

Heterochrony in Hybrid Macaques

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Zoological Studies **47**(6): xxx-xxx. 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. <http://zoolstud.sinica.edu.tw/Journals/47.6/xxx.pdf>

Key words: Ontogeny, Growth allometry, Hybridization, Primates, Heterosis.

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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 1st 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.

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
Hybridization	The interbreeding of individuals from genetically distinct taxa (Harrison 1990)

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 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, hypermorphism, and hypomorphism, 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 of a trajectory associated with that of the ancestor (hypermorphosis). Hypermorphosis requires an increase in size, thus resulting in a new form (size + shape).

Pedomorphosis (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).

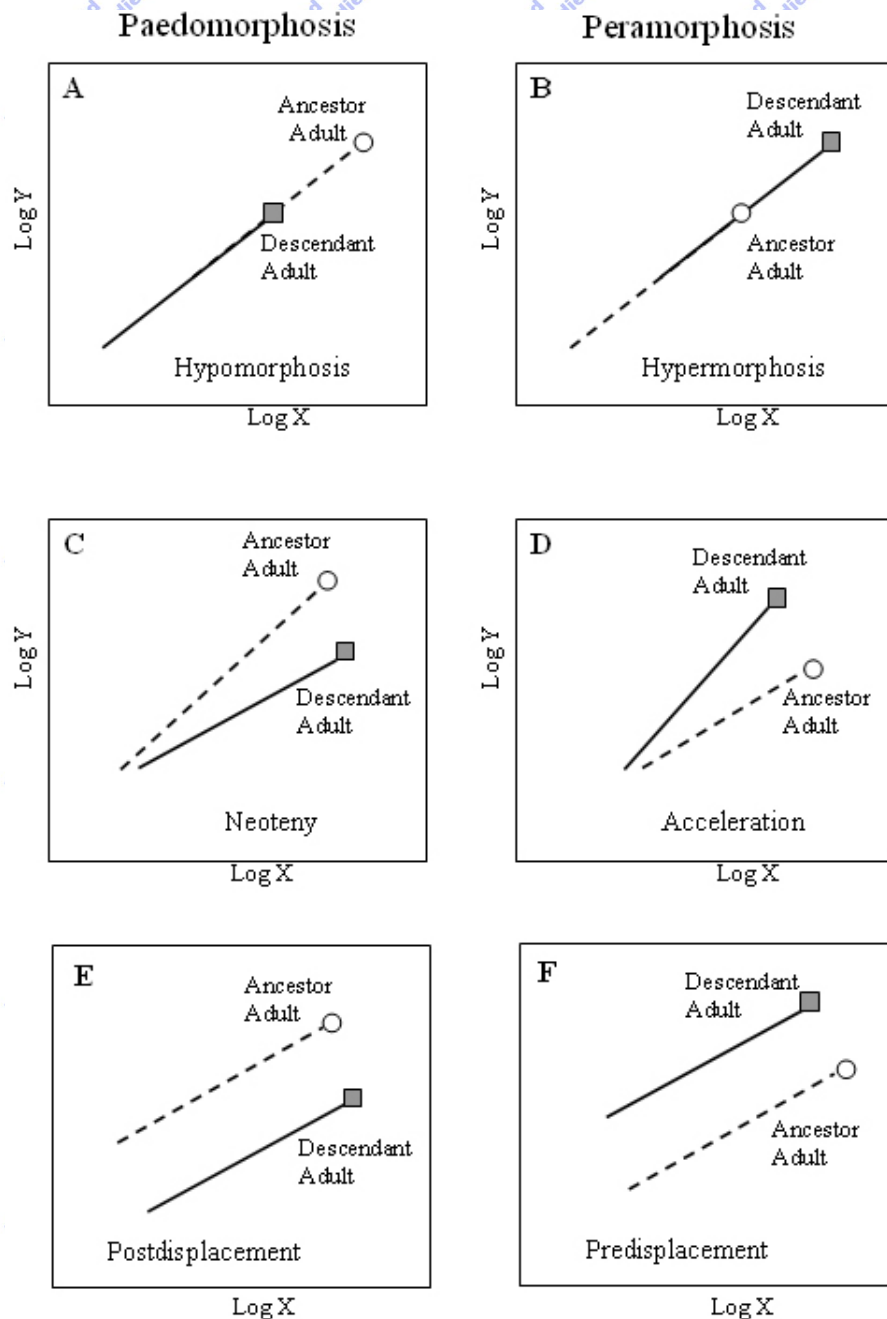


Fig. 1. Regression models describing heterochronic patterns and processes (after Leigh et al. 2003, Fig. 4). Each column describes one of 2 heterochronic patterns for the descendant comparison group: pedomorphosis and peramorphosis. Heterochronic processes are

included here. (A) Hypomorphosis; (B) hypermorphosis; (C) neoteny; (D) acceleration; (E) postdisplacement; (F) predisplacement. Negative and positive allometries were not separately considered here.

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, rather than the dental, ages of the monkeys, and their hybrid status are known. In addition, the comparative groups shared the same feeding protocols, thus 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 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 these values were both 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 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).

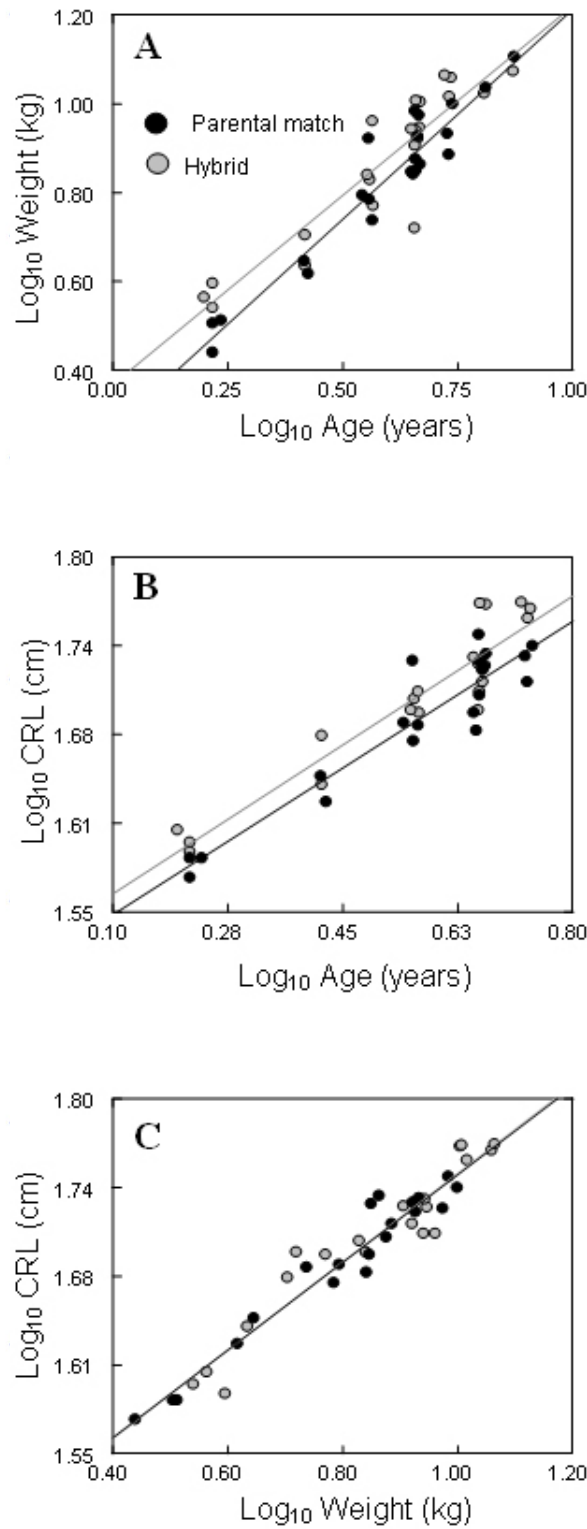


Fig. 2. Least squares regression of weight on age (A), crown-rump length (CRL) to age (B), and CRL on weight (C) in male rhesus macaques. Hybrids are represented

by gray shaded circles and the gray regression line. Parental matches are represented by solid black circles and the black regression line.

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.

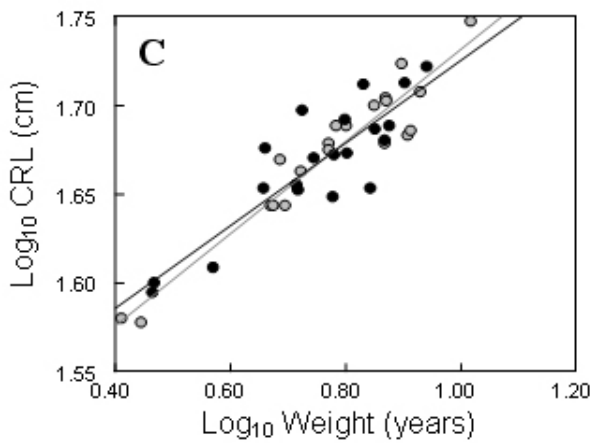
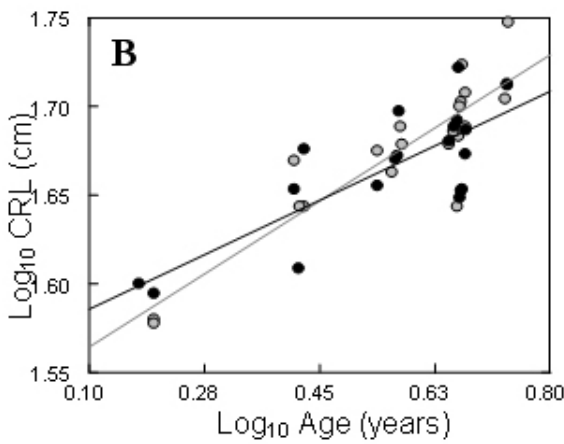
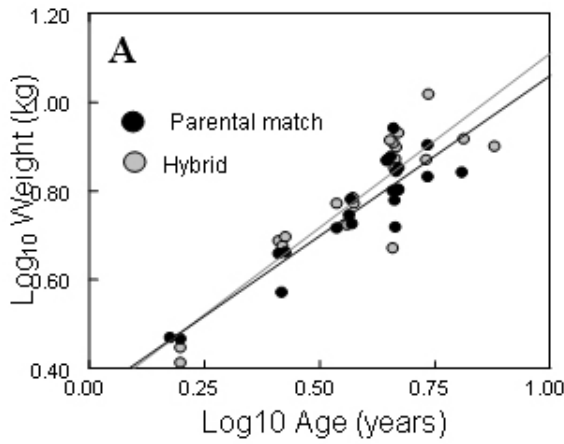


Fig. 3. Least squares regression of weight on age (A), crown-rump length (CRL) on age (B), and CRL to weight (C) in female rhesus macaques. Hybrids are represented by gray shaded circles and the gray regression line. Parental matches are represented by solid black circles and the black regression line.

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 et al. (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

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