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Heterochrony in Hybrid Macaques

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Nicole D. Taylor and Michael A. Schillaci (2008) Heterochrony in hybrid macaques. *Zoological Studies* **47**(6): 713-719. In this report, we examine the effects of hybridization on growth allometry and the heterochronic growth process in a sample of hybrids of *Macaca mulatta*. Comparisons of regression parameters describing the linear relationships of age with body weight and body length, and the allometric relationship between body weight and body length indicate that hybridization may be associated with predisplacement (body weight and length to age) and hypermorphosis (length to weight) in males. Only the comparison of the male weight-to-age regression was statistically significant. Female hybrids exhibited a visible pattern of acceleration (body weight and length to age), or slight acceleration coupled with slight hypermorphosis (length to weight). None of the female patterns, however, were statistically significant. The results of our study indicate hybridization can affect growth patterns, although the magnitude of the difference varies and may be sex specific.
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Key words: Ontogeny, Growth allometry, Hybridization, Primates, Heterosis.

Hybridization among phenotypically distinct phylogenetic species is ubiquitous within the order Primates, particularly cercopithecine monkeys. In primates, hybridization (and its effects on the adult phenotype) has been a topic of considerable research in biological anthropology because of its implications for interpreting the fossil record (e.g., Jolly 2001, Ackermann et al. 2006, Jolly et al. 1997). The effect of hybridization on the primate phenotype, especially growth and development, however, is not well understood and has received little attention in the literature. In this report, we examine the effects of hybridization on heterochronic growth processes and growth allometry (Table 1) using a published dataset on a sample of hybrid macaques and their parental match of Indian origin (*Macaca mulatta mulatta*). We focus on heterochrony because small changes in developmental timing and growth rates caused by hybrid heterosis can substantially affect the hybrid adult phenotype.

The first published study on the effects of hybrid heterosis on primate growth was presented by Smith and Scott (1989). Their analysis identified a sex-specific heterosis effect on age-adjusted body weight and body length values in subspecific hybrids of *M. mulatta*. In that study, males, but not females, exhibited greater age-adjusted values than nonhybrids. A study by Schillaci et al. (2005) identified a hybrid pattern of craniofacial growth allometry characterized by increased regression slope values and reduced intercept values for a sample of male macaques from Sulawesi. This observed pattern of increased allometries did not, however, correspond well with the observed pattern of adult heterosis.

Growth and heterochronic processes

Heterochrony was defined by Gould (1977) as “phyletic change in the onset or timing of development, so that the appearance or rate

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of development of a feature in a descendant ontogeny is either accelerated or retarded relative to the appearance or rate of development of the same feature in an ancestor's ontogeny". The processes of heterochronic growth, i.e., predisplacement, postdisplacement, acceleration, neoteny, hypermorphosis, and hypomorphosis, have one of 2 consequences (patterns) on the descendant adult phenotype (Fig. 1). The development of a new descendant adult shape, termed peramorphosis (Alberch et al. 1979), can be caused by dissociation from ancestral trajectories by way of increased descendant regression slope values (acceleration), increased intercept values (predisplacement), or by a continuation along an ancestral trajectory (hypermorphosis). Hypermorphosis requires an increase in size, thus resulting in a new form (size + shape). Paedomorphosis (Alberch et al. 1979) is the development of a juvenilized descendant adult shape relative to the ancestral adult shape and can be caused by dissociation from ancestral allometric trajectories by way of a decreased slope (neoteny), decreased intercept values (postdisplacement), or truncated growth along the ancestral trajectory (hypomorphosis) (Fig. 1).

MATERIALS AND METHODS

For the present study, we used morphometric data on body weight and body length (crown-rump length; CRL) from a cross-sectional ontogenetic sample of 40 (20 males and 20 females) captive subspecific hybrid rhesus macaques published by Smith and Scott (1989). We also included a cross-sectional sample of 40 full-blooded parental "matches" of Indian origin. This is a valuable dataset because the chronological, ages of the monkeys, and their hybrid status are known. In addition, the comparative groups shared the same feeding protocols, eliminating nutrition as a confounding factor in the study.

The hybrids were a product of cross-breeding between captive groups of macaques of Chinese (*M. m. littoralis* and *M. m. vestitus*) and Indian (*M. m. mulatta*) origin (also see Smith and McDonough 2005). The level of cross-breeding between the Chinese subspecies is not known. Both the hybrid and parental-match groupings were housed and reared in the same way, and were subjected to the same diet and feeding protocols (Smith and Scott 1989). The animals ranged in age from juveniles (1.58 yr) to subadults (5.48 yr) (Smith and Scott 1989). In addition, we included data on adult body weight from a subsequent study on the same population (Smith 1994).

Ontogenetic data from the parental matches of Chinese origin were not collected and thus are not available. Adult weight comparisons between full-blooded Chinese and full-blooded Indian rhesus macaques indicated that in both males and females, the Chinese macaques were statistically significantly smaller than the Indian macaques (Smith and Scott 1989).

Data analysis

A least-squares (LS) regression was used to describe the linear relationships of age with weight, age with body length, and weight with body length. All variables were $\log_{10}$-transformed prior to analysis. Bootstrapping was used to minimize any potential bias associated with smaller sample sizes. Bootstrapped estimates of regression slopes, intercepts, and 95% confidence intervals (CIs) were calculated based on 1000 resampling iterations. A model of heterochrony (see above) was used to interpret the growth process associated with differences in the observed patterns between hybrids (descendant condition) and parental matches (ancestor condition).

The hybrid regression parameters were compared to the bootstrapped estimates of the 95% CIs to assess the significance of observed differences in growth patterns. The hypothesis of isometry was tested by determining if the hybrid and parental-match 95% CIs included a slope

Table 1. Terms and definitions

Term	Definition
Growth allometry	Size-related shape changes during ontogeny
Heterochrony	Changes in the relative time of the appearance and rate of development in the descendant taxon (Gould 1977)
Heterosis	A condition of increased heterozygosity resulting in hybrid trait sizes that are greater than the average of the 2 parental species (Falconer and Mackay 1996)
Hybridization	The interbreeding of individuals from genetically distinct taxa (Harrison 1990)

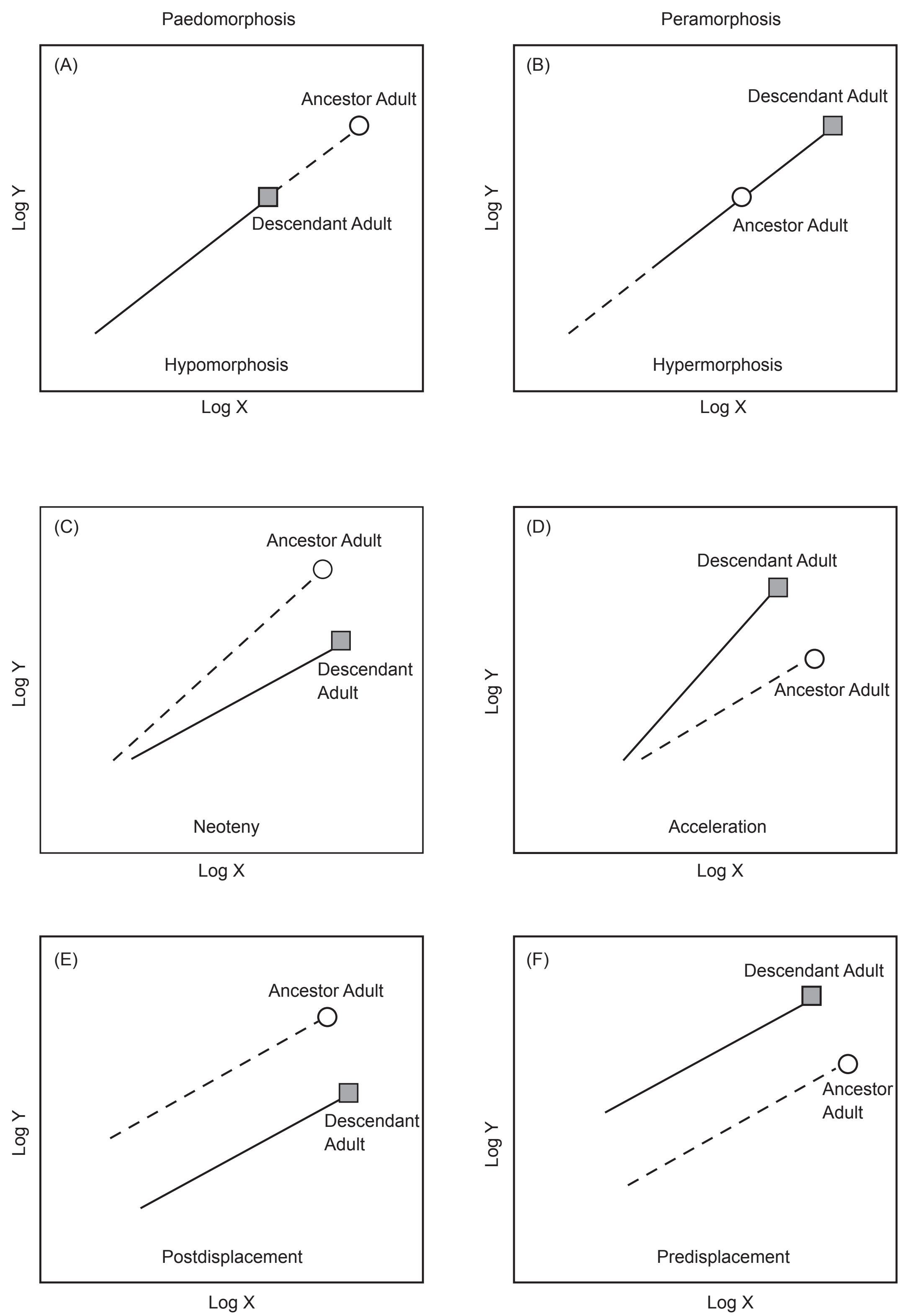

Fig. 1. Regression models describing heterochronic patterns and processes (after Leigh et al. 2003, Fig. 4). Each column describes one of 2 heterochronic patterns for the descendant comparison group: paedomorphosis and peramorphosis. Heterochronic processes are included here. (A) Hypomorphosis; (B) hypermorphosis; (C) neoteny; (D) acceleration; (E) postdisplacement; (F) predisplacement. Negative and positive allometries were not separately considered here.

value of 0.33 (i.e., isometry in a linear/weight comparison). Positive allometry was identified when both the upper and lower 95% CI values were > 0.33, while negative allometry was identified when both these values were less than isometry.

RESULTS AND DISCUSSION

The bootstrapped estimates for the slopes and intercepts of the regressions of male and female hybrid and parental-match macaques are listed in table 2. Bivariate regression plots for males and females are presented in figures 2 and 3. In male macaques, the hybrid LS regression lines for weight to age and CRL to age were visually positioned above the regression line for the parental-match animals (Fig. 2A, B). LS slope values for both male groupings were largely equivalent with the parental-match values, which fell well within the hybrid 95% CIs. Although the male hybrid LS intercept values were slightly higher than the parental-match values, the observed difference was statistically significant only for male weight-to-age growth. This pattern was consistent with predisplacement, or an earlier growth onset, for hybrid body length. Here, predisplacement and peramorphosis were associated with a hybrid condition. The observed pattern for male body weight growth was consistent with predisplacement for juvenile growth, but did not seem to result in a different adult phenotype. The higher Y-intercept values suggest that the difference between hybrid and non-hybrid growth trajectories had already been established by 1.58 yrs of age, the earliest

Table 2. Results of regression analyses of hybrid and parental-match growth trajectories. Significant comparisons are in boldface

	Males		Females	
	Parental Match	Hybrids	Parental Match	Hybrids
Males				
Weight to age				
LS slope	0.948	0.862	0.723	0.774
Standard error	0.045	0.062	0.064	0.094
95% CI	0.856-1.033		0.602-0.863	
LS intercept	0.266	**0.363***	0.339	0.333
Standard error	0.028	0.037	0.034	0.052
95% CI	0.213-0.324		0.255-0.399	
R^2	0.909	0.833	0.822	0.782
CRL to age				
LS slope	0.294	0.301	0.173	0.230
Standard error	0.020	0.021	0.030	0.030
95% CI	0.263-0.337		0.126-0.245	
LS intercept	1.519	1.533	1.570	1.541
Standard error	0.012	0.012	0.018	0.017
95% CI	1.495-1.535		1.527-1.597	
R^2	0.870	0.879	0.612	0.765
CRL to weight				
LS slope	0.309	0.312	0.231	0.258
Standard error	0.012	0.022	0.027	0.020
95% CI	0.286-0.335		0.195-0.303	
LS intercept	1.438	1.436	1.495	1.473
Standard error	0.009	0.020	0.021	0.015
95% CI	1.413-1.452		1.439-1.520	
R^2	0.942	0.912	0.735	0.897

CI, confidence interval; LS, least squares.

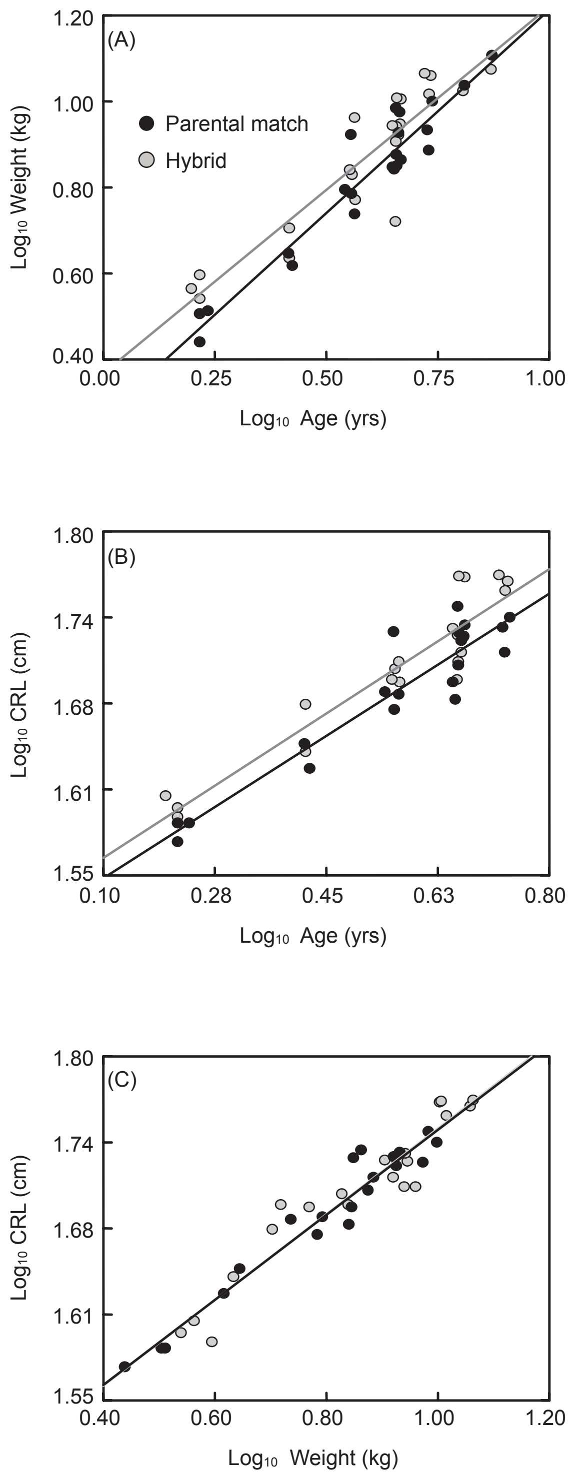

Fig. 2. Least squares regression of weight on age (A), crown-rump length (CRL) to age (B), and CRL on weight (C) in male rhesus macaques. Hybrids are represented by gray shaded circles and the gray regression line. Parental matches are represented by solid black circles and the black regression line.

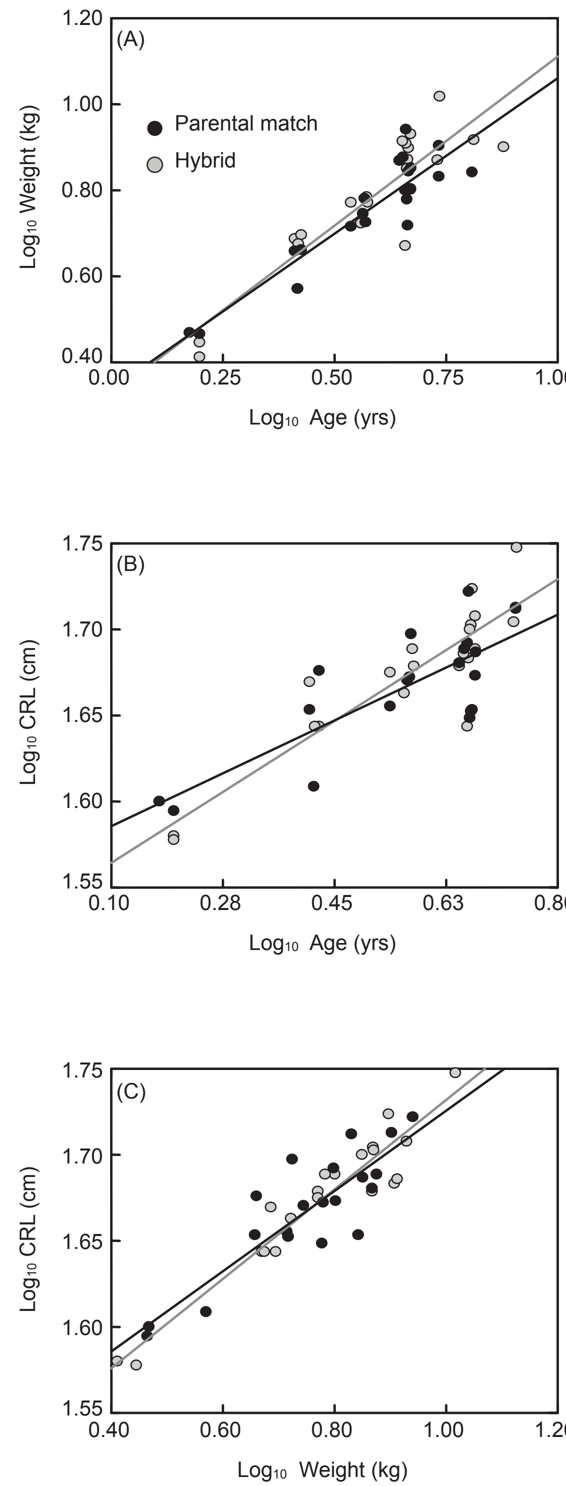

Fig. 3. Least squares regression of weight on age (A), crown-rump length (CRL) on age (B), and CRL to weight (C) in female rhesus macaques. Hybrids are represented by gray shaded circles and the gray regression line. Parental matches are represented by solid black circles and the black regression line.

age for which we have data. Hybrids, therefore, must grow faster than non-hybrids early in life either in utero or during the 1st year after birth (but see Smith et al. 1987).

Figure 2C shows no variation in the relationship between CRL and weight in male hybrids vs. the parental matches. The slope and Y-intercept estimates fall within the 95% CIs of each other, indicating that male hybrids and parental matches share the same allometric relationship throughout ontogeny. The maximum values for the descendant hybrids were beyond those of the parental matches, a pattern consistent with hypermorphosis through ontogenetic scaling. A comparison of the 95% CIs to a slope value of 0.33 indicates that the hypothesis of isometry cannot be rejected for either the male hybrids or their parental counterparts.

Our results indicate that female hybrids weighed less (Fig. 3A) and were shorter (Fig. 3B) at the initial age, but achieved slightly higher weight and CRL by the final age along a slightly steeper trajectory. The parental-match slope and intercept estimates fell within the 95% CIs of the hybrids, indicating that an association between the 2 growth trajectories cannot be rejected. The allometric relationship of CRL to weight in female hybrids vs. parental matches (Fig. 3C) was not identical as it was in males, but the regression lines were very similar and fell within the 95% CIs of each other, indicating closely associated allometric trajectories. A comparison of the 95% CIs to a slope value of 0.33 indicates negative allometry, and thus the hypothesis of isometry can be rejected for female hybrids.

The results of our analysis indicated that hybridization may affect the heterochronic process. This effect, however, was not statistically significant for all but 1 comparison, and it may be sex-specific, with predisplacement indicated for hybrid males but not for hybrid females. Hybrid and parental patterns of growth allometry based on weight-related changes in body length during ontogeny were largely the same. Hypermorphosis was apparent for males but not females. Interestingly, in their assessment of hybrid craniofacial morphology, Ackermann (2007) did not find a significant sex x taxon interaction effect for metric variables included in their analysis but did find differences in sex-specific patterns of the expression of non-metric trait variations.

Our results contribute to an emerging literature on hybridization and intraspecific variations in growth patterns by demonstrating that hybridization can affect the heterochronic process in macaques. These results are important because they demonstrate that largely similar, visible, and statistically significant (i.e., male body mass growth) differences in growth patterns between parental and hybrid populations can occur, despite their being completely cross-fertile. This may call into question the use of growth patterns for identifying species-level taxonomic distinctions in the fossil record.

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APPENDIX. Age, weight, and crown-rump length (CRL) values for Chinese-Indian hybrids and their Indian parental matches

Males						Females					
Hybrids			Parental Match			Hybrids			Parental Match		
Age[1]	CRL[2]	Weight[3]	Age[1]	CRL[2]	Weight[3]	Age[1]	CRL[2]	Weight[3]	Age[1]	CRL[2]	Weight[3]
7.42[4]	N/A	11.84	7.46[4]	N/A	12.77	7.58[4]	N/A	7.94	N/A	N/A	N/A
6.42[5]	N/A	10.55	6.47[5]	N/A	10.87	6.50[5]	N/A	8.25	6.44[5]	N/A	6.94
5.44	58.0	11.45	5.48	54.6	9.98	5.45	55.9	10.41	5.43	51.6	8.00
5.39	57.1	10.38	5.38	51.5	7.68	5.39	50.6	7.41	5.43	51.5	6.78
5.27	58.6	11.59	5.34	53.7	8.56	4.69	48.8	6.33	4.70	48.6	7.10
4.66	58.4	10.10	4.66	53.9	7.30	4.69	51.0	8.51	4.69	47.1	6.35
4.64	52.9	8.84	4.63	52.8	9.42	4.64	52.9	7.90	4.64	45.0	6.97
4.60	51.5	8.33	4.60	52.5	8.44	4.62	50.4	7.43	4.62	44.9	5.22
4.56	58.5	10.16	4.56	53.2	7.07	4.60	50.1	7.08	4.60	44.5	6.00
4.55	50.7	8.72	4.55	50.4	7.51	4.58	48.2	8.09	4.58	52.7	8.73
4.54	53.0	8.05	4.54	55.6	9.63	4.56	44.0	4.68	4.56	49.2	6.30
4.53	49.2	5.24	4.50	47.6	6.94	4.50	48.5	8.19	4.51	48.8	7.52
4.46	53.6	8.76	4.46	49.0	7.02	4.43	47.7	7.38	4.43	47.9	7.38
3.68	49.0	5.89	3.67	48.0	5.46	3.76	47.7	5.90	3.72	49.8	5.31
3.62	50.1	6.74	3.61	46.8	6.09	3.74	48.8	6.08	3.70	47.0	6.03
3.67	50.7	9.14	3.60	53.3	8.35	3.63	46.0	5.28	3.67	46.8	5.56
3.58	49.2	6.92	3.49	48.2	6.22	3.45	47.3	5.90	4.45	45.2	5.19
2.62	47.2	5.06	2.66	42.4	1.14	2.58	46.7	4.86	2.58	45.0	4.55
2.62	43.6	4.31	2.61	44.2	4.42	2.67	44.0	4.96	2.67	47.4	1.58
1.65	39.7	3.47	1.72	38.7	3.25	2.63	44.0	4.73	2.62	40.6	3.72
1.65	39.1	3.94	1.65	37.5	2.75	1.58	38.0	2.58	1.58	39.3	2.92
1.58	40.5	3.66	1.65	38.7	3.20	1.58	37.8	2.79	1.50	39.8	2.94

[1]Age (yr). [2]CRL, crown-rump length (cm). [3]Body weight (kg). [4]Adult age and body weight taken from Smith (1994, table 1). [5]Data on average age and body weight derived from Smith (1994, table 1).