.4	26.4	68.7	3.6	412.6	36.7	66.5	2.8
21	472.5	25.9	69.0	3.6	414.4	37.8	67.3	2.9
22	470.6	26.3	69.4	3.6	416.1	37.5	67.6	2.7
23	468.8	26.2	69.7	3.7	417.7	37.6	68.0	2.9
24	467.1	27.3	69.9	3.7	419.2	38.4	68.4	2.9
25	465.4	28.1	70.1	3.7	420.7	39.4	68.6	2.9
26	463.9	29.5	70.5	3.7	422.2	39.5	69.0	3.0
27	462.4	29.6	70.7	3.7	423.6	38.7	69.3	3.3
28	460.9	29.5	71.0	3.8	424.9	41.2	69.7	3.1
29	459.5	28.0	71.3	3.8	426.2	38.8	69.9	2.9
30	458.1	30.2	71.4	3.7	427.5	39.4	70.1	2.8
31	456.9	29.4	71.7	3.8	428.7	38.8	70.4	3.0
32	455.7	26.1	71.9	3.7	429.9	38.1	70.8	3.1
33	454.5	26.0	72.1	3.3	431.0	36.5	71.1	3.3
34	453.3	26.7	72.4	3.8	432.1	34.8	71.3	3.0
35	452.2	25.9	72.6	3.8	433.2	34.2	71.5	3.2
36	451.1	24.2	72.7	3.6	434.3	33.3	71.8	3.5

¹ X, mean values; SD, standard deviations.

TABLE 4. Bivariate analysis for femur length and indices¹

Equation and group	Regression parameters						ANOVA		
	<i>r</i>	<i>r</i> ²	<i>a</i>	<i>t_a</i>	<i>b</i>	<i>t_b</i>	<i>F_m</i>	RSS	RMS
Equation: $Y = a + bx$									
Control males									
Femur length	0.995	99.0	64.4	169.2**	0.57	37.9**	1,435.9**	5.66	0.26
Neurocranial index	0.720	51.8	37.9	557.1**	0.06	22.1**	490.8**	0.18	0.01
Facial index	0.840	70.6	30.9	258.0**	0.09	19.3**	370.5**	0.56	0.03
Pelvic index	0.921	84.8	23.8	125.4**	0.14	18.7**	350.8**	1.41	0.06
Neurofacial index	0.878	77.1	81.7	285.9**	0.10	8.6**	74.2**	2.76	0.13
Pelviofemoral index	0.772	59.6	36.8	98.4**	-0.08	-5.7**	59.9**	0.71	0.56
Control females									
Femur length	0.996	99.2	65.9	205.6**	0.51	40.1**	1,609.6**	4.01	0.18
Neurocranial index	0.775	60.1	37.0	133.1**	0.07	5.9**	35.1**	3.02	0.40
Facial index	0.931	86.7	29.4	312.4**	0.11	28.7**	822.0**	0.93	0.04
Pelvic index	0.998	99.6	25.6	170.4**	0.19	31.9**	1,014.9**	0.88	0.04
Neurofacial index	0.680	46.2	80.0	123.0**	0.11	4.3**	18.6**	1.13	0.05
Pelviofemoral index	-0.245	6.0	39.0	121.9**	-0.02	-1.2	1.5		
Undernourished males									
Femur length	0.977	95.5	65.0	140.7**	0.36	20.0**	397.9**	8.34	0.38
Neurocranial index	0.652	42.5	36.7	97.6**	0.10	6.8**	46.3**	5.52	0.25
Facial index	0.741	40.7	29.6	106.7**	0.09	8.7**	75.0**	3.01	0.14
Pelvic index	0.753	56.7	24.0	195.7**	0.06	12.3**	151.8**	0.59	0.03
Neurofacial index	0.341	11.6	80.7	144.7**	0.04	1.7	2.9		
Pelviofemoral index	-0.351	12.3	35.0	59.9**	-0.04	-1.7	0.1		
Undernourished females									
Femur length	0.981	96.2	62.8	149.0**	0.40	22.7**	516.4**	7.86	0.36
Neurocranial index	0.667	44.5	36.3	164.2**	0.09	10.8**	116.2**	1.90	0.09
Facial index	0.864	74.7	28.8	186.2**	0.11	17.4**	302.2**	0.93	0.04
Pelvic index	0.994	98.8	22.2	264.8**	0.17	50.9**	2,591.3**	0.27	0.01
Neurofacial index	0.570	32.5	79.9	168.2**	0.06	3.3**	10.6**	1.12	0.05
Pelviofemoral index	0.081	0.7	35.8	84.4**	0.02	0.8	0.7		

¹ *r*, correlation; *r*², determination coefficient; *a*, intercept; *b*, slope; *F_m*, validity of the model; RSS, residual sum of squares; RSM, residual mean of squares; ***P* ≤ 0.01.

males, and the pelviofemoral index in control males, are all partially explained by the simple regression equation. The unexplained fraction of the variation ranged from 13% (facial index in control females) to 67% (neurofacial index in undernourished females).

Tetra function equation type fitting

The components in which more than 5% of the variation was not explained by simple regression were fitted by one of the four four-function equations with intercept of the type $y = a + bx + cf1(x) + df2(x) + ef3(x)$ (Table 5; Figs. 2, 3). The adjustment was defined by the determination coefficient (*r*²), and by both the variance analysis (*F_m*) and the standard error (*SE_m*) of the model. The highly significant *F_m* values assessed the validity of the regression model in all comparisons: the smallest *F_m* was 169.1 (*P* < 0.01), for the pelvic index in undernourished males; and the greatest one was 1554.4 (*P* < 0.01), for the facial index in undernourished females.

The variation fraction explained by the curves ranged from 98.0% to 99.7%. The unexplained variation was 1.3 % on average. The adjusted standard errors ranged from 0.05 (neurocranial index in control males) to 0.12 (pelvic index in control males), and are low enough to reject any significance of the residuals.

Multiple regression

The multiple regression tests showed which of the independent variables (factors) acted on the patterns described by the four-function equations (Tables 6, 7). The results in Table 7 show the validity of the model through the highly significant (*P* < 0.01) *F_m* values. On average, the model explained more than 99% of the variation, since the determination coefficient range is 0.994 (neurocranial index) to 0.997 (pelvic index). Six of the seven tested factors had (except for age in neurocranial index) highly significant (*P* < 0.01) influence on old indices. Water consumption was of lesser but signif-

femur length in control females

equation $y=a+bx$

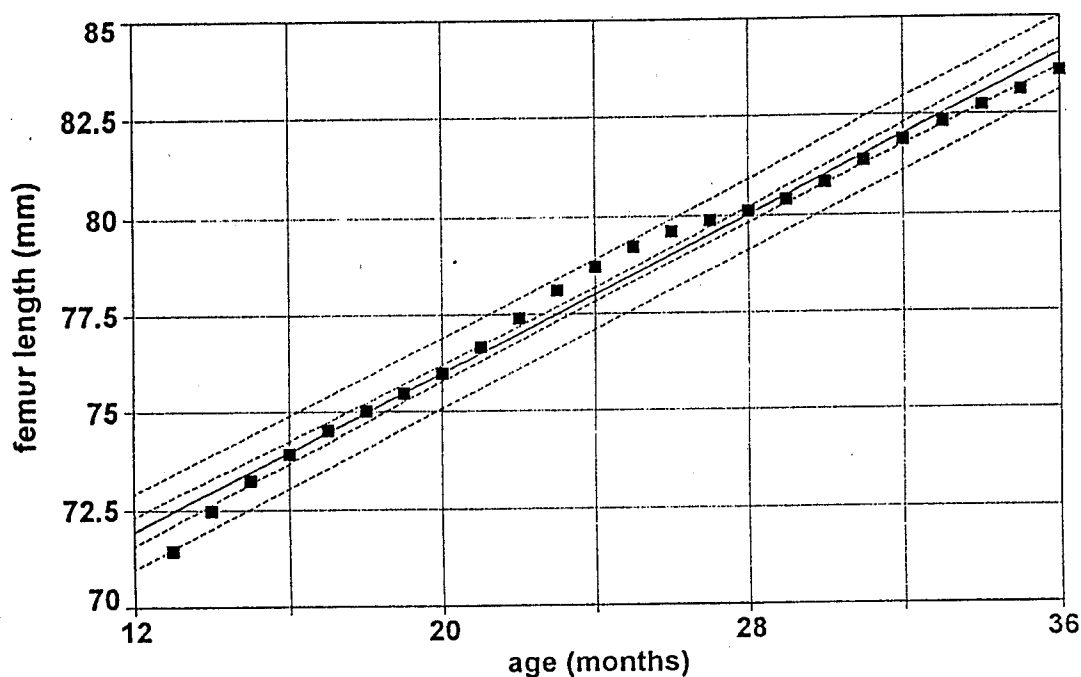


Fig. 1. Example of simple linear growth in control females. The central straight line means that growth explained more than 98% of the variation in femur length. The proximal lines are the confidence intervals. The lateral ones limit the prediction intervals.

icant ($P < 0.05$) influence in all of the comparisons (Table 6).

DISCUSSION

There is consensus about the difficulty of fitting linear equations to biological data (Koops, 1986; Jolicoeur and Pirlot, 1988; German et al., 1994). This is true not only for simple regressions but also for more complex linear relationships. The main problem stems from the fact that growth is neither a constant, nor an even or an infinite process. It has a starting point (conception, birth), uneven velocity (growth spurts), and asymptotic trends towards the end of the growth period. Because of this complexity, nonlinear equations are employed in the study of long-lasting growth spans in mammals with monosexual or bisexual spurts of adolescence. Nonlinear exponential (Hiyaoka et al., 1989; German et al., 1994); logistic

(Pearl, 1925; Bock and Thissen, 1976; Preece and Baines, 1978; Lebeau et al., 1986; Jolicoeur and Pirlot, 1988; Tanner, 1988; Hiyaoka et al., 1989); asymptotic (Jolicoeur et al., 1988, 1992; Kanefuji and Shohoji, 1990; Humphrey, 1998); and Lowess (Cleveland, 1979; Cleveland and Devlin, 1988; Efron and Tibshirani, 1991; Leigh, 1992, 1994, 1996) regression models, among others, have been successfully employed for studies in human and nonhuman primates.

An exception can be made in favor of the linear models. When short periods of growth are studied in genera such as *Saimiri*, which does not display a plain growth spurt in adolescence (Leigh, 1996), the linear models are suitable and easier to interpret than the nonlinear ones. Two main restrictions, however, have to be considered. First, the linear equations define a line that extends infinitely in both directions. No mat-

TABLE 5. Components of growth fitted by complex linear equations¹

Group and equation	ANOVA			Regression parameters				
	(r ²)	SE _m	F _m	a	b	c	d	e
Control males, equation: $Y = a + bx + c\frac{x}{\ln x} + \frac{d}{\ln x} + \frac{e}{x}$								
Neurocranial index	99.0	0.05	468.8	14,640.9	173.1	-1,049.4	-44,287.8	74,533.6
Facial index	98.8	0.08	358.5	24,557.2	291.5	-1,766.7	-74,328.1	53,523.8
Pelvic index	98.9	0.12	396.2	23,350.7	271.8	-1,653.9	-71,011.9	119,732.5
Control females, equation: $Y = a + bx + cx^2\sqrt{x} + dx^3 + ee^{-x}$								
Neurocranial index	98.0	0.10	214.9	31.8	0.8	-0.0	0.0	-0.0
Facial index	98.3	0.11	275.5	26.4	0.5	-0.0	0.0	-0.0
Undernourished males, equation: $Y = a + bx + cx\sqrt{x} + \frac{d}{\ln x} + \frac{e}{x}$								
Neurocranial index	99.3	0.08	715.6	6,523.7	-57.4	4.3	-23,103.4	39,872.4
Facial index	98.8	0.09	395.8	4,939.9	-43.0	3.2	-17,516.7	30,284.7
Pelvic index	98.2	0.08	169.1	-1,486.5	14.1	-1.1	5,352.5	-9,213.1
Undernourished females, equation: $Y = a + bx + cx\sqrt{x} + dx^2\ln x + e\frac{x}{\ln x}$								
Neurocranial index	98.0	0.11	226.3	7,883.7	1,557.6	-85.8	0.6	-4,802.6
Facial index	99.7	0.05	1,554.4	3,162.3	619.1	-33.8	0.2	-1,913.8

¹ The components of growth were fitted by the four four-function (b, c, d, e) standard linear equations with intercept (a), of the type $y = a + bx + cf1(x) + df2(x) + ef3(x)$, with determination coefficient (r²), and ANOVA standard error (SE_m), and significance for the model (F_m).

ter how high or low a value of X is proposed, the equation can predict a Y value. This assumption is rarely reasonable in biological data. Nevertheless, we can preserve the model by employing the predictors of the model only within the range of X values defined by the experiment (Motulsky, 1995). Second, the relationship between X and Y is usually employed not to depict the best possible fit, but to know which proportion of the variation can be explained by age as an independent variable. In these circumstances, a simple regression equation has been successfully employed in previous studies on *Saimiri* (Hamano et al., 1990; Dressino, 1991; Dressino and Pucciarelli, 1997, 1999).

Neural structures such as the brain and the eyes show fast early growth, with the structures approaching adult size during childhood. The body organs, however, follow general somatic trends and reach adult size after puberty (Humphrey, 1998). These patterns are observed in the results obtained in the present study. The growth of *Saimiri* skeletal functional components was described by three different patterns. 1) The *simple linear* one comprised components whose variability was entirely explained (r² ≥ 95%) by the $Y = a + bx$ equation. These components were femur length in control and undernourished males and fe-

males, with the highest regression slopes (b_x = 0.46), and the pelvic index in control and undernourished females, with medium slope values (b_x = 0.18). 2) The *complex linear* pattern involved components with an average of 40.8% of the variation unexplained by the simple regression, with the smallest regression slopes (b_x = 0.09). The highest percentages of explanation (r² ≥ 95%) were obtained by four four-function standard linear equations of the type: $y = a + bx + cf1(x) + df2(x) + ef3(x)$. Each equation described the growth of the components from one specific group. Consequently, the components are genetically (sex) and environmentally (nutrition) influenced (Table 5; Figs. 2, 3). 3) The *noncorrelated with age* pattern was reserved for morphometric indices that test the linearity of growth between the components. Hence, these indices were not included in the fitting of complex linear equations. Their nonsignificant simple regression models stated, e.g., that a linear relationship of growth exists between the pelvis and the femur. On the other hand, linear growth between the neurocranium and the face was absent, since significant regression models were found in most of the cases.

In this study, the null hypothesis proposed that all major skeletal components of

neurocranial index in control males

$$\text{equation } y=a+bx+cx/\ln x+d/\ln x+e/x$$

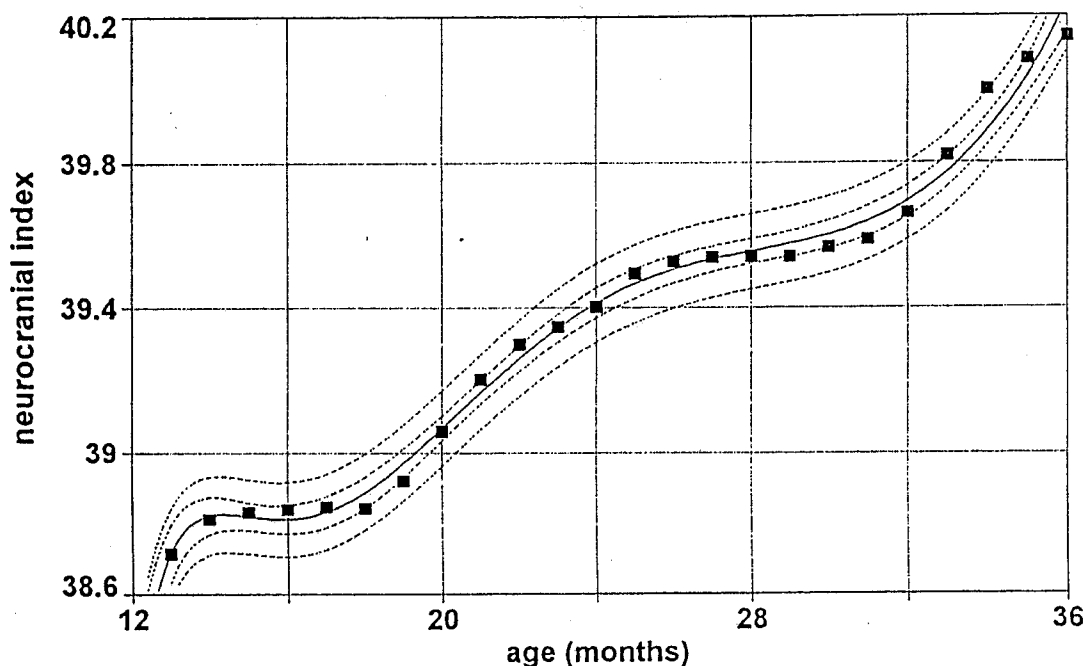


Fig. 2. Example of complex linear growth in control males. The central curved line means that growth explained about 97% of the variation in neurocranial components. The proximal lines are the confidence intervals. The lateral ones limit the prediction intervals.

the platyrrhine body grow linearly, regardless of different demands for different functions. Accepting the null hypothesis implies that linear growth in the skeletal frame of *Saimiri* would be expected. The results, however, allowed us to reject the hypothesis. The skeleton did not grow evenly but according to functional demands imposed by related soft tissues and body cavities. The simple linear pattern seen in the femur of both sexes may be linked to the steady growth in height of the young animals. The same may occur in the female pelvic index, maintaining the normal bony conditions for parturition, in both the control and stressed environments.

Because complex linear equations were necessary for explaining skeletal growth, a nongenetic mechanism influences growth in the *Saimiri* genus. This implies that factors independent of age were acting. Age incre-

ments explained only part of the variation in the complex linearly patterned components. The remainder of the variation was due to the sum of other independent variables. Because the sinuous trajectory found in the complex linear components is not an artifact (Jandel, 1994), eco-geographical factors may explain this pattern. For example, several observations have been made about the intraspecific differences in size due to the latitude, habitat, and rainfall affecting *Macaca* (Albrecht, 1978, 1980; Hamada et al., 1986; Albrecht and Miller, 1993; Fooden and Albrecht, 1993; Turner et al., 1997) and *Callithrix* (Albrecht, 1982) genera. This suggests that eco-geographic variation in primates may be multifactorial, i.e., with different factors influencing different situations. The strong oscillation in environmental temperature, food intake, and body weight seen in our experiment on squirrel monkeys corre-

facial index in undernourished females

$$\text{equation } y = a + bx + cx^{1.5} + dx^2 \ln x + ex / \ln x$$

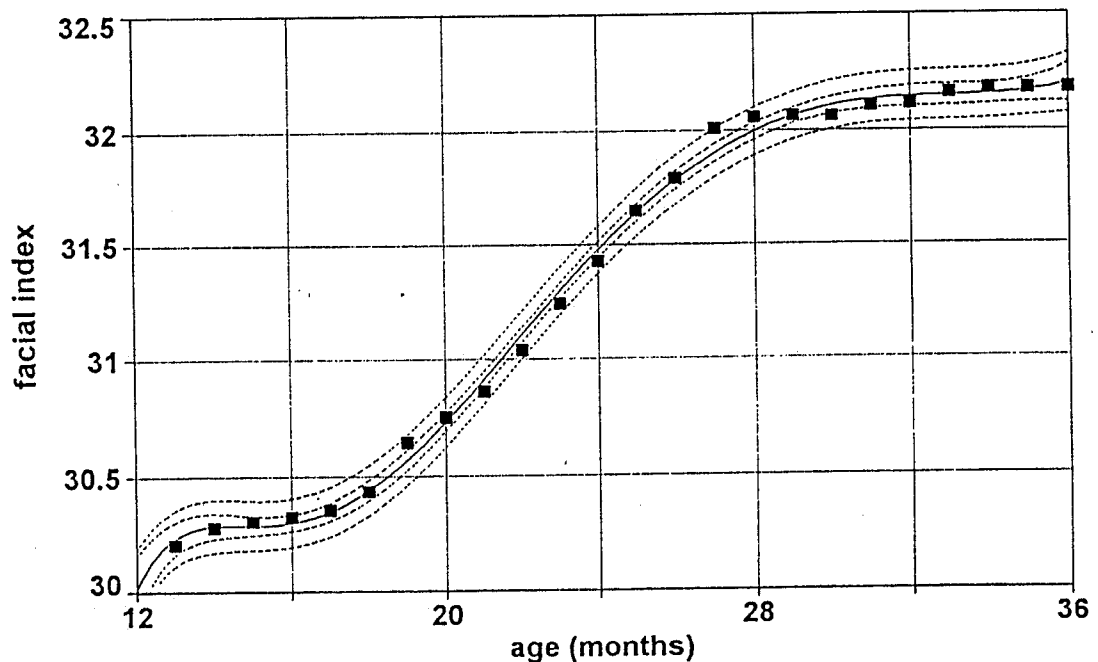


Fig. 3. Example of complex linear growth in undernourished females. The central curve line means that growth explained more than 99% of the variation in facial components. The proximal lines are the confidence intervals. The lateral ones limit the prediction intervals.

TABLE 6. Multiple regression tests for total sample

Index	Age	Sex	Body weight	Food intake	Water intake	Environmental temperature
Neurocranial	1.0	7.3**	21.9**	13.3**	3.9**	2.4*
Facial	5.4**	11.2**	14.9**	3.5**	4.1**	2.3*
Pelvic	6.5**	3.6**	21.3**	2.2**	2.9**	2.1*

* $P < 0.05$.

** $P < 0.01$.

sponds to that of the tropical forest in which significant seasonal variation occurs. The cool-rainy season (winter) lasts from December to April, and the warm-dry one (summer) from May to November (Murrieta et al., 1989). Alternate conditions make food production and food reserves cyclic (Rosenblum and Coe, 1985). The dry season, with high temperatures, low relative humidity, and food scarcity, might decrease growth rates, which are responsible for the lowest slopes of the four-function curves. The rainy season, with moderate temperatures and greater quality and

TABLE 7. Adjusted ANOVA for multiple regression model¹

Index	MS	SE	F	Adj. r^2	D-W
Neurocranial	31,725.6	6.4	4,926.0*	99.4	6.441
Facial	43,601.5	5.3	8,279.3*	99.6	2.295
Pelvic	22,007.6	2.2	9,951.4*	99.7	0.513

¹ MS, mean square values; SE, standard error of the mean squares; F, F significance of indices; Adj. r^2 , adjusted determination coefficients expressed as percent; D-W, Durbin-Watson test. * $P < 0.01$.

availability of food, might increase growth rates, which are responsible for the highest slopes of the complex linear equation curves.

In fact, the *simple linear* growth components also suggest an undulating trend, although masked by the high growth rate of the components involved (see Fig. 1).

CONCLUSIONS

The null hypothesis tested in the present experiment was rejected in regard to the following considerations.

1. The skeletal components of the squirrel monkey behaved according to two defined patterns of growth. The femur in all of the groups, and the pelvis of the females, grew *straight and fast*. The face and the neurocranium in all of the groups and the pelvis of the males grew *slowly and in an undulating fashion*. These growth modalities were imposed by several different functional demands. The neurocranium and the face grew mostly during lactation. In the present experiment, only the final growth stages of these two components were detected, each with a feeble increment, and having a nonlinear relationship between them. The femur went on growing actively, following the increment in stature. Sexual dimorphism was evident in the growth pattern of the pelvis. The linear growth showed by the pelviofemoral index is interpreted as a greater pelvic growth rate in females than in males, presumably to ready the female organism for reproductive activity.
2. Undernutrition affected growth in height in both sexes and pelvic growth only in males. The pelvis in females and the neurocranium and the face in both sexes were not affected. This fact reinforced the idea of functional demands acting on growth. The skull components were protected from undernutrition due to their early growth. The "better pelvic growth canalization of the females" may be closely related to reproduction.
3. The undulating growth trend observed in the complex linear growing components might be related to the feeding behavior of the primates of the tropical forest. The rising slopes of the four-function curves may be evoked in the rainy season, when food quality and quantity are better than in the dry one. The downhill slopes may

be evoked during the dry season, when food quality and quantity generally turn poorer than in the rainy season.

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