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Patterns of variation in the ontogeny of primate body size dimorphism

This study investigates variability in the ontogeny of sexual dimorphism in body weight in anthropoid primates. Specifically, the hypothesis that the ontogenetic bases of dimorphism vary in primates is tested with a large comparative sample. This sample allows both specification of the range of variability in patterns of dimorphic growth and careful examination of some correlates of ontogenetic variability.

The analysis is based on body weight growth in 45 species of captive primates. Growth curves are estimated for each sex in each species using a non-parametric regression technique (locally weighted least squares regression). These regressions facilitate estimation of the degree of differences in age at body weight maturation, the proportion of total adult dimorphism arising from sex differences in rate of growth, and the proportion of total dimorphism attributable to sex differences in duration of growth.

Primates show great diversity in how adult weight dimorphism develops. Although males tend to reach adult weight later than females, cases in which rate differences are exclusively responsible for body weight dimorphism are observed. More generally, sex differences in both rate and duration of growth occur together to produce dimorphism, but these differences may occur independently. Relationships between these processes and size appear complex, as do relations between these processes and dimorphism. These results suggest that primates have evolved a number of developmental pathways that lead to similar levels of adult dimorphism. It is expected that male patterns of growth respond primarily to sexual selection, but that female patterns of growth respond to natural selection.

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Introduction

Sexual dimorphism in body size is a common and well-recognized phenomenon in primates and in many other taxa (Ralls, 1977). Recent analyses of the evolution of primate sexual dimorphism delineate a number of correlations between body size dimorphism and socio-ecological variables. The ideas proposed to explain such variation in sexual dimorphism include sexual selection, allometric or size-related phenomena, ecological factors and phylogenetic inertia (see Cheverud *et al.*, 1985; Ely & Kurland, 1989; Gaulin & Sailer, 1984; Leutenegger & Cheverud, 1982, 1985; Rensch, 1959). Despite the high level of interest in the study of adult dimorphism, relatively few studies have provided detailed insight into the ontogeny of dimorphism. Moreover, ontogenetic studies of dimorphism have tended to be contradictory in their findings (see Watts, 1986).

The present study attempts to provide a basic understanding of the range of variability in dimorphic growth in primates. Specifically, this study expands previous research presented by Shea (1986) which shows that the ontogenetic bases of sexual dimorphism vary among primate species [see also Jarman (1983) and Georgiadis (1985) for terrestrial herbivores]. These studies indicate that there is interspecific diversity in the contribution of sex differences in rate of growth and duration of growth that lead to adult dimorphism. In other words, there are species-specific ways in which comparable levels of sexual dimorphism develop. Although these studies provide evidence for the presence of variability, the nature of this variation remains inadequately specified because relatively few species have been investigated, particularly for primates. Definition of the variability in dimorphic growth processes provides a foundation for more detailed explanatory analyses (see Leigh, 1992).

Ontogeny and dimorphism

Ontogeny is important in gaining an understanding of dimorphism because similar levels of body size dimorphism could, theoretically, be produced through quite disparate developmental processes. If the developmental processes that ultimately account for dimorphism vary substantially among primate species, then the presence of variable processes requires explanation. Previous researchers (Jarman, 1983; Fedigan, 1982; Ralls, 1977; Shea, 1985, 1986) have addressed the possibility that ontogenetic bases vary among species and have discussed the significance of actual or potential variation. However, the patterns of variation in the ontogenetic processes that result in primate body size dimorphism are not well documented.

The presence of marked variation in the ontogenetic processes that lead to adult body size dimorphism would imply that, in some instances, similar levels of adult dimorphism reflect differing evolutionary causes. For example, equivalent levels of adult dimorphism might be observed in two species even though rate differences in growth produced dimorphism in one species while duration differences resulted in dimorphism in another species. An attempt to explain the presence or degree of dimorphism in an interspecific analysis without knowledge about the underlying ontogenetic trajectories risks evaluation of a variable (adult dimorphism) that may be a consequence of distinct ontogenetic processes. Adult dimorphism can be seen as a result of such processes, reflecting the presence of such processes but not their nature. This problem is recognized by Shea, who suggested that interspecific variability in the developmental processes that produce dimorphism may be the outcome of "fundamentally different evolutionary pathways" (1986:98). This general theoretical approach follows Gould (1977) quite closely in anticipating that the evolution of widely divergent ontogenetic processes may produce similar adult morphologies. This perspective may imply that analyses of adult dimorphism have yielded inconsistent results and proven controversial (Ely & Kurland, 1989), because they focus on the consequences of dimorphic growth and not on the actual processes that generate dimorphism.

A number of previous studies investigated the relations between ontogeny and dimorphism. In a pioneering analysis, Wiley showed that bimaturism [which he defined as "a sexual difference in the age at onset of breeding" (1974:241)] is positively correlated with polygyny, large body size and body size dimorphism in grouse. According to Wiley, bimaturism can evolve when delays in male breeding confer reproductive advantages to males. In grouse, bimaturism most likely evolves because young males cannot compete effectively with older birds for mates. Moreover, females may tend to choose older males, limiting reproductive opportunities for young males. As a result of these (and other) factors, bimaturism evolves.

Jarman (1983) modified and enhanced Wiley's concept of bimaturism. Jarman defined bimaturism as a sex difference in duration of growth (usually body weight growth) and evaluated associations between bimaturism and dimorphism in *Bovidae* (antelope, sheep, cattle, etc.), *Cervidae* (deer) and *Macropodidae* (kangaroos, wallabies, rat kangaroos, etc.). In these taxa, sex differences in rate of growth may occur, but dimorphism always seems to be associated with bimaturism. Georgiadis (1985) offered comparable results for an analysis of body weight growth and sexual dimorphism in African ruminants. Georgiadis found that "no males attain asymptotic weight before conspecific females" (1985:79) and that bimaturism is much more important in the production of dimorphism than rate differences.

These studies of terrestrial herbivores would suggest that variability in body size dimorphism is a consequence of variable ontogenetic processes. As pointed out by Jarman, there are

species-specific ways in which dimorphism develops (1983:513). Variation in patterns of ontogeny that result in dimorphism are seen as evolutionary responses to a number of factors which may include territoriality, mate competition and resource distribution plus interactions between these and other factors. In general, however, Jarman expects bimaturism to evolve when:

“Males that eventually breed will be those that, as young males, adopted strategies of survival rather than competing dangerously for matings against the older males” (1983:487).

It should be noted that Jarman's findings were based primarily on evaluation of literature data. Moreover, the growth data used include body weight for some species but skeletal dimensions for others [such as skull weight in dall sheep (1983:493) and mandibular length in caribou (1983:496)]. Jarman's cross sectional growth curves were often based on somewhat limited data, and growth curves fitted by eye. Consequently, Jarman's results may be rather tentative. Georgiadis' (1985) analysis, which is technically more rigorous because it was based on regression analysis of body weight growth, does not conflict with Jarman's general assessment.

Shea (1986) approached the problem of ontogenetic variability and dimorphism in primates through a heterochronic analysis. In comparisons involving groups of closely related species, he found that variation in levels of bimaturism (defined as a sex difference in age at body weight maturity) was positively correlated with size and dimorphism among certain primate species. These species include macaques, baboons and African apes. In contrast, Shea found that in some West African forest monkeys (guenons), dimorphism apparently resulted mainly from sexual rate differences in growth.

Although Shea's study was rather general, it points to considerable diversity among groups of closely related primate species in the role that rate and duration differences in ontogeny play in the production of dimorphism. In some cases, similar levels of dimorphism may arise through rate differences, but in others, sex differences in the duration of the growth period (bimaturism) seem to account for dimorphism.

Growth studies of linear skeletal dimensions in primates may suggest less diversity in the ontogenetic processes that lead to dimorphism than is indicated by Shea's study of weight growth. It should be noted that such studies may not be directly comparable to analyses based on body weight primarily because analyses of skeletal growth describe growth in a single morphological system. In contrast, analyses of weight simultaneously incorporate growth of all morphological components. While the skeletal system contributes to mass and weight, the relation between this system and others is not well known in non-human primates. Nevertheless, in a discussion of detailed longitudinal studies of long bone growth based on rhesus macaques, chimpanzees and humans, Watts suggested that skeletal “sexual dimorphism in the tempo of maturation appears to have been conserved” among primate species (1986:162). This implies that interspecific variation in rate differences in growth are largely, but as Watts cautions, not exclusively, responsible for production of variable levels of skeletal length dimorphism in primates. This view contrasts with an earlier study by Gavan & Swindler (1966) who indicated that intraspecific differences in sitting height dimorphism among these taxa are largely the outcome of variation in bimaturism. Gavan & Swindler detected statistically significant sex differences in adolescent chimpanzee growth rates (1966: 184–185) and in rhesus growth rates. However, Gavan & Swindler (1966) attributed the differences in chimpanzee growth rates to small sample sizes rather than to developmental processes, possibly explaining the disparity between their findings and those of Watts (1986).

Review of these investigations illustrates that, although there is strong evidence for diversity in the developmental processes that result in sexual size dimorphism, there is some controversy as to the nature and degree of variation. In general, detailed comparative knowledge about the ontogenetic processes that result in dimorphism is lacking (in both weight and length). Because of this lack of information, the present study attempts to delineate the range of variability in processes of dimorphic growth in anthropoid primates. Exploration of this variability provides a foundation for further explanatory analyses of primate sexual dimorphism. Variability in the ontogenetic processes (rate and duration of growth) that result in dimorphism is anticipated in primates (Shea, 1986). The degree of bimaturism is also expected to vary. It is further expected that bimaturism is often size-related within groups of closely related primate species, as hypothesized by Shea (1986:107). An additional objective of this study is to provide basic descriptions of body weight growth in several primate species that reflect variability in patterns of dimorphic growth.

Materials and methods

Materials

The data consist of chronological age (years) and body weight measurements (kg) for captive primates. Forty-five anthropoid species are included in the analysis (Table 1).

Chronological age and body weight measurements were obtained from veterinary records for 2637 monkeys and apes. These animals are maintained at United States Regional Primate Research Centers and European and United States zoological parks and research laboratories. Additional data gathered from the veterinary records include species, subspecies, sex, individual identification number or name, health status, reproductive status, general body condition and health history. Animals were observed and photographed whenever possible.

Most of the data were obtained during routine physical examinations and tuberculosis tests. Data from animals requiring veterinary care as a result of trauma (such as lacerations and fractures) are also utilized, provided weights were obtained shortly after occurrence of trauma. Weights from pregnant, chronically ill, dehydrated or congenitally abnormal animals are excluded. A small number of animals identified in health records as obese (usually based on palpation by veterinary staff) are omitted from the analysis. No animals were designated as obese prior to attainment of adult weight. Nearly all animals are of known chronological age, accurate to the day of birth. Data from animals of unknown date of birth are utilized but only those data points collected after the animals had been in captivity for at least 10 years. For gorillas and orang-utans, only weights from animals in captivity for at least 15 years were used from wild-caught individuals.

The use of weight as a size variable requires careful scrutiny. Specifically, it is important to consider whether or not reliable evolutionary inferences can be based on an analysis of weight. Weight may mask differences in body composition that may be important in inter-specific analyses. In addition, it is well known that weight is easily affected by environmental factors. As a result, weight can fluctuate markedly, especially after maturity.

These liabilities are balanced by several factors. First, nearly all previous literature on primate body size dimorphism focuses on weight (Cheverud *et al.*, 1985; Clutton-Brock, 1985; Clutton-Brock & Harvey, 1977; Clutton-Brock *et al.*, 1977; Gaulin & Sailer, 1984; Leutenegger & Cheverud, 1982, 1985). The reason for investigation of weight is obviously related to sexual selection theory, particularly hypotheses about the role of intermale

Table 1 Species for which growth data were collected and key for plot abbreviations

Species	Plot abbreviation	Individuals	
		Male	Female
<i>Cebuella pygmaea</i>	CPYG	29	36
<i>Callithrix jacchus</i>	CJAC	33	39
<i>Callimico goeldi</i>	CLGOE	42	47
<i>Saguinus fuscicollis</i>	SFUS	18	19
<i>Saguinus geoffroyi</i>	SGEO	9	10
<i>Saguinus imperator</i>	SIMP	11	14
<i>Saguinus oedipus</i>	SOED	46	18
<i>Leontopithecus r. rosalia</i>	LR0S	26	31
<i>Saimiri sciureus</i>	SSCI	32	28
<i>Cebus apella</i>	CAPEL	26	28
<i>Callicebus moloch</i>	CMOL	30	23
<i>Aotus trivirgatus</i>	ATRI	25	23
<i>Ateles geoffroyi</i>	AGEO	29	30
<i>Alouatta caraya</i>	ACAR	27	26
<i>Allenopithecus nigroviridis</i>	ANIG	6	10
<i>Cercopithecus aethiops</i>	CAET	30	30
<i>Cercopithecus diana</i>	CDIA	25	26
<i>Cercopithecus neglectus</i>	CNEG	29	23
<i>Cercopithecus mitis</i>	CMIT	27	37
<i>Erythrocebus patas</i>	EPAT	41	52
<i>Miopithecus talapoin</i>	MTAL	16	27
<i>Cercocebus torquatus atys</i>	CTOR	38	71
<i>Macaca arctoides</i>	MARC	52	58
<i>Macaca cyclopis</i>	MCYL	25	20
<i>Macaca fascicularis</i>	MFAS	13	13
<i>Macaca mulatta</i>	MMUL	52	58
<i>Macaca nemestrina</i>	MNEM	39	64
<i>Macaca nigra</i>	MNIG	27	31
<i>Macaca radiata</i>	MRAD	28	26
<i>Macaca silenus</i>	MSIL	39	41
<i>Papio cynocephalus</i>	PCYN	33	53
<i>Papio (Mandrillus) leucophaeus</i>	PLEU	5	10
<i>Papio (Mandrillus) sphinx</i>	PSPH	49	59
<i>Colobus guereza</i>	CGUE	46	49
<i>Presbytis cristata</i>	PCRI	9	19
<i>Presbytis entellus</i>	PENT	29	24
<i>Presbytis obscura</i>	POBS	19	17
<i>Pygathrix nemaeus</i>	PNEM	13	12
<i>Hylobates lar</i>	HLAR	24	25
<i>Hylobates syndactylus</i>	HSYN	19	21
<i>Pongo pygmaeus</i>	PPYG	42	41
<i>Pan paniscus</i>	PPAN	13	23
<i>Pan troglodytes</i>	PTRO	22	23
<i>Gorilla gorilla</i>	GGOR	59	50

Only those species listed in Tables 2 and 3 are included in plots. Because longitudinal data are pooled, regressions are based on larger numbers of data points than individuals. Results for species with fewer than about 20 individuals for each sex should be treated with caution.

competition in the evolution of dimorphism. Sexual selection should favor heavier males in cases where male–male competition (most directly, combat) influences mating success (Darwin, 1871). When sexual selection does produce larger males, it can be expected to do so similarly among species, probably through increased size of the musculo-skeletal system. It should be noted that this expectation does not obviate a role for natural selection in the determination of male body size. Second, and more generally, weight is recognized as a key variable in ecological, physiological, morphological, allometric and life history studies because it is an accurate approximation of mass (Jungers, 1985:350–351). As such, weight is inextricably linked to nearly all aspects of an organism's biology. Thus, weight offers an appropriate variable for many types of biological investigations, including the present study.

It is also necessary to consider the value of captive data in addressing evolutionary hypotheses. For the present analysis, two assumptions facilitate evolutionary inferences. First, it is assumed that captivity affects both sexes similarly. This study examines sex differences, and it is unlikely that captivity has differential effects by sex. Therefore, inferences about patterns of sexually differentiated growth in captive animals should reflect similar patterns in non-captive animals. Second, it is assumed that captivity affects all species similarly. Clearly, neither assumption can be tested with data currently available, and future research should focus on these assumptions.

There are notable advantages to using captive data. First, nearly all ages are exact and all weights are actual (see above). This is a very important feature because all previous analyses of adult body size dimorphism and some studies of ontogeny and dimorphism are based on developmentally aged samples. Limited data gathered for the present study suggest that dental maturity may not correspond to cessation of body weight growth. Dental eruption often appears complete (sometimes substantially) before attainment of adult weight, particularly in males (Leigh, 1992). As a result, estimates of adult weight based on dentally adult individuals may not reflect weight of animals after body weight growth cessation.

Second, the majority of the data are mixed-longitudinal (Cock, 1966), allowing some knowledge about individual variation in growth. Although the focus of this study is on comparisons among species, repeated measures (longitudinal data) are considered for all species.

Third, all the animals in this study have received good nutrition and veterinary care, minimizing disruptions to growth trajectories resulting from illness or parasites. Fourth, veterinary records, daily logs, interviews with animal care staff and direct observation allow some familiarity with a number of the animals studied. It should be added that data from zoos and regional primate research centers seem comparable, with no apparent differences in growth or in adult weight.

Methods

All data for each species are plotted with age as the independent variable and weight as the dependent variable. The data are treated cross-sectionally (or as pooled time-series data; Dielman, 1989). Evaluation of longitudinal data in this manner loses information about individual variation in growth. However, this approach can be employed because cross-sectional regression coefficients approximate the mean of longitudinal regression coefficients (Cock, 1966; Tanner, 1978) and because groups (e.g., males *vs.* females) are compared in this study. Tanner (1978) and Eveleth & Tanner (1990) recommend cross-sectional data in group comparisons. Finally, comparisons of results based on analyses of longitudinal and

cross-sectional data drawn from the same samples suggest that both types of data supply adequate information for the present study (Leigh, 1992).

Non-parametric locally weighted least squares regression (lowess) is used to describe growth in these species. This method is employed because it makes no assumptions about the form of growth curves, an important consideration when numerous species are compared. According to Cleveland & Devlin (1988), lowess regression is analogous to calculation of moving averages in time series analysis.

Lowess regression fits small portions of a bivariate distribution of points through several steps (Efron & Tibshirani, 1991). Initially, a small "window" of points is selected in which there is a single "target" point. A weighting function is centered on this target point, with the highest weight at the target point. Weights at either side of the target point decrease, falling to zero at the edges of the window. The window and weighting function determine the position of a linear regression centered on the target point and calculated for all the points in the window. Data near the target point have a large influence on the position of the linear regression because weights are highest at this point. Iterative shifting of the target point and window results in a solid line through the entire bivariate distribution.

Varying the size of the window controls the linearity of the fit to the bivariate distribution. For example, a window that includes all data points would fit a linear weighted least squares line to the data. Conversely, extremely small windows could conceivably fit all points with unique x and y values. Efron & Tibshirani (1991) provided a non-technical description of this method, while Cleveland (1979) and Cleveland & Devlin (1988) detailed its mathematical foundations. All lowess regressions in the present analysis were performed using Systat packaged programs (Wilkinson, 1990).

Lowess regressions facilitate visual estimates of the two variables studied in this analysis (Figure 1; see also Cheverud *et al.*, 1992). These variables are the degree of bimaturism (in years), the proportion of dimorphism due to growth rate differences (pr) and the proportion of dimorphism resulting from body weight bimaturism (pt). **Bimaturism is defined in the present study as a sex difference in age at cessation of body weight growth. Bimaturism is measured by subtracting age at female growth cessation from age at male growth cessation.** The proportion of dimorphism due to difference in rate of growth is estimated by measuring the percentage of total dimorphism observed at the age of female growth cessation (Figure 1). In other words, the rate proportion is estimated by dividing r by the total dimorphism (D). The proportion due to difference in age at growth cessation is simply one minus the proportion due to rate. These two proportions measure the effects of rate differences and bimaturism, respectively, on dimorphism.

Values for pr and pt are calculated only for those species in which dimorphism exceeds 1.25. This procedure is necessary because pr and pt do not reflect varying degrees of dimorphism; even minute levels of dimorphism could be partitioned into rate and duration compounds by this method. For example, a mean sex difference of 1 g can be parcelled into pr and pt as easily as 100 kg of dimorphism. Thus, pr and pt are "dimorphism free" measures of ontogenetic sex differences. This property may preclude extensive use of pr and pt values in statistical hypothesis tests directed toward explaining variation in dimorphism.

Exclusion of non-dimorphic species helps ensure that the phenomenon of dimorphism is not confounded with monomorphism because of arithmetic artifacts. Limiting the analysis in this manner removes all callitrichids, *Aotus trivirgatus*, *Callicebus moloch*, *Presbytis obscura*, *Presbytis cristata* and hylobatids, resulting in a sample of 31 species. There are no species in the sample of 45 species with estimates of dimorphism between 1.15–1.25.

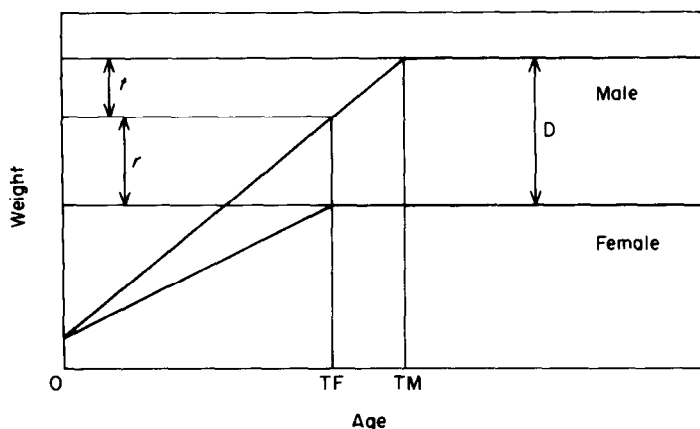


Figure 1. Idealized growth curves illustrating measurement of proportional contributions to dimorphism. Ontogenetic components of total adult dimorphism (D) are estimated by r , resulting from rate differences and t resulting from duration differences. Division of r by D gives the proportion of total dimorphism due to sex differences in rate of growth (pr). Division of t by D provides an estimate of proportion of total dimorphism arising from sex differences in duration of growth (pt).

Derivation of accurate estimates of bimaturism, pr and pt hinges on the ability to estimate ages at growth cessation. These estimates are obtained visually from lowess plots and accuracy to the nearest 3 months is attempted. Specifically, an inflection separating a post-natal growth rate from a flatter adult regression is taken as the age at growth cessation (see Figure 1). A straight-edge ruler is placed perpendicular to the x -axis on a printed copy of the lowess regression. An inflection defining age at female growth cessation is designated and male weight at this age is determined by intersection of the male lowess curve and the straight-edge (see Figure 1). Male age at growth cessation is estimated in a similar manner. Adult weights are calculated by averaging all data points at ages in excess of 1 year past the estimated age at growth cessation.

This method is subjective. In some cases, female growth decelerates over a long period of time, making a precise estimate of age at growth cessation difficult. This problem is, however, fairly infrequent. Longitudinal data were inspected in situations where estimation of growth cessation was problematic and these estimates were generally consistent with cross-sectional estimates.

Intraobserver error is evaluated for the percentage of dimorphism resulting from rate differences in growth (pr). Means for two trials over the sample of 31 species for which pr (and therefore, pt) are calculated are nearly identical (trial 1 pr mean = 0.517, trial 2 pr mean = 0.544). A t -test comparing these means suggests no significant differences ($t = 0.352$, $P < 0.73$). Thus, estimates seem consistent, at least within a single observer.

Dimorphism is measured as the mean of male adult weights divided by the mean of female adult weights. Female weight is taken as a measure of species size.

Results

Variation in bimaturism

Bimaturism is very commonly observed in primate species and there appears to be considerable diversity in the degree of bimaturism among primate species (Table 2). The length of the

Table 2

Ages at growth cessation, bimaturism (measured as male-female) and duration of female growth as a percentage of male growth period

Species	Age at growth cessation			Percent bimaturism
	Male	Female	Bimaturism	
<i>S. fuscicollis</i>	2.00	2.00	0.00	1.00
<i>S. geoffroyi</i>	1.00	1.00	0.00	1.00
<i>S. imperator</i>	1.50	1.50	0.00	1.00
<i>S. oedipus</i>	2.00	2.00	0.00	1.00
<i>L. r. rosalia</i>	2.00	2.50	-0.50	1.25
<i>C. goeldi</i>	1.50	2.00	-0.50	1.33
<i>C. jacchus</i>	2.25	2.25	0.00	1.00
<i>C. pygmaea</i>	1.50	1.50	0.00	1.00
<i>S. sciureus</i>	4.50	3.50	1.00	0.78
<i>C. apella</i>	7.50	4.50	3.00	0.60
<i>C. moloch</i>	3.50	3.50	0.00	1.00
<i>A. trivirgatus</i>	2.80	3.20	-0.50	1.36
<i>A. geoffroyi</i>	6.50	5.50	1.00	0.85
<i>A. caraya</i>	7.50	4.50	3.00	0.60
<i>A. nigroviridis</i>	5.50	4.50	1.00	0.82
<i>C. aethiops</i>	5.50	4.00	1.50	0.72
<i>C. diana</i>	8.50	6.50	2.00	0.76
<i>C. mitis</i>	7.50	9.00	-1.50	1.20
<i>C. neglectus</i>	5.50	5.25	0.25	0.95
<i>E. patas</i>	6.00	4.50	1.50	0.75
<i>M. talapoin</i>	7.50	5.50	2.00	0.73
<i>C. t. atys</i>	7.00	5.75	1.25	0.82
<i>M. arcoides</i>	9.75	8.00	1.75	0.82
<i>M. cyclopis</i>	8.50	8.50	0.00	1.00
<i>M. fascicularis</i>	8.50	6.50	2.00	0.76
<i>M. fuscata</i>	11.00	8.00	3.00	0.72
<i>M. mulatta</i>	9.50	5.50	4.00	0.58
<i>M. nemestrina</i>	8.50	6.75	1.75	0.79
<i>M. nigra</i>	8.50	8.50	0.00	1.00
<i>M. radiata</i>	8.75	6.50	2.25	0.74
<i>M. silenus</i>	7.50	4.50	3.00	0.60
<i>P. cynocephalus</i>	9.00	7.50	1.50	0.83
<i>P. (M.) leucophaeus</i>	9.00	9.00	0.00	1.00
<i>P. (M.) sphinx</i>	9.50	7.75	1.75	0.82
<i>C. guereza</i>	6.00	5.00	1.00	0.83
<i>P. cristata</i>	4.50	4.50	0.00	1.00
<i>P. entellus</i>	6.25	5.50	0.75	0.88
<i>P. obscura</i>	5.50	5.50	0.00	1.00
<i>P. nemeaeus</i>	4.50	4.50	0.00	1.00
<i>H. lar</i>	6.25	6.25	0.00	1.00
<i>H. syndactylus</i>	7.50	7.50	0.00	1.00
<i>P. pygmaeus</i> ¹				
<i>P. paniscus</i>	10.50	8.50	2.00	0.81
<i>P. troglodytes</i>	12.00	11.50	0.50	0.96
<i>G. gorilla</i>	12.50	8.50	4.00	0.68

¹See text for discussion.

female growth period averages about 90% of the male growth period. For the 31 dimorphic species, the average length of the growth period for females in comparison to males decreases to about 80%.

Variability in bimaturism occurs within groups of closely related species (Table 2). An increase in bimaturism is observed when squirrel monkeys (*Saimiri sciureus*) are compared to black-capped capuchins (*Cebus apella*). Comparable variability is observed in atelines [*Ateles geoffroyi* (spider monkeys) and *Alouatta caraya* (black howler monkeys)]. It should be noted that results for howler monkeys are somewhat tentative.

Bimaturism is highly variable in guenons, ranging from 3.5 years in diana monkeys (*Cercopithecus diana*) to **– 1.5 years in blue monkeys (*Cercopithecus mitis*)**. **Negative bimaturism (defined as attainment of male adult weight prior to attainment of female adult weight) is an unexpected result, particularly for a species as dimorphic as *C. mitis* (see below)**. Minimal levels of negative bimaturism are also noted (but with differing causes and consequences) for some non-dimorphic species (Table 2, see below).

In macaques, the best-represented clade in this study, there is extreme variation in bimaturism. *Macaca mulatta* (rhesus macaque) shows approximately 4 years of bimaturism, a value that is high both in comparison to some other macaques and to anthropoids in general. Two macaque species [*Macaca cyclopis* (Taiwan macaques) and *Macaca nigra* (Sulawesi black “ape”)] exhibit dimorphism in the absence of bimaturism.

Although underrepresented in this data base, baboons (including *Mandrillus* species) seem to show rather limited bimaturism. Data for *Papio* (*Mandrillus*) *leucophaeus* are limited. Similarly, bimaturism is restricted in colobines, but this taxon is also not well sampled.

Variability in bimaturism is pronounced in hominoids. About 2 years of bimaturism characterize bonobos (*Pan paniscus*), but there is little bimaturism in common chimpanzees (*Pan troglodytes*). Bimaturism is expressed in gorillas (*Gorilla gorilla*) and female gorillas grow for about the same amount of time as female bonobos. Orang-utans (*Pongo pygmaeus*) are highly unusual in that male body weight growth may not cease (i.e., unlimited male growth).

A scatterplot of bimaturism against size for the dimorphic species suggests no clear relations between these variables (Figure 2), at least at a broad level. Comparisons among groups of closely related species are presented in subsequent sections.

Variability in the effects of rate and duration differences in growth

Proportions *pr* and *pt* measure the contributions of rate differences and bimaturism to dimorphism, respectively. Analysis of 31 dimorphic species in this sample suggests that differences in rate of growth and differences in duration of growth are both very important in production of body size dimorphism (Table 3). On average, rate differences in growth (*pr*) account for about 54% of the total dimorphism while duration differences (*pt*) account for the remaining 46% of the total dimorphism.

There appears to be considerable variation in the effects of rate and duration differences on dimorphism (Table 3). In addition, comparable levels of dimorphism are clearly the outcome of variation in both rate and duration of growth (Table 4). In some cases, rate differences account for virtually all the observed dimorphism (*pr* = 1.00). In other instances, bimaturism almost exclusively results in dimorphism. Thus, summary of *pr* and *pt* by averages is somewhat misleading because of the presence of extreme values.

The proportion of dimorphism resulting from rate differences (and consequently, the proportion due to bimaturism) appears independent of species size when all 31 species are considered (Figure 3). Comparison of closely-related species may suggest more complexity in

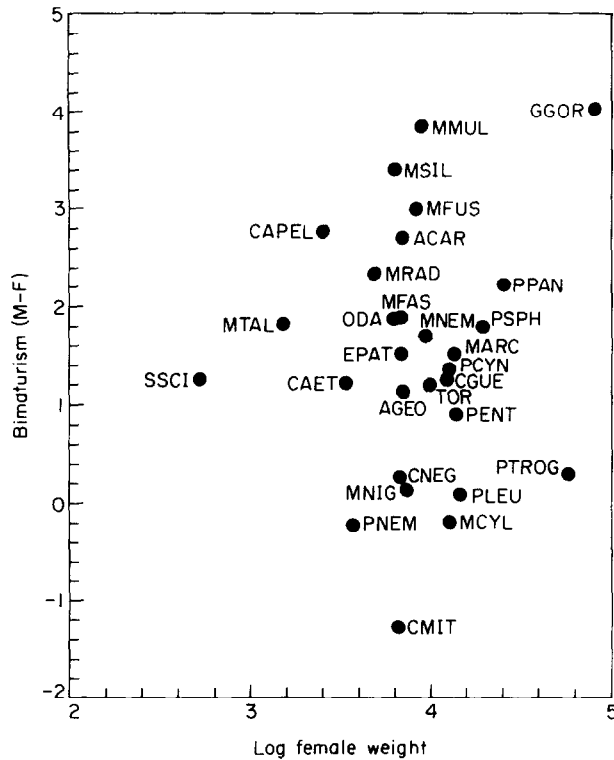


Figure 2. Scatterplot of bimaturism (sex difference in age at body weight growth cessation) *vs.* size (log female adult weight).

the relations between proportional ontogenetic components of dimorphism, size and adult dimorphism. Small sample sizes complicate statistical assessment of this possibility. In addition, variation in *pr* and *pt* is independent of variation in dimorphism. This property may limit the strength of assessments of relations between these variables (Figure 4).

In *Cebidae*, represented by *Cebus apella* and *Saimiri sciureus*, increased differences in duration of growth correspond to increased size and dimorphism. The reverse appears to be true for guenons, with bimaturism in *Miopithecus talapoin* (talapoin) and *Cercopithecus aethiops* (vervets) giving way to increased rate differentiation in progressively larger and more dimorphic *C. diana*, *C. mitis* and *Cercopithecus neglectus* (DeBrazza's guenon). In other words, rate differentiation appears to be correlated with increased species size and dimorphism in guenons.

Macaques show great diversity in values of *pr* and *pt*. Associations between size, dimorphism and either rate or duration differences do not seem to show clear patterns.

In *Papio cynocephalus papio* (guinea or red baboons), rate differences seem most important in the production of dimorphism [see Coelho, 1985; Glassman *et al.*, 1984, for *Papio cynocephalus anubis* (olive baboons)] and the same appears generally true for *Mandrillus* species. A group composed of mangabeys (represented here by *Cercocebus torquatus atys*) and baboons might suggest that increases in size and adult dimorphism correspond to increases in the importance of rate differences. The lack of additional papionins complicates interpretation of these results.

Table 3 Proportional components to dimorphism in anthropoid primates

Species	pr ¹	pt ²	Dimorphism ³	Female weight (kg)	Female growth cessation age (years) ⁴
<i>S. sciureus</i>	0.62	0.38	1.44	0.67	3.50
<i>C. apella</i>	0.21	0.79	1.91	3.20	4.50
<i>A. geoffroyi</i>	0.70	0.30	1.34	6.46	5.50
<i>A. caraya</i>	0.74	0.26	1.86	3.77	4.50
<i>A. nigroviridis</i>	0.83	0.17	1.71	4.66	4.50
<i>C. aethiops</i>	0.08	0.92	1.53	3.45	4.00
<i>C. diana</i>	0.44	0.56	1.82	4.94	6.50
<i>C. mitis</i>	1.00	0.00	1.84	5.59	9.00
<i>C. neglectus</i>	0.86	0.14	1.89	5.66	5.25
<i>E. patas</i>	0.80	0.20	1.89	6.69	4.50
<i>M. talapoin</i>	0.00	1.00	1.32	1.23	5.50
<i>C. l. atys</i>	0.61	0.39	1.54	7.82	5.75
<i>M. arctoides</i>	0.68	0.32	1.47	12.1	8.00
<i>M. cyclopis</i>	0.93	0.07	1.36	11.2	8.50
<i>M. fascicularis</i>	0.13	0.87	1.53	5.15	6.50
<i>M. fuscata</i>	0.27	0.73	1.47	11.0	8.00
<i>M. mulatta</i>	0.17	0.83	1.60	8.37	5.50
<i>M. nemestrina</i>	0.50	0.50	1.93	7.50	6.50
<i>M. nigra</i>	1.00	0.00	1.75	8.88	8.50
<i>M. radiata</i>	0.13	0.87	1.79	5.90	6.50
<i>M. silenus</i>	0.06	0.94	1.63	5.80	4.50
<i>P. cynocephalus</i>	0.61	0.39	1.65	14.3	7.50
<i>P. (M.) leucophaeus</i>	1.00	0.00	2.14	15.3	9.00
<i>P. (M.) sphinx</i>	0.60	0.40	2.17	16.4	7.75
<i>C. guereza</i>	0.89	0.11	1.33	9.26	5.00
<i>P. entellus</i>	0.60	0.40	1.49	13.5	5.50
<i>P. nemeaus</i>	1.00	0.00	1.53	6.86	4.50
<i>P. pygmaeus</i>	0.50	0.50	2.04	60.9	15.0
<i>P. paniscus</i>	0.31	0.69	1.38	33.9	8.50
<i>P. troglodytes</i>	0.73	0.27	1.27	45.0	11.5
<i>G. gorilla</i>	0.39	0.61	1.93	80.8	8.50

¹pt represents the percentage of adult dimorphism attributable to sex differences in duration of growth. ²pr is a measure of the percentage of adult dimorphism attributable to sex differences in rate of growth. ³Dimorphism is measured by the ratio of (male adult weight/female adult weight). ⁴Ages at body weight growth cessation are estimated from lowess regression (see text for further discussion).

The colobines are probably insufficient for adequate comparisons. Effects of rate differences do, however, consistently exceed effects of duration differences in these species.

The hominoids exhibit diversity in patterns of dimorphic growth, illustrating quite clearly that there are species-specific ways in which dimorphism develops. Gorillas and bonobos show a tendency for duration differences to account for adult dimorphism, but common chimpanzees exhibit a large rate component. Longitudinal and cross-sectional data suggest that growth in male orang-utans may be unlimited, making estimates of pr and pt somewhat arbitrary for orang-utans.

Examples of ontogenetic variability

Evaluation of pr and pt values offers an overview of ontogenetic processes that lead to dimorphism. However, additional variation can be illustrated by comparisons of body weight growth curves among selected species. For example, rate differences bring about

Table 4 Proportional components to dimorphism in anthropoid primates ranked according to level of dimorphism

Species	pr ¹	pt ²	Dimorphism ³
<i>P. troglodytes</i>	0.73	0.27	1.27
<i>M. talapoin</i>	0.00	1.00	1.32
<i>C. guereza</i>	0.89	0.11	1.33
<i>A. geoffroyi</i>	0.70	0.30	1.34
<i>M. cyclopis</i>	0.93	0.07	1.36
<i>P. paniscus</i>	0.31	0.69	1.38
<i>S. sciureus</i>	0.62	0.38	1.44
<i>M. arctoides</i>	0.68	0.32	1.47
<i>M. fuscata</i>	0.28	0.73	1.47
<i>P. entellus</i>	0.60	0.40	1.49
<i>C. aethiops</i>	0.08	0.92	1.53
<i>M. fascicularis</i>	0.13	0.87	1.53
<i>P. nanaeus</i>	1.00	0.00	1.53
<i>C. l. atys</i>	0.61	0.39	1.54
<i>M. mulatta</i>	0.17	0.83	1.60
<i>M. silenus</i>	0.06	0.94	1.63
<i>P. cynocephalus</i>	0.61	0.39	1.65
<i>A. nigroviridis</i>	0.83	0.17	1.71
<i>M. nigra</i>	1.00	0.00	1.75
<i>M. radiata</i>	0.13	0.87	1.79
<i>C. diana</i>	0.44	0.56	1.82
<i>C. mitis</i>	1.00	0.00	1.84
<i>A. caraya</i>	0.74	0.26	1.86
<i>C. neglectus</i>	0.86	0.14	1.89
<i>E. patas</i>	0.80	0.20	1.89
<i>C. apella</i>	0.21	0.79	1.91
<i>M. nemestrina</i>	0.50	0.50	1.92
<i>G. gorilla</i>	0.39	0.61	1.93
<i>P. pygmaeus</i>	0.50	0.50	2.04
<i>P. (M.) leucophaeus</i>	1.00	0.00	2.14
<i>P. (M.) sphinx</i>	0.60	0.40	2.17

¹pt represents the percentage of adult dimorphism attributable to sex differences in duration of growth. ²pr is a measure of the percentage of adult dimorphism attributable to sex differences in rate of growth. ³Dimorphism is measured as male adult weight divided by female adult weight.

adult dimorphism in spider monkeys (Figure 5). Dimorphism in this species can be seen largely as a result of female growth deceleration and slight bimaturism. A contrasting pattern is illustrated by *C. mitis* (Figure 6) in which rate differences result in dimorphism due to pronounced growth spurts in males and to an extended female growth period. Female growth appears to have two distinct phases prior to attainment of adult weight, a pattern not seen in other species. Males reach adult body weight prior to females. This assessment is strongly supported by detailed longitudinal data (Leigh, 1992).

A pattern of significant rate differentiation is seen in guinea (red) baboons (Figure 7). Female growth is prolonged and decelerates over an extended period of time. Although males grow for a longer period of time than females, growth rate differences seem mainly responsible for the observed dimorphism. The longer duration of male growth accounts for a small degree of additional dimorphism because the male growth rate is slow during this period (cf. *A. geoffroyi*; Figure 5).

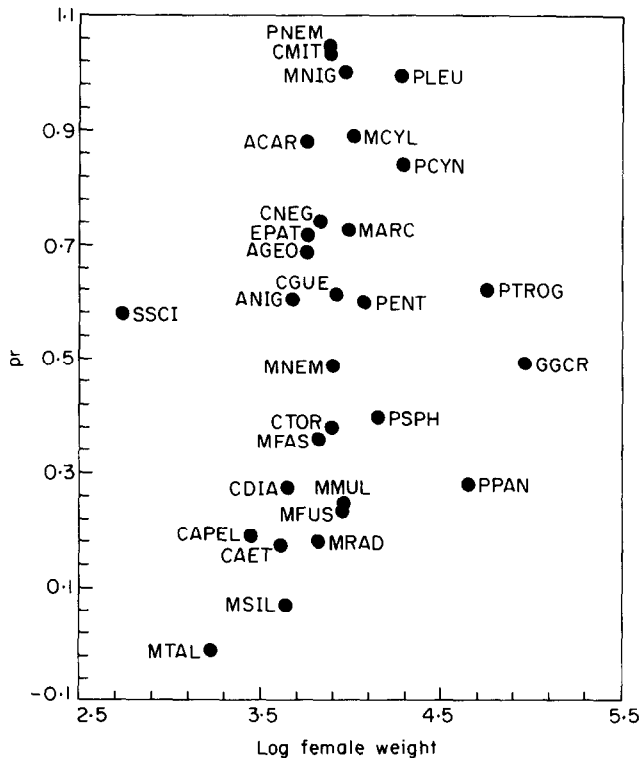


Figure 3. Scatterplot of proportion of total dimorphism resulting from sex differences in rate of growth *vs.* size (log female adult weight).

Taxa in which bimaturism almost exclusively results in dimorphism include *Cebus apella* (black-capped capuchins; Figure 8) and *Macaca silenus* (lion-tailed macaques; Figure 9). Roughly equal contributions of bimaturism and rate differences seem to account for dimorphism in *Macaca nemestrina* (pig-tailed macaques; Figure 10).

Monomorphic species follow the general pattern of decelerating growth seen for *A. trivirgatus* (Figure 11). The decelerating pattern is also observed in large-bodied monomorphic species such as siamangs (*Hylobates syndactylus*). There may be slight differences in rates of growth in monomorphic species, but these are balanced by countervailing differences in duration of growth (Figure 11). More specifically, males of some monomorphic species may grow slightly faster than conspecific females. However, male growth duration is shorter than female growth duration in some monomorphic species (negative bimaturism) in these cases. This pattern characterizes *A. trivirgatus*, *Callimico goeldi* and *Leontopithecus rosalia rosalia*, but cannot be unambiguously detected in other monomorphic species.

Discussion

The results of this study allow clarification of a number of issues, centering on the variability of bimaturism in primates, variability in the effects of rate differences and duration differences on dimorphism and correlations between these variables, size and dimorphism. Finally, patterns of variation in growth are considered.

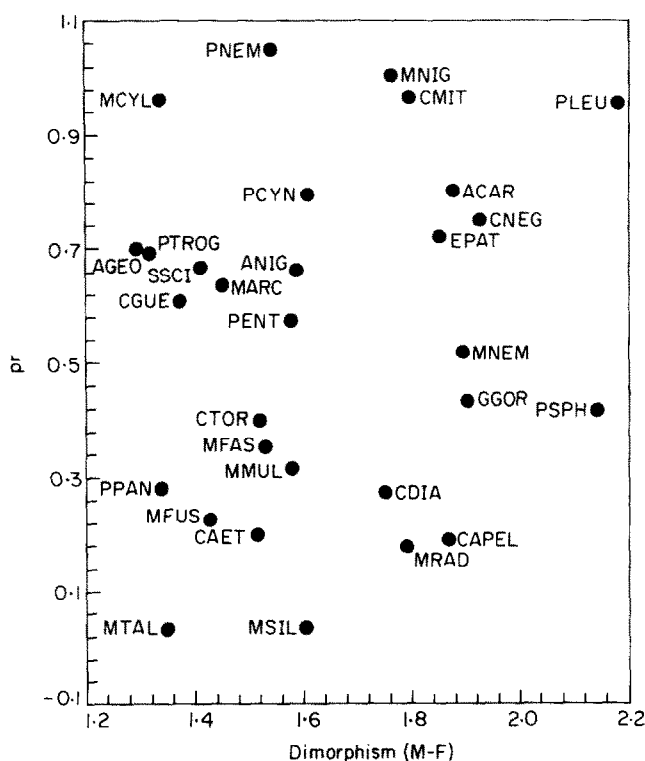


Figure 4. Scatterplot of proportion of total dimorphism resulting from sex differences in rate of growth *vs.* dimorphism (male adult weight/female adult weight).

The expectation that the ontogenetic bases of adult dimorphism vary interspecifically (Georgiadis, 1985; Jarman, 1983; Shea, 1986) is well substantiated by the present study. The presence of bimaturism is very common, and it is highly variable in its degree. This is also illustrated by numerous cases in which sex differences in rate of growth account for the vast majority of adult dimorphism. Putting aside variation in types of rate differences, this result would suggest that there are potentially very marked differences in the ways that primate species attain adult dimorphism. Moreover, the presence of dimorphism in association with negative bimaturism (*C. mitis*) or in the absence of bimaturism [*M. cyclopis*, *M. nigra*, *P. (Mandrillus) leucophaeus*, *Pygathrix nemaeus*] is an unexpected result. Of these cases, that of *C. mitis* is best documented. Additional data would be helpful in further verifying the absence of bimaturism in these other species [especially in *P. (Mandrillus) leucophaeus*].

This study indicates that bimaturism and sexual rate differences may be independent of one another. In other words, the absence of bimaturism leads either to monomorphism or dimorphism. Furthermore, the lack of bimaturism does not imply either the presence or absence of a sex difference in rate of growth. Bimaturism (positive bimaturism) always leads to some level of dimorphism. Combinations of these two processes are most important in producing adult dimorphism, but it is essential to realize they can impact dimorphism independently.

The present analysis permits a more detailed understanding of the variability in ontogenetic processes that lead to dimorphism than previous analyses (Shea, 1986; Watts, 1986).

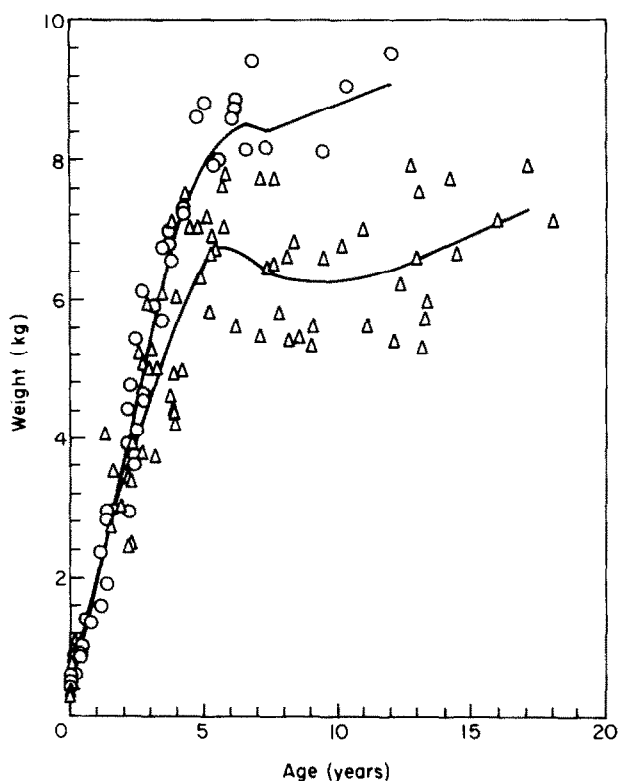


Figure 5. Lowess estimated growth curves for *Ateles geoffroyi*. Persistent deceleration of female growth seems to account for a large portion of the observed dimorphism. Male growth decelerates and ceases later than female growth.

Shea argues that body weight bimaturism is a common feature of primate growth and suggests that there may be great variation in the role that bimaturism plays (1986:108). The present study confirms Shea's point through investigation of a much more complete and better documented data base. High levels of dimorphism can be attained in the absence of major differences in duration of growth, a result that parallels Shea's (1986) earlier result for guenons.

Reconsideration of Watts' (1986) assessment of ontogenetic inputs into dimorphism may be required if findings for weight growth are generalizable to growth in length. Specifically, her finding of conservative (perhaps nearly constant) interspecific levels of skeletal bimaturism contrasts with the results of the present study. Limited variation in bimaturism would imply that dimorphism is produced mainly through rate differences in growth. The diversity observed in the present analysis contrasts with this idea. Differences in conclusions between Watts and the present study may be due either to greater species diversity in the present study or to differences in the variables analysed.

Negative bimaturism is observed for some non-dimorphic species and at least one strongly dimorphic species (*C. mitis*). Males and females reach adult body weight at the same time in several dimorphic species. Unlimited growth in *P. pygmaeus* implies extreme body weight bimaturism. A similar pattern is reported by Jolicœur (1985) for male elephant seals

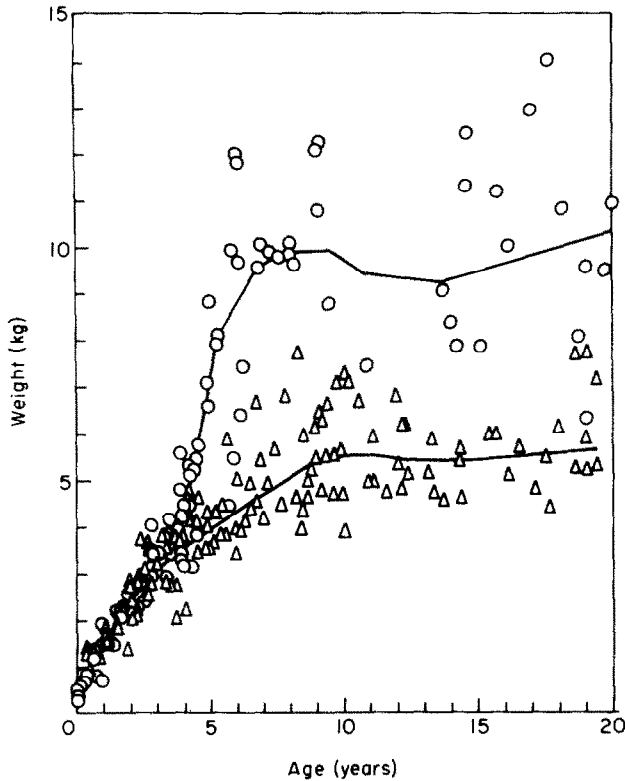


Figure 6. Lowess estimated growth curves for *Cercopithecus mitis*. A marked increase in the rate of male growth seems to account for dimorphism in this species.

(*Mirounga leonina*) and by Jarman (1983) for several species of large terrestrial herbivores. Thus, the present study indicates that there is variation in bimaturism and especially in the effects of bimaturism on dimorphism.

The diversity in the ways that macaques attain dimorphism requires special attention. The variation in this genus is not paralleled by other genera and might imply that better representation of other genera would show comparable diversity. In any case, it is clear that macaques have apparently evolved a number of different pathways to dimorphism.

It should be noted that *M. mulatta* (rhesus) shows a very high level of bimaturism, which is not readily apparent from some previous studies of weight growth in this species. Previous studies often did not include sufficient data for older males to allow accurate estimation of growth cessation. For example, van Wagenen & Catchpole (1956) report male weights up to 8 years of age, Gavan & Hutchinson (1973) up to 7.5 years and Kirk (1972) up to 8 years. Given that *M. mulatta* seems derived in terms of a high level of body weight bimaturism, it is extremely interesting that, in terms of length growth bimaturism, this species shows a pattern comparable to other species (see Watts, 1986).

The present analysis does not unambiguously support the hypothesis that bimaturism is consistently correlated with size within groups of closely related species (cf. Shea, 1986: 107); a more complex situation is revealed. For example, within groups of closely related cercopithecoids (guenons, mangabeys and baboons), size, dimorphism and differences in

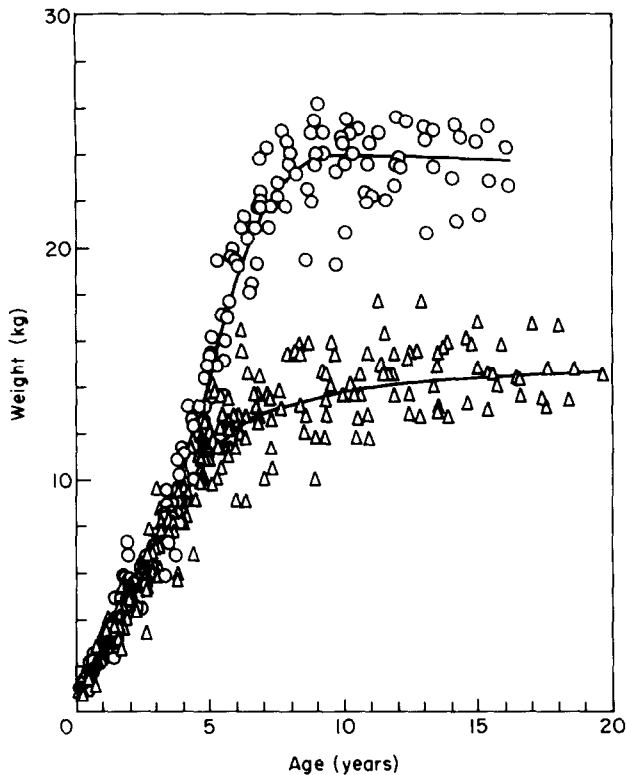


Figure 7. Lowess estimated growth curves for *Papio cynocephalus papio*. An increase in male growth rate plus prolonged female growth deceleration account for the majority of the dimorphism in this taxon.

rate of growth may be positively associated. There are no consistent associations of this kind within *Macaca*. Bimaturism shows associations with size in *Cebidae* (*S. sciureus* to *C. apella*) and a positive association between dimorphism, size and bimaturism could be suggested for hominoids. The lack of consistency in size-relatedness of these variables may imply that other ecological or social variables play major roles in determining the presence and degree of rate differences and bimaturism in primates. Research currently in progress addresses such issues (Leigh, 1992).

Variation by sex among species in growth rate and duration illustrates the complexity of developmental processes that result in dimorphism. For example, males of many species often exhibit marked growth spurts. These growth spurts frequently have large effects on adult dimorphism. Generally, the effects of growth spurts on dimorphism seem more substantial than the effects of male growth prolongation because late male growth rates are often very slow.

Male growth spurts tend to define rate-dimorphic species (e.g. *C. mitis*, *P. c. papio*). In these species, the male growth rate increases, quickly separating male and female growth trajectories. However, in duration-differentiated species, male growth rates tend to be stable, with little or no increase in growth rate (e.g., *M. silenus* and *C. apella*). Consequently, two basic patterns of male growth can be distinguished, involving either a growth spurt or prolonged period of growth.

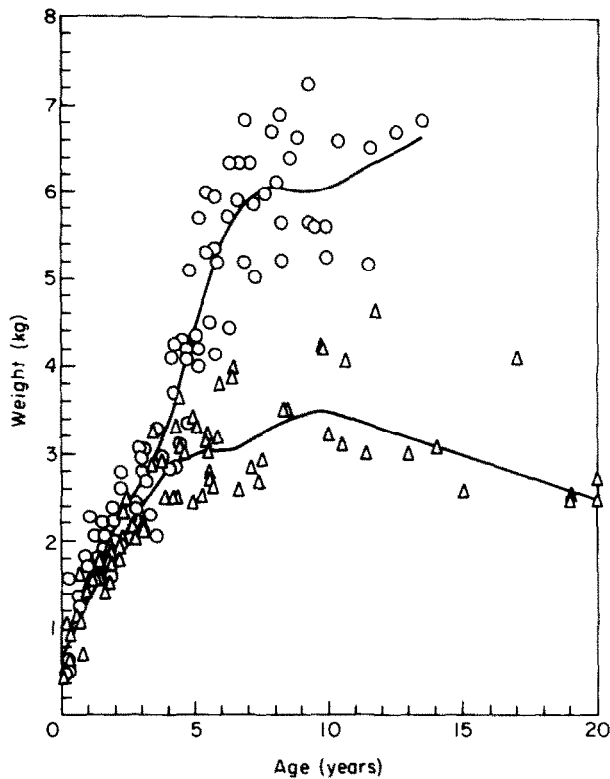


Figure 8. Lowess estimated growth curves for *Cebus apella*. Prolonged male growth is primarily responsible for the level of dimorphism observed in this species.

It is possible that these two contrasting male developmental trajectories have differing evolutionary bases. Dimorphism in some species may be largely the outcome of evolutionary factors that increase male growth rate. In other species, factors that prolong male growth duration may be seen as causes of dimorphism. Thus, an explanation of adult dimorphism would require identification of these factors and a model of how they influence ontogeny. Focus on adult dimorphism confounds these potentially separate underlying growth processes.

It is generally assumed that evolutionary modification of male ontogenetic trajectories is the primary factor in producing variation in dimorphism. Although variation in male growth rate and duration is obviously important, the present study indicates that variation in female growth rate and duration are key to the ontogeny of dimorphism (Fedigan, 1982; Shea, 1986; Willner & Martin, 1985). For example, prolongation of female growth in *C. mitis* and *P. c. papio* (see above) can be seen as a mechanism that, *ceteris paribus*, limits dimorphism in these species. In other words, cessation of female growth in these species at younger ages would produce extremely high levels of dimorphism. Prolongation of female growth in *C. mitis* is particularly important in producing rate-based dimorphism. In contrast, the pattern of fairly abrupt cessation of female growth in some species (e.g., *C. apella*, *M. silenus*) would tend to increase levels of adult dimorphism. Compared to closely related species, ages at growth cessation in female *Erythrocebus patas* (Rowell, 1977) and in *G. gorilla* (Shea, 1986) may be

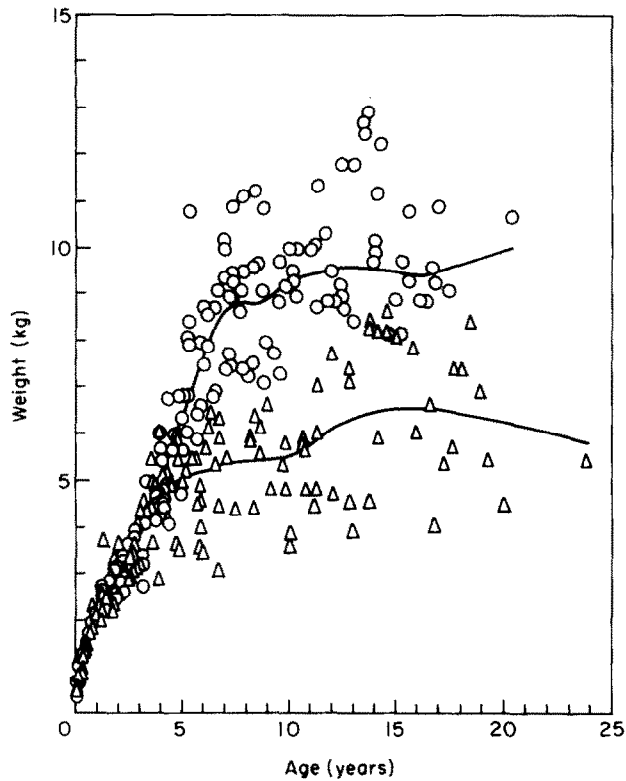


Figure 9. Lowess estimated growth curves for *Macaca silenus*. Duration differences in growth produce the majority of dimorphism in this species.

early. However, the situation for African apes is not straightforward because female *P. paniscus* and *G. gorilla* share approximately equal ages at growth cessation. This would suggest that *P. troglodytes* exhibits a derived pattern of prolonged female growth relative to bonobos and gorillas. In general, however, these results suggest that high levels of dimorphism in these species are related to factors that influence female growth rate and duration (see Shea, 1986). As with diversity in male growth, the “female component” of dimorphism is unrecognizable in studies of adult dimorphism, but can be detected in comparative ontogenetic analyses (Leigh, 1992). Moreover, the effects of female growth on dimorphism may be largely responsible for the lack of consensus as to the evolutionary correlates of dimorphism in primates (see Gaulin & Sailer, 1984; Leutenegger & Cheverud, 1982, 1985; Ely & Kurland, 1989).

It is possible that variation in male growth is ultimately most strongly influenced by sexual selection, which should increase dimorphism. The presence of variation in male ontogenetic pathways may reflect differences in kinds of sexual selection or variability in responses to sexual selection. The expectation of major effects of sexual selection does not deny a role for natural selection. However, this prediction differs both from Watts’ (1986:162) suggestion that natural selection substantially affects male growth and from Shea’s (1986:108) proposition of a more general role for natural selection.

Variation in female growth may be primarily the outcome of natural selection. Natural selection on female growth rate and duration could serve to increase or decrease dimorphism.

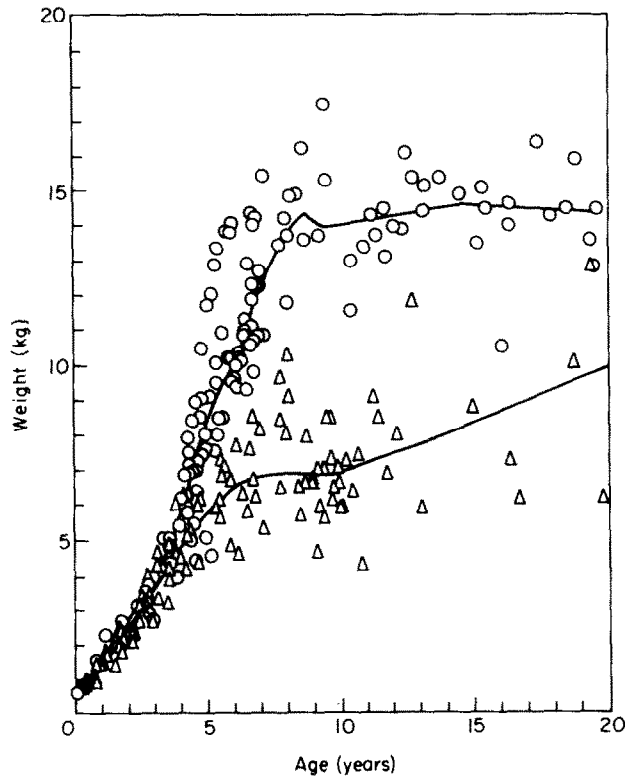


Figure 10. Lowess estimated growth curves for *Macaca nemestrina*. Differences in rate and duration of growth produce similar quantities of dimorphism in this species.

Analyses of body weight growth allow some insight into the processes that influence female growth and, therefore, dimorphism.

It is the interplay of these (and other) factors that produces a given level of dimorphism. Although investigation of the evolutionary bases of the sex differences in growth detailed here are beyond the scope of the present study, it is important to recognize that diversity in ontogenetic bases of dimorphism is characteristic of primates. An ontogenetic perspective lends the opportunity to address, in much more detail than is available by comparison of adult endpoints, the causal factors that are involved in the evolution of dimorphism. Such studies must attempt to explain variation in rate and duration of growth in each sex. Investigation of sex differences in these parameters should lead to a fuller understanding of primate dimorphism.

Summary and conclusions

This analysis investigates the ontogeny of body weight dimorphism in 45 species of anthropoid primates. The study attempts to supplement previous analyses of ontogenetic diversity in primates (Shea, 1986) through analysis of an extensive sample of captive primates. Previous studies of primates (Shea, 1986) and terrestrial herbivores (Georgiadis, 1985; Jarman, 1983) found variation in the ontogenetic bases of sexual dimorphism.

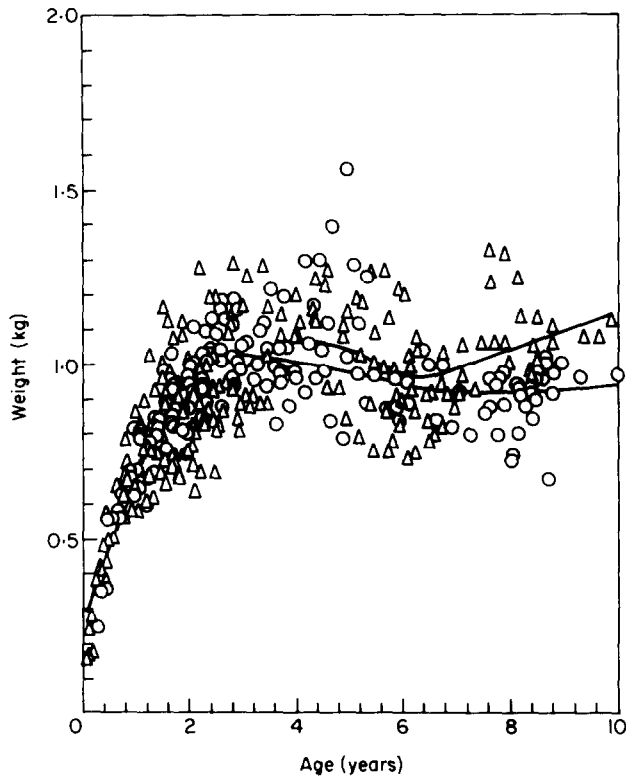


Figure 11. Lowess estimated growth curves for *Aotus trivirgatus*. Males seem to grow slightly faster in this species, but cease growth earlier than females. The male curve lies below the female curve between the ages of 4 and 10 years.

The contributions of sex differences in rate and duration of weight growth are evaluated in this study. In addition, the relations between size and bimaturism and between varying levels of dimorphism and bimaturism are investigated. These problems are addressed using estimates of sex differences in growth derived from non-parametric regression.

The results of this analysis suggest that there is considerable diversity in the ontogenetic processes that lead to body weight dimorphism in anthropoid primates. Bimaturism varies considerably within groups of closely related species. In addition, rate differences are important in producing adult dimorphism, but their contributions to dimorphism vary substantially among groups of closely related species. In some cases, this variation is correlated with size and dimorphism, but additional studies that explore evolutionary factors that underlie these correlations must be undertaken. The large degree of variability in ontogenetic processes that result in adult dimorphism in primates may imply that analyses of adult dimorphism are of limited value in explaining the evolution of body size dimorphism.

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