Nonhuman Primate Models of Human Ontogeny

Steven R. Leigh
Department of Anthropology
University of Illinois
Urbana, IL USA 61801

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ABSTRACT

The lack of formal comparative analyses of human growth and development has limited the usefulness of primates as models of human ontogeny. Thus the present study undertakes qualitative and metric comparisons of primate growth and development in order to identify candidates for models of human ontogeny. First, growth curves from a variety of species are presented and discussed. Second, specific elements of body mass growth curves are compared across the sample. Third, multivariate comparisons of growth in mass across species are presented. Analogs for human male growth are more readily identifiable than analogs for human females. Several species can be identified as candidates for models of human male growth including: *Pan troglodytes, Macaca silenus, Cercocebus atys,* and *Cebus apella*. Human female growth can be best modeled by primate species that exhibit female growth spurts. Specific analogs could include *Macaca fascicularis, Cercopithecus aethiops,* and *Papio hamadryas papio.*

INTRODUCTION

Nonhuman primates provide essential referential models for studies of human biology. Their value as models is most evident for either pathological or normative processes that are difficult to study in humans. Human growth and development is one such process, given that human growth normally requires at least 18 years to complete [1]. Consequently, investigating clinical problems such as growth deficiencies can be a costly and time-intensive undertaking. Moreover, experimental studies of human growth and development are typically not feasible. These limitations greatly complicate attempts to understand the fundamental principles that govern both normal and abnormal human ontogeny.

Study of nonhuman primate growth and development can help mitigate these limitations. In order for analyses of nonhuman primate growth to contribute to increasing our understanding of human growth, a more thorough empirical understanding of the similarities and dissimilarities between human and nonhuman primate ontogeny is required. Only a few species have been thoroughly analyzed as models of human growth. More specifically, several species of macaques and common chimpanzees have been analyzed (i.e., rhesus macaques (*Macaca mulatta*) [2-5]; pig-tailed macaques (*Macaca nemestrina*) [6-8]; chimpanzees (*Pan troglodytes*) [9-11]). Although these particular species are indispensable to biomedical research, they may not be the most adequate models of many human physiological processes, including growth. A related difficulty is that primate ontogeny varies considerably, both within [3] and among species [12-14]. This variation has tremendous potential to reveal mechanisms that control growth, but it has not been explored with special reference to identifying models of human growth.

Finally, a wide array of primate species are currently employed in biomedical research. Basic information on growth in nontraditional species contributes to a more complete understanding of normative biology in such taxa, and opens possibilities for avenues of future research.

It is well-known that, in general, nonhuman primates tend to have shorter growth periods than humans [15], effectively compressing the time (and costs) needed for a complete study of growth and development. Thus, these species would appear to provide efficient models of human growth. Nonhuman primate species will contribute essential information to studies of hormonal mechanisms, given the increasing pace of hormonal research. For example, insulin-like growth factor I (IGF-I) therapies are in an early stage of development [16]. The deployment of such therapies could be accelerated through access to primate experimental models, but this requires better information about primate ontogeny than is currently available. Therefore, this study conducts a comparative analysis of anthropoid primate body weight growth in order to assess the potential value of several species as candidates for models of human growth and development. The research attempts to evaluate quantitative similarities between humans and other primate species in terms of body weight growth using inspection of growth rate (growth velocity) curves, allometric techniques, and multivariate cluster analyses.

Criteria for models of human growth

Evaluation of alternative models of human growth requires well-defined criteria for recognizing candidates as models of human growth. The late Elizabeth Watts advanced three criteria, noting that nonhuman catarrhine primates (Old World monkeys and apes) are characterized by "a delayed development, prolonged pre- and postnatal

growth periods, and an adolescent growth spurt" [15:2]. These three qualitative attributes should, as recognized by Watts, serve as basic criteria for appraising candidates for models of human growth. However, increases in our knowledge of primate growth, along with steady improvements in analytical techniques, enable enumeration of several more specific criteria. Thus, species with the closest metric similarity to humans in terms of body weight growth may be the most desirable as models of human ontogeny, pending investigation of skeletal growth and hormonal analysis of primates. (Body weight growth is analyzed here because data for analyses of skeletal length in primates are not sufficient for comparative analysis [see 17]). In this study, metric similarity is assessed in two ways. First, similarities in specific features of growth can be explored. In other words, species that are most similar to humans on the basis of single variables (e.g., peak velocity) are identified. This information allows recognition of primate models that reflect critical periods of growth, such as the initiation of subadult growth spurts. Second, nonhuman primates that appear to be most similar to humans in terms of overall or aggregate patterns of growth are identified. These species may be quite valuable for studying the long-term effects of diseases or therapies on growth and development.

Both specific and aggregate similarities to humans can be evaluated at two additional levels, including absolute and relative similarities to humans. Comparison of absolute measures of growth are of limited value, and illustrate only the most general kind of similarities between humans and nonhuman primates. Relative measures of growth trajectories, on the other hand, calibrate similarities between humans and other primates in relation to a size-based expectation. This approach is important because it allows identification of species that depart from a size-based expectation in directions

that are comparable to humans (either relatively low or high values). Analysis of relative values allows identification of species that are similar to humans without the confounding influence of body size. Such information is especially important given that most species used in biomedical research are smaller than humans. Consequently, the present paper attempts to identify those species that are relatively most-similar to humans. In all, resemblances between human and nonhuman species are assessed by visual inspection of growth curves, bivariate allometric analysis, and by multivariate cluster analyses.

MATERIALS AND METHODS

Materials

Body weight measures (in kilograms) for 2395 captive primates representing thirty-four species were analyzed for this study (Table 1). These animals are housed at zoological parks and primate centers throughout the world. All subjects are clinically normal, and observations were obtained from records of routine veterinary examinations (usually tuberculosis tests). Additional details regarding the nature of this sample are reported elsewhere [17-20]. Data from nonhuman primate species are compared to human weight growth from Buckler's study of adolescents in Leeds, England [21], which provides highly detailed information about adolescent growth for a number of variables. Plots of human weight velocity are derived from 50th percentile standards presented by Tanner *et al*. [1, 22].

Methods

Data Analyzed

Longitudinal data for each individual nonhuman specimen were visually inspected, but all data are analyzed cross-sectionally. This involves treating each weight

observation as an independent data point, and complicates statistical testing of differences between sexes and among species. Cross-sectional analysis precludes study of individual variation in growth. In addition, Tanner [22] notes that cross-sectional treatment of human growth data may lead to artificially depressed estimates of growth spurt magnitudes. This forces some caution regarding interpretation of the degree of differences among species. However, problems related to cross-sectional data are minimized in the present study because the species studied have short growth periods relative to humans. Shorter growth periods limit the time available for variance in growth spurts [17].

Statistical Techniques

Statistical analyses include several steps. The first steps provide regression estimates of average weight-for-age ("distance") and growth rate ("velocity") curves [12,13]. Subsequent analyses of these data involve measurements obtained from velocity curves. Bivariate allometric analyses comprise the next stage of the analysis, and contribute to specific information on growth by describing the relation of each growth curve measure to size (average adult weight for each species). Lastly, the analysis utilizes multivariate clustering of growth curve measures. This procedure enables identification of species that show the closest overall similarities to human growth. Males and females are analyzed separately.

Description of growth. Nonparametric lowess regressions describe growth for each sex in each species [23-25]. Techniques for applying lowess regression techniques to these data are detailed elsewhere [13, 14]. Approximations of instantaneous growth rates for nonparametric regressions are obtained by dividing the difference in successive

predicted weight values (Y) by the difference in successive age values (X) (equivalent to Coelho's [26] pseudo-velocity curves). Pseudo-velocity curves are presented for a number of the species in this study, and yield estimates of the first derivative for each case. Additional procedures for evaluating these data are described elsewhere [17].

The subadult growth spurt serves as a primary feature in assessing the suitability of a primate model of human growth [9]. The subadult growth spurt is broadly defined as a unimodal, visually detectable increase, peak, and decline in growth rate that occurs at some point during the last two-thirds of the growth period. The term "subadult growth spurt" is used because the endocrine correlates of these changes in growth rates remain unknown, thus precluding their designation as adolescent growth spurts. For example, human adolescent growth spurts represent increases in velocity that peak between puberty and attainment of asymptotic size [27]. It is not currently possible to ascertain whether or not the subadult growth spurts of the nonhuman primates in this sample occur during a homologous developmental period. The terms "growth spurt" and "subadult growth spurt" are used interchangeably throughout the text. Plots of pseudo-velocities for selected species are presented so as to allow qualitative assessments of growth in selected species.

Bivariate allometric analyses. The basic analyses for this study center on regressions of measurements derived from velocity curves. These regressions allow an understanding of the degree of similarity between humans and nonhuman primates for specific variables, and are directed towards defining relative similarities in growth between humans and nonhuman primates for specific variables. A total of seven variables are evaluated relative to adult weight (size), including: peak velocity, weight at

peak velocity, age at peak velocity, "take-off" velocity (defined as minimum pre-spurt growth rate), age at "take-off" velocity, age at return to "take-off" velocity, and duration of spurt (the difference in ages at "take-off" and return to "take-off" velocities) (Fig. 1). These data are subjected to allometric regressions after transformation to natural logarithms. Human growth data analyzed in the present study are summarized in Buckler's Table 8.1 [21]. These data include averages for peak velocity, age at peak weight velocity, weight at peak velocity, and weight at 18 years of age (as a measure of adult size). Estimates of "take-off" velocities, ages, and weights are obtained from Buckler's appendices. Because they are not calculated in precisely the same way as the nonhuman data, they may not be fully congruent with estimates for other species. Moreover, these data differ from Tanner *et al*'s [1] standards by showing higher female take-off velocity, lower female peak velocity and slightly higher male peak velocity. In addition, the substantial variation in human growth [28, 29] is not analyzed by the current study. It is assumed that intraspecific variation probably does not exceed the interspecific variability that is the primary focus of the present analysis. The subtlety of female growth spurts for some species complicates measurements: For these cases, a fairly liberal definition of growth spurts is utilized.

Allometric analyses are accomplished with reduced major axis regressions. These regressions account for error in both the dependent and independent variables [30], and are calculated in Systat's Nonlin module [31]. Residuals from reduced major axis regressions are defined by a perpendicular line that extends from the estimated regression line to the data point. Humans are excluded from calculation of reduced major axis regression lines, but human bivariate data points are superimposed on the plots along

with bivariate data points for other species and estimated regression lines. Excluding humans from the regressions permits a measure of the degree of similarity between humans and other taxa without the influence of human data on the regression. Allometric results are presented mainly as plots (rather than as tables) because plots preserve the relations among data points. Finally, interspecific allometric analyses may have serious limitations arising from the lack of independence among data points. Consequently, procedures outlined by Garland and Adolf, which involve calculation of independent contrasts, are employed [32, 33]. This approach gives a general view of the effects of phylogeny.

Multivariate analyses. The last stage of the study presents a series of cluster analyses. This segment of the analysis complements the bivariate portion of the study by identifying species that seem to present a general or overall similarity to humans in terms of ontogeny. Cluster analyses are undertaken on logged measures described previously (Fig. 1) using single-linkage algorithms with either Euclidean distances (if variables are measured on the same scale) or Pearson correlations (if variables are measured on different scales). In addition, residuals from reduced major axis regressions are subjected to cluster analyses in order to describe the overall similarity in *relative* values between humans and other species. An alternative approach would be to divide each measure by body weight. This approach was not taken because the objective of clustering is to identify the species in this sample with the closest similarity to humans. Furthermore, several species present values of zero for age at initiation of growth spurts, precluding calculation of ratios. Cluster analyses are separated into several distinct categories (Table 2). All statistical analyses are accomplished with Systat statistical software [31].

RESULTS

Patterns of variation in growth

Subadult growth spurts are observed in several species within each of the three anthropoid superfamilies (Ceboidea, Cercopithecoidea, and Hominoidea). Species with growth spurts are expected to provide the most robust models of human growth. Growth spurts occur in both female and male primates, with clearly-defined spurts occurring more frequently in males than in females. New World monkeys that weigh less than about 1 kilogram do not generally exhibit growth spurts and are not considered further (see [13, 34]).

The only New World monkey in this sample with an unambiguous growth spurt is the black-capped capuchin (*Cebus apella*) (Fig. 2). Male growth velocity peaks at about 4.8 years of age at about 1.1 kg/yr. Males may also show a growth acceleration at about 1.5 years of age. On the other hand, female capuchins do not exhibit a detectable growth spurt. The shape of the velocity curve for capuchins is generally similar to the human male growth curve (and possibly human female growth curve). Specifically, there is a substantial delay in the initiation of the growth spurt, with a long period of slow growth prior to the spurt.

Growth spurts are a very common feature of ontogeny in Old World monkeys, which suggests that these species may provide good models of human growth. For instance, cercopithecoids show considerable variation in the shapes of velocity curves. In cercopithecini, male growth spurts are highly variable in duration and magnitude and, to a lesser degree, in the timing of peak velocity (Fig. 3). Moreover, a clearly-defined female growth spurt exists only in the patas monkey (*Erythrocebus patas*). Female

vervet monkeys (*Cercopithecus aethiops*) also exhibit a growth spurt, but it is comparatively small. Female blue monkeys (*C. mitis*) and DeBrazza's guenon (*C. neglectus*) lack growth spurts, but show additional variation in patterns of growth rate deceleration. Sex differences in growth rates at young ages probably result from small sample sizes.

Variation in growth among macaques is substantial (Fig. 4). Males exhibit a growth spurt in all species examined. Females are more variable than males with respect to the presence of growth spurts. In addition, there are sex differences in the magnitude, duration, and timing of peak velocities in these species. The range in male peak velocity extends from 3.72 kg/yr in stump-tailed macaques (*Macaca arctoides*) to .97 kg/yr in crab-eating macaques (*M. fascicularis*). Males of these species seem to have a secondary plateau in growth rates. Unfortunately, it is difficult to ascertain whether this is an artifact of cross-sectional data or a real phenomenon. Obvious female growth spurts are evident in rhesus (*Macaca mulatta*), pig-tailed (*Macaca nemestrina*), and Japanese (*Macaca fuscata*) macaques. Female growth spurts are poorly defined in lion-tailed (*Macaca silenus*), and crab-eating macaques. Female stump-tailed macaques (*M. arctoides*) apparently lack growth spurts.

Male red baboons (*Papio hamadryas papio*) and mandrills (*Mandrillus sphinx*) are characterized by extremely high growth rates (Fig. 5). However, female papioninans generally show minimal growth spurts. The peak absolute magnitude of the male mandrill growth spurt exceeds that for all primates other than large-bodied hominoids. Growth spurt timing and magnitude differs among colobines (Fig. 6). In addition,

females in the two available species evaluated exhibit well-defined growth spurts. Female growth spurts in these species are among the most obvious of all taxa studied.

Apes vary substantially in body size ontogeny (Fig. 7). Growth spurts are absent in gibbons and siamangs. Growth in orangutans, particularly males, is unusual with respect to other primates. Mass growth for males appears to be indeterminate (unlike any other primate species), with a peak velocity reached at around 13.5 years of age. Orangutans are excluded from interspecific allometric analyses because of their unusual pattern of growth (considered in more detail by [19, 20]). Female orangutans seem to lack a single-peaked growth spurt that is comparable to other species. Growth spurts are apparent in the African apes and in humans. However, female common chimpanzees appear to lack a well-defined growth spurt, contrasting with other African ape species [19,20]. Tanner *et al.*'s [1] data for humans show clearly-defined growth spurts (Fig. 9).

Allometric Analyses

Phylogenetic adjustments imply that that there are no mean differences between raw correlations and correlations calculated through Felsenstein's method [33]. Rregression lines are largely determined by Old World monkey data points, and may not adequately represent unbiased, "primate-wide" relations. The fact that species were selected on the basis of the presence growth spurts may further exacerbate this phenomenon. However, the prevalence of Old World monkeys in the regression is advantageous in the sense that these species are among the most accessible in biomedical research.

Age at take-off velocity and size are not correlated (Fig. 9). (Females are designated by *italic* lettering in these figures. Species codes are presented in Table 1.)

Take-off velocity and size are closely correlated (Fig. 10). Humans tend to exhibit relatively low take-off velocities, particularly males. Across primates, female take-off velocities are relatively higher than male take-off velocities, as indicated by the separation between the female and male reduced major axis regression lines. Thus, at common sizes, female primates can be expected to have higher take-off velocities than males. This feature probably results in the generally more obvious nature of the male growth spurt because it helps produce an obvious peak in the velocity curve. It should be noted that female take-off velocities only rarely exceed male take-off velocities within species.

The relationship between peak velocity and size is very consistent across this sample. Moreover, expected values for male and female peak velocities are comparable at common sizes (Fig. 11). Humans are only slightly below the female anthropoid regression line. Thus, humans are not extreme relative to other primates in terms of their peak velocities. Several species return residual values within 20% of the male human value (Table 3). Comparison of weight at peak velocity relative to adult weight suggests that humans are large relative to other primates at peak velocity (Fig. 12) (Table 3). Across primates and at any given size, males are minimally heavier than females at peak velocity. However, human females appear to be relatively heavier than male humans at peak velocity. Female vervets (*Cercopithecus aethiops*) and crab-eating macaques exhibit relatively high values for weight at peak velocity. Colobus monkey (*Colobus guereza*) females are unusually small at peak velocity relative to other species.

Humans reach peak velocity at absolute ages that are in excess of any other primate species (Fig. 13). Although humans are quite distinct from an absolute

standpoint, they are not atypical in relative terms. Capuchins (*Cebus apella*), lion-tailed macaques (*Macaca silenus*), and sooty mangabeys (*Cercocebus atys*) are most similar to human males for these variables (Table 3). It is also important to note that there is considerable variation among primates in terms of both absolute and relative age at peak velocity. Female vervets are closest to humans in relative terms. It can be noted that crab-eating macaques reach peak velocity very late. This may be a consequence of the subtlety of the growth spurt in this case. However, eliminating this case from the regression would bring the regression line much closer to the human female bivariate data point, resulting in a smaller residual value.

Age at return to take-off velocity and size are positively correlated (Fig. 14). In addition, the ages of males at return-to-take-off velocity can be expected to exceed female values at common sizes. Human ages at return to take-off velocity are relatively and absolutely quite high (as could be expected based on the lateness of the human growth spurt). Other species with late male ages at return to take-off velocity include crab-eating macaques and capuchins. For females, crab-eating (*Macaca fascicularis)* and Japanese macaques (*Macaca fuscata)*, as well as pygmy chimpanzees (*Pan paniscus*) show relatively late ages at return to take-off velocity.

The duration of the growth spurt, like many of the other variables analyzed, is postively correlated with size (Fig. 15). The human female growth spurt duration is relatively short. It should be noted that this could be a consequence of differences in measurement techniques. The duration of the human male growth spurt is also relatively short, but the departure from the regression line is less dramatic for males than for

females. Across the remainder of the sample, anthropoid primates exhibit great variation in the duration of growth spurts across smaller size ranges (1.25 to 3 ln units of mass).

Cluster analyses

"Raw" variables.

Cluster analyses for males based on all seven measures of growth confirm the results of bivariate analyses, illustrating that human growth is fairly distinctive relative to other primate species. Cluster analyses for seven-variable analyses are based on Pearson correlation measures of distance, which accounts for differences in scale of variables (e.g., rate vs. age estimates). For all seven variables, a partial cluster diagram (showing only those species most similar to humans) illustrates that human males are loosely bracketed by a number of species (Fig. 16A). As might be expected based on allometric analyses that show size correlations, none of these species is especially close to humans for overall growth. The cluster with which humans are most closely aligned contains species with obvious or high-peaked growth spurts. The cluster analysis for females based on all variables (not shown) provides roughly the same result as for males, with human females not closely aligned with other taxa. However, human females are part of a loose cluster with red baboons (*Papio hamadryas papio*).

Analyses of unadjusted rates suggests that human males cluster closely with chimpanzee species (Fig. 16B). The next most similar species is the pygmy chimpanzee (*Pan paniscus*). In general, these clusters probably reflect differences in the absolute magnitude of growth spurts. They may also reflect comparable body sizes, given the tight correlation between growth rates and size. For females, analyses of rates return results that suggest a loosely organized cluster placing humans with large-bodied ape species (*Pan paniscus* and *Gorilla gorilla*).

The distinctness of human growth is very obvious given cluster analyses of unadjusted growth timing variables, a result that is expected based on allometric analyses (Fig. 16C). Male humans are clearly separated from other primate species for these variables. There do not appear to be close similarities between human males and other species based on these variables. Human females are greatly separated from other species for age measures.

Relative Measures.

Relative measures of growth variables allow similarities between humans and other species to be gauged in relation to departures from allometric expectations. These data are especially important because clusters are formed based on relative measures of growth. Analyses of all seven growth variables suggest that human males can be included within a relatively tight cluster (Fig. 16D). Overall, common chimpanzees (*Pan troglodytes*) and a group of monkey species seem to be most similar to humans. Specifically, humans and chimpanzees are equally distant from a group that includes capuchins (*Cebus apella*), lion-tailed macaques (*Macaca silenus*), and sooty mangabeys (*Cercocebus atys*). Several Old World monkey species fall into the next set of clusters.

Cluster analyses for rate variables show the greatest similarities between humans and black-capped capuchins (*Cebus apella*) (Fig. 16E). This cluster is very shallow when compared to others, with a total cluster distance of only .20. Analyses of age variables place humans into a larger cluster that includes sooty mangabeys (*Cercocebus atys*) and lion-tailed macaques (*Macaca silenus*) (Fig. 16F) These species are included in a still-larger group of several Old World monkey species. .

Analyses of female ontogeny in relative terms indicate that vervet monkeys display overall similarities to humans (Fig. 17). Relative measures for human females are not easily linked to other species on the basis or relative variables. The scarcity of female species in the analysis complicates interpretation of these results.Human females are distinctive relative to other species, with the exception of crab-eating macaques (*Macaca fascicularis*).

DISCUSSION

Human growth in body mass is comparable to several other anthropoid primate species, implying that a number of species can potentially provide informative models of human growth. Moreover, similarities between humans and other primates are detectable at a variety of analytical levels. First, qualitative similarities are evident based on inspection of velocity curves. Qualitative analyses suggest that species with extreme growth spurts can serve as models of human growth. Second, allometric analyses calibrate similarities between humans and other primates for specific ontogenetic variables, highlighting both absolute and relative similarities to particular components of human growth. Finally, cluster analyses, particularly cluster analyses of relative growth variables, quantitatively measure aggregate similarities between humans and other primates.

Qualitative Analyses

Humans are not unique in exhibiting both a male and female growth spurt in mass. This is an important finding because the presence of a growth spurt may signal that certain parts of ontogeny are homologous among species. Homology with respect to discrete elements of growth curves could imply that similar hormonal regulators govern

growth. Moreover, it is likely that species with both male and female growth spurts can be productive as models of human growth. However, the rarity of species with female growth spurts complicates identification of optimal models of human female growth. In light of this uncertainty, gaining additional knowledge about human female growth may require investigation of species with exaggerated growth spurts. Species with obvious female growth spurts include colobine primates and patas monkeys (*Erythrocebus patas*). Thus, these species are probably good potential models of human female growth and development.

Inspection of velocity curves suggests that models of overall or general human male growth might productively utilize those species with delayed growth spurts. Several species exhibit this qualitative pattern, including capuchins (*Cebus apella*), sooty mangabeys (*Cercocebus atys*), and common chimpanzees (*Pan troglodytes*). The discreteness of the growth spurt in these species, as well as in humans, may be partly a product of the delay in the initiation of the growth spurt. Therefore, these species appear to meet the Watts' criterion of delayed development [9]. In contrast, both sexes of several species apparently begin postnatal growth with a body mass growth spurt (e.g., patas monkeys (*E. patas*), hanuman langurs (*P. (S.) entellus*), black-and-white colobus (*C. guereza*). Although growth in these species may not show close metric similarities to humans, they could provide insight into the hormonal mechanisms that control growth spurts. Assuming that androgens play a role in the initiation of growth spurts [35], then it is possible that androgens are present at high levels very early in life in these species. If true, then these species could serve as good models for problems such as precocious puberty.

Allometric Analyses

Allometric analyses illustrate fundamental distinctions between scaling patterns of human growth rates and the scaling of timing of human growth events. Human growth rates tend to be consistent with expectations based on other primate species. On the other hand, the age at which human growth events occur (e.g., age at take-off velocity) are typically much-delayed relative to other taxa. These findings imply that attempts to model human growth should analytically separate investigations of growth rates from those of growth timing.

The close correlation between growth rates and size implies that a number of primate species could contribute to an understanding of the factors that control human growth rates. Moreover, variation around allometric regression lines for growth rates is limited, suggesting that a broad range of species could be used as models for human growth rates. Female and male patterns of growth rate scaling are similar for peak velocity, implying that peak velocities could be modeled independent of sex. However, sex differences in the scaling of take off-velocities require separate models of this component of growth. Scaling analyses illustrate several species with residual values that are comparable with those of humans. By this criterion, sooty mangabeys (*Cercocebus atys*) are perhaps the most adequate model of human male growth. Capuchins (*Cebus apella*), crab-eating macaques (*Macaca fascicularis*), rhesus macaques (*Macaca mulatta*), and common chimpanzees (*Pan troglodytes*) also present at least one residual value within 20% the human range. For females, crab-eating macaques (*Macaca fascicularis*) are the only species within 20% of the human value (for two measures).

Human growth differs most from other primate species for measures of age variation. The timing of the events measured by this analysis (age at initiation of growth spurt, age at peak velocity, age at cessation of growth spurt, and growth spurt duration) almost always occurs absolutely later in humans than in other primate species. In particular, the age at initiation of the growth spurt is absolutely very late in humans, and is the only variable in this study that fails to show a clear correlation with size. This result may imply that few species provide suitable models of factors that influence human growth spurt initiation. However, the presence of size-free variation indicates that further comparative study can pinpoint the factors that induce growth spurts without the potentially confounding influence of size. For other timing variables, male and female scaling patterns differ consistently across the size range, implying that growth timing should be modeled separately in each sex.

Allometric analyses of timing variables suggest that capuchins (*Cebus apella*) can probably provide the best references to humans for age variables. This species is within 20% of the human residual value for three of four regressions. Common chimpanzees (*Pan troglodytes*) meet this criterion for two values, while gorillas (*Gorilla gorilla*), sooty mangabeys (*Cercocebus atys*), and lion-tailed macaques (*Macaca silenus*) each fall within 20% of the human value for one measure. Females are again more difficult to characterize, with vervets (*Cercopithecus aethiops*) and baboons (*Papio hamadryas*) within 20% of the residual value for one measure each.

Cluster Analyses

Cluster analyses demonstrate the close similarities in total growth between humans and several other primate species. Results for unadjusted estimates of growth

parameters typically show that humans are fairly distinct from other species in an absolute sense. For these variables, humans are typically separated from other species by substantial distances. As could be expected based on bivariate analyses, variables that measure the age of growth events distinguish humans from nonhuman primates most clearly.

Cluster analyses of relative values are much informative than clusters on raw variables for defining adequate models of human growth because they track the multivariate departure of humans and other species from a size-based expectation. Models of male growth are again easier to define than models of female growth. For males, cluster analyses tend to regularly align humans with several other several species. Specifically, capuchins (*Cebus apella*) cluster with humans for rate measures, and occur consistently in larger clusters with as humans for all variables. Other species that share clusters with humans include lion-tailed macaques (*Macaca silenus*) (all variables, age variables) and sooty mangabeys (*Cercocebus atys*) (all variables, age variables). Common chimpanzees (*Pan troglodytes*) are equally close to capuchins, lion-tail macaques, and sooty mangabeys for cluster analyses of all variables. In all, the consistent presence of capuchins, sooty mangabeys, and lion-tail macaques in clusters with human males strongly suggests that these species have very high potential as models of human growth. Of these species, sooty mangabeys are the most common in captivity.

Female cluster analyses present an ambiguous pattern, complicating designation of good models. However, vervets (*Cercopithecus aethiops*) cluster closely for all variables. Crab-eating macaques (*Macaca fascicularis*) are grouped with humans for rate

variables. As noted, species with obvious growth spurts, regardless of specific similarities, might provide the most adequate model of human female growth.

CONCLUSIONS

Nonhuman primate species vary substantially in the degree to which their patterns of growth resemble human patterns of growth. Metric evaluation of this variation, along with direct comparison to male and female human patterns of growth, enables identification of possible models for human growth and development. This study assesses these similarities both with and without size-adjustments. In general, species that exhibit growth spurts probably provide the best candidates for models of human growth. Tight correlations with size across species imply that most species can serve as good models for factors that influence growth velocities. However, for variables that reflect the timing of growth events, only a few species closely resemble humans. For males, species such as capuchins (*Cebus apella*), lion-tailed macaques (*Macaca silenus*), and sooty mangabeys (*Cercocebus atys*) seem to be the best candidates for models of processes that control growth timing. Multivariate analyses strengthen this conclusion, illustrating close similarities between these species and human males when size adjustment is undertaken. Female models are more difficult to identify. Species with prominent growth spurts, including patas monkeys (*Erythrocebus patas*), colobine species, gorillas (*Gorilla gorilla*), and pygmy chimpanzees (*Pan paniscus*) may provide the most adequate models of human female growth.

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Table 2

Protocol for cluster analyses. Males and females are analyzed separately.

1. Pearson correlation cluster based on correlations among all variables.
2. Euclidean distance-based cluster analysis on rate variables.
3. Euclidean distance-based cluster analysis on timing variables.
4. Euclidean distance-based cluster analysis on residual variables from all RMA regressions
5. Euclidean distance-based cluster analysis on residual variables from RMA regressions on growth rates
6. Euclidean distance-based cluster analysis on residual variables from RMA regressions on growth timing variables.

Table 3.

Species that fall within + or - 20% of the human residual value for bivariate regressions. Species within 20% for females are followed by the designation "F." Otherwise, results apply to male regressions.

Regression analysis (figure number)	Species
Age at take-off velocity (9)	*Macaca fascicularis* (F only)
Take-off velocity (10)	*Cebus apella* *Macaca fascicularis* (M,F)
Peak velocity (11)	*Macaca mulatta* *Macaca arctoides* *Gorilla gorilla* *Pan troglodytes*
Weight at peak velocity (12)	*Cercocebus atys* *Macaca fascicularis* (F only)
Age at peak velocity (13)	*Cebus apella*
Age at return to take-off velocity (14)	*Cebus apella* *Macaca fascicularis*
Growth spurt duration (15)	*Pan troglodytes* *Papio h. papio* (F only)

Figure Legends

Figure 1. Representation of variables measured. This diagram shows an average velocity curve for male baboons (*Papio hamadryas papio*). Measures along the Y-axis include peak velocity (PV) and take-off velocity (TOV). Measures along the X-axis include age-at-take-off velocity (ATOV), age-at-peak velocity (APV), and age-at-return-to-take-off velocity (ARTOV). Two additional measures were obtained for each species, including weight at peak velocity (derived from weight-for-age curves) and growth spurt duration (ARTOV-ATOV). Allometric analyses utilize log transforms of these variables.

Figure 2. Velocity curves for squirrel monkeys (*Saimiri sciureus*) and black-capped capuchins (*Cebus apella*). Females are shown as solid lines, males as dashed lines.

Figure 3. Velocity curves for guenons. Species shown include *Cercopithecus mitis* (blue monkey), *Cercopithecus neglectus* (DeBrazza's guenon), *Cercopithecus aethiops* (vervet monkey), and *Erythrocebus patas* (patas monkey). Females are shown as solid lines, males are shown as dashed lines.

Figure 4. Velocity curves for macaques. Species shown include *Macaca mulatta* (rhesus macaque), *Macaca nemestrina* (pig-tailed macaque), *Macaca fuscata* (Japanese macaque), *Macaca silenus* (lion-tailed macaque), *Macaca fascicularis* (crag-eating macaque), and *Macaca arctoides* (stump-tailed macaque). Females are shown as solid lines, males are shown as dashed lines.

Figure 5. Velocity curves for *Cercocebus atys* (sooty mangabey), *Mandrillus sphinx* (mandrill monkey), and *Papio hamadryas papio* (red or Guinea baboon). Females are shown as solid lines, males are shown as dashed lines.

Figure 6. Velocity curves for colobine monkeys. Species analyzed include *Presbytis (Semnopithecus) entellus* (Hanuman langur), *Presbytis obscura* (spectacled langur), and *Colobus guereza* (black-and-white colobus monkey). Data for female *Presbytis obscura* are not sufficient for the present analysis. Females are shown as solid lines, males are shown as dashed lines.

Figure 7. Pseudo-velocity curves for apes, including *Hylobates lar* (lar gibbon), *Hylobates syndactylus* (siamang), *Pongo pygmaeus* (orangutan), *Gorilla gorilla gorilla* (western lowland gorilla), *Pan paniscus* (pygmy chimpanzee), and *Pan troglodytes* ("common" chimpanzee). Females are shown as solid lines, males are shown as dashed lines.

Figure 8. Growth standards derived from Tanner et al., 1966. Data used for the present study are similar to these values (see text for discussion).

Figure 9. Age at take-off velocity (kg/year) plotted against average adult weight (kg). Species codes are presented in Table 1. Female data points are shown as italicized letters, males as regular fonts. Human females are identified by E, males are shown by

W. Note that humans have the latest ages at take-off velocity. This variable appears to be independent of size.

Figure 10. Take-off velocity (kg/year) plotted against average adult weight (kg). Female data points are shown as italicized letters, males as regular fonts. Human females are identified by E, males are shown by W.

Figure 11. Peak velocity (kg/year) plotted against average adult weight (kg). Female data points are shown as italicized letters, males as regular fonts. Human females are identified by E, males are shown by W.

Figure 12. Weight at peak velocity (kg) plotted against average adult weight (kg). Female data points are shown as italicized letters, males as regular fonts. Human females are identified by E, males are shown by W.

Figure 13. Age at peak velocity (years) plotted against average adult weight (kg). Female data points are shown as italicized letters, males as regular fonts. Human females are identified by E, males are shown by W.

Figure 14. Age at return to take-off (years) velocity plotted against average adult weight (kg). Female data points are shown as italicized letters, males as regular fonts. Human females are identified by E, males are shown by W.

Figure 15. Growth spurt duration (years) plotted against average adult weight (kg). Female data points are shown as italicized letters, males as regular fonts. Human females are identified by E, males are shown by W.

Figure 16. Partial cluster diagrams emphasizing species that show close similarities to humans. Less-similar species have been edited out of the diagram.

A. Cluster results for unadjusted data on all seven measures. Humans are loosely associated with a large group of catarrhines.

B. Cluster results for unadjusted rate variables.

C. Cluster results for unadjusted timing variables. Humans are distinct from other taxa.

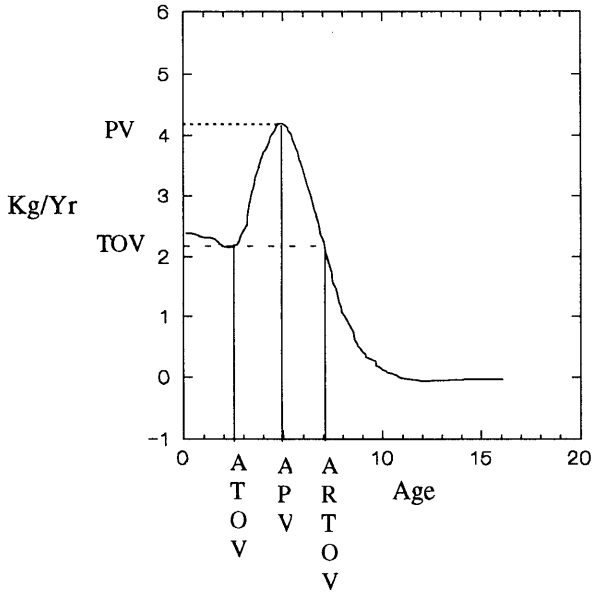
D. Cluster analysis for all variables after size-adjustment.

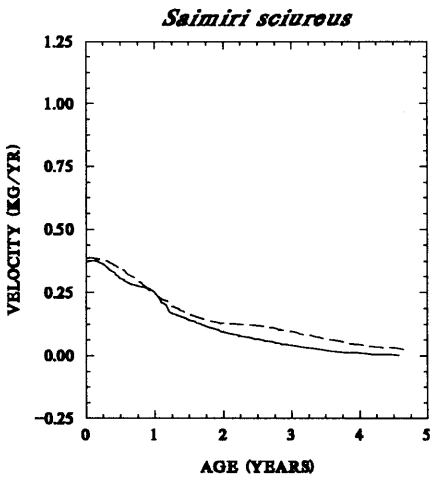
E. Cluster analysis for rate variables after size-adjustment.

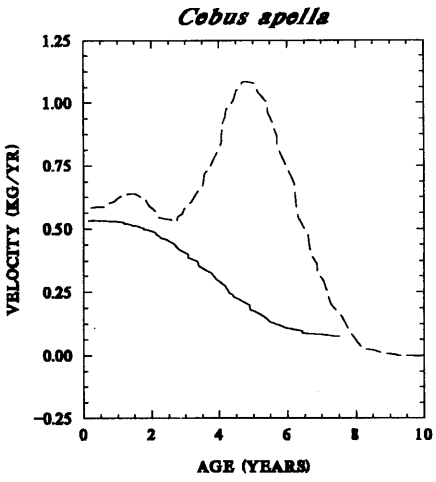
F. Cluster analysis for timing variables after size-adjustment.

Figure 17. Cluster analysis for females, based on all variables following size adjustment.

Papio h. papio




Saimiri sciureus
VELOCITY (KG/YR)
1.25
1.00
0.75
0.50
0.25
0.00
-0.25
0
1
2
3
4
5
AGE (YEARS)


Cebus apella
VELOCITY (KG/YR)
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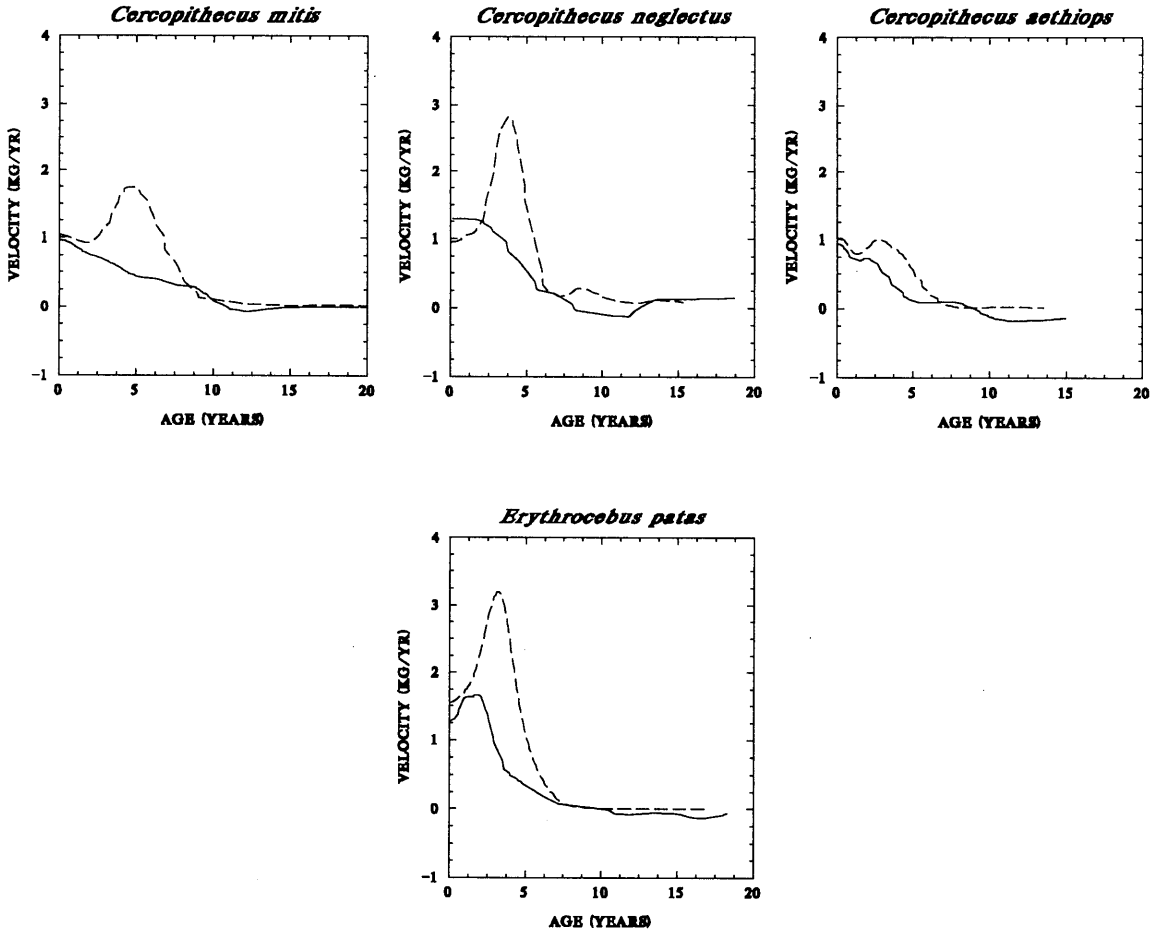
0.50
0.25
0.00
-0.25
0
2
4
6
8
10
AGE (YEARS)


Cercopithecus mitis
Cercopithecus neglectus
Cercopithecus aethiops
Erythrocebus patas
VELOCITY (KG/YR)
AGE (YEARS)
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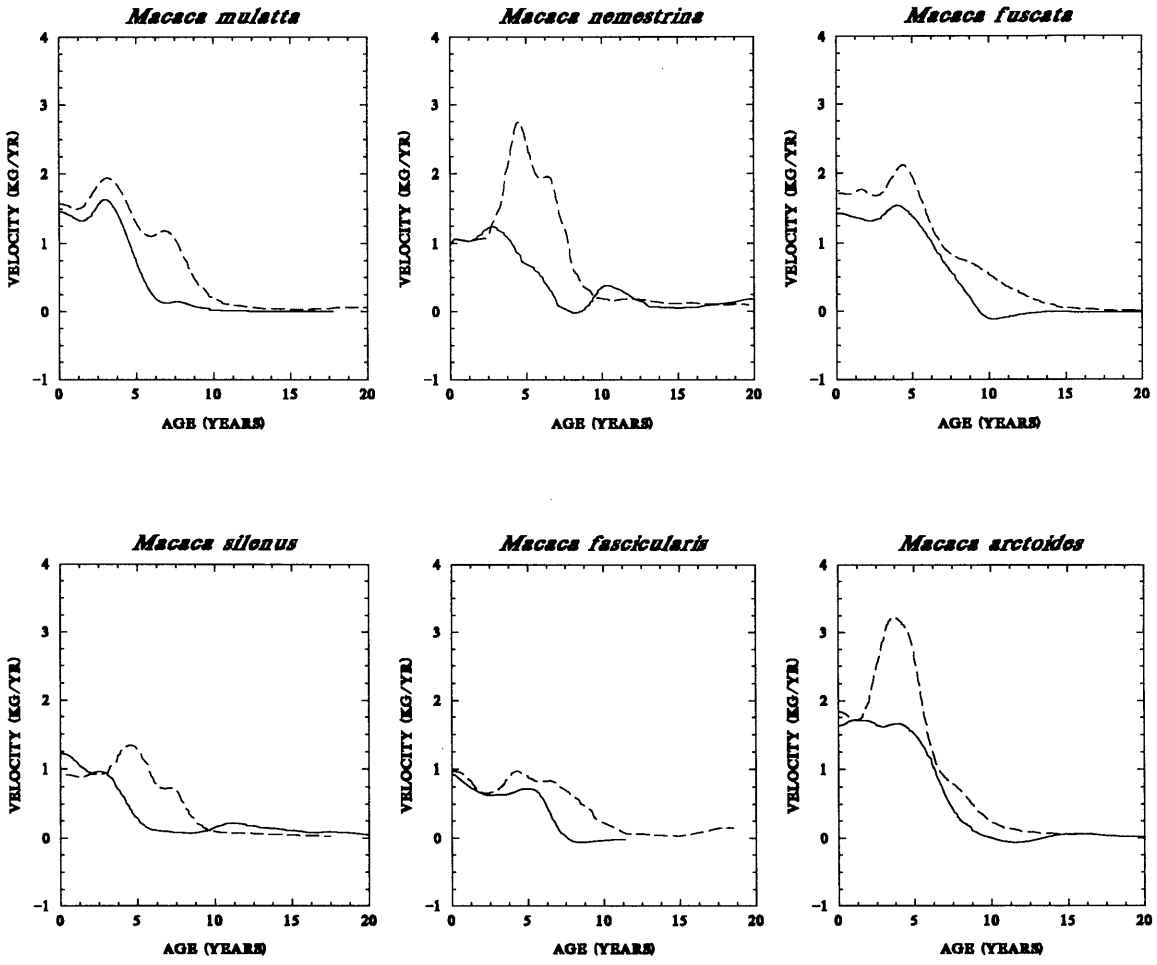
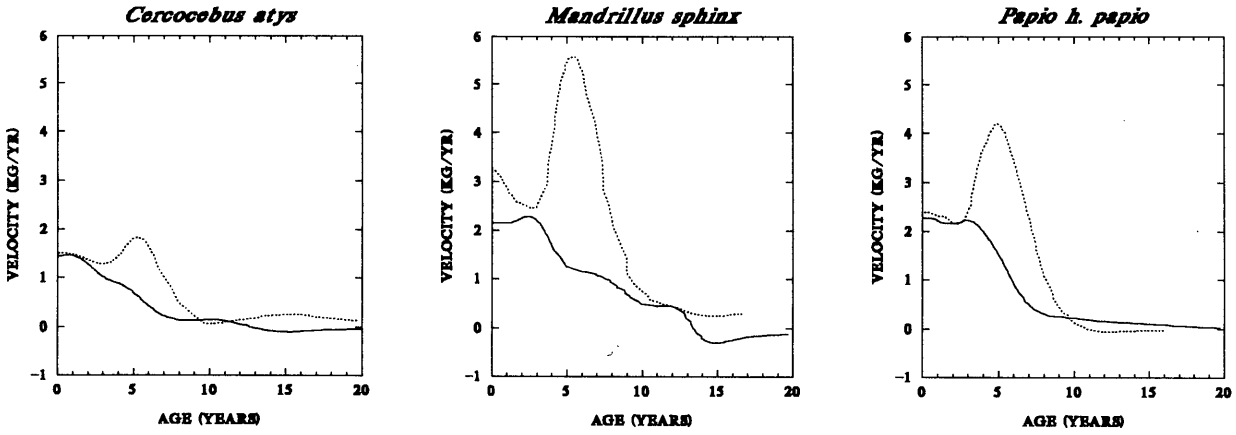
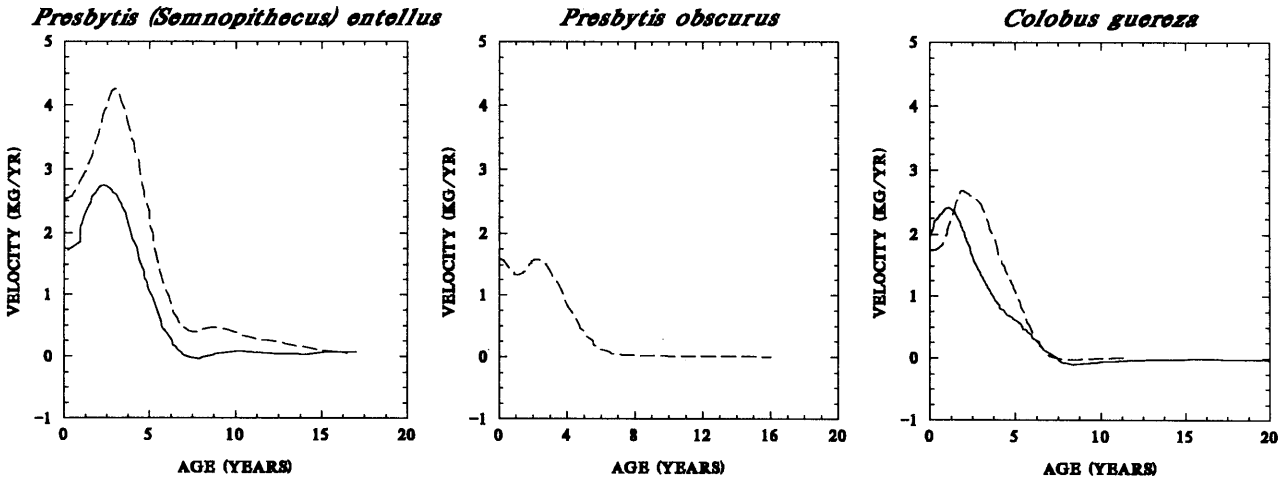
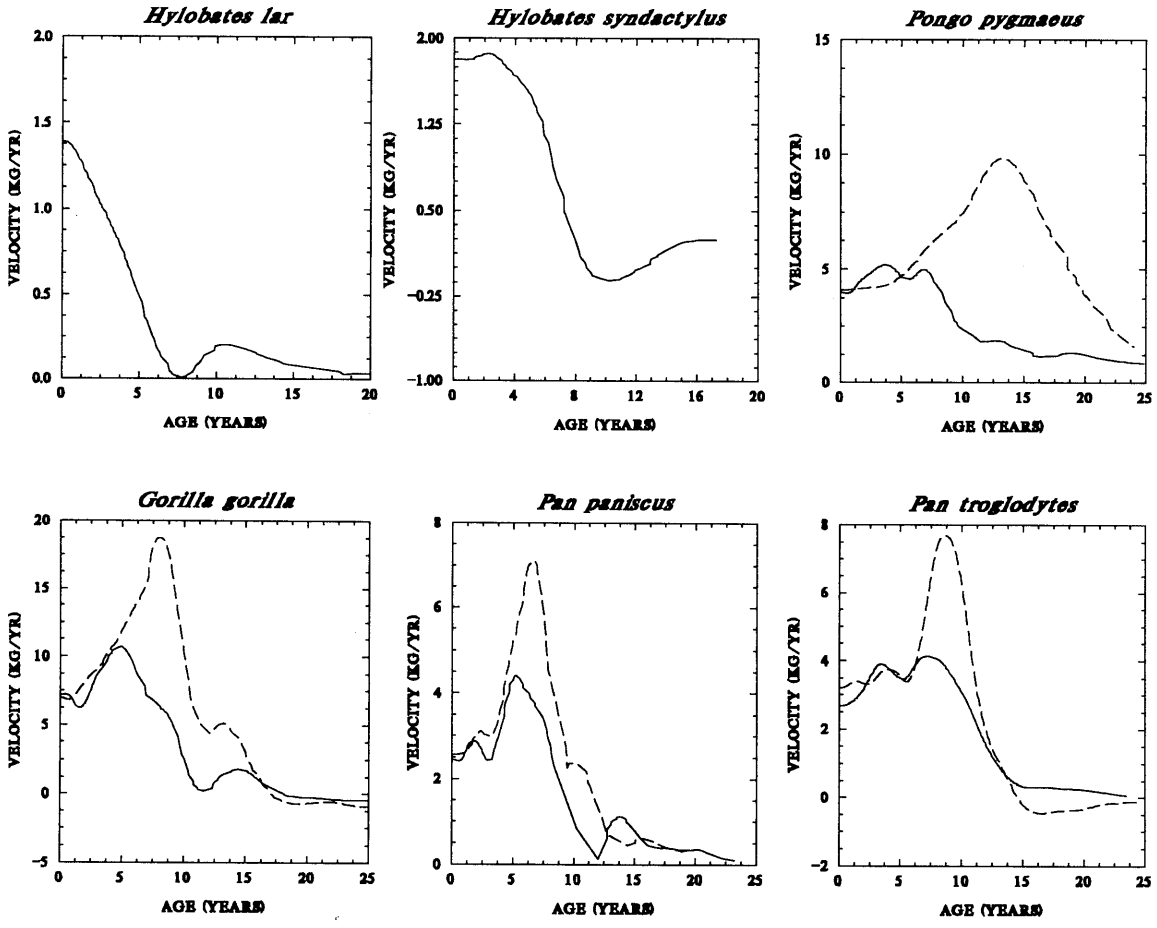
3
2
1
0
-1
0
5
10
15
20


Macaca mulatta
Macaca nemestrina
Macaca fuscata
Macaca silenus
Macaca fascicularis
Macaca arctoides
VELOCITY (KG/YR)
AGE (YEARS)
4
3
2
1
0
-1
0
5
10
15
20


Cercocebus atys
Mandrillus sphinx
Papio h. papio
VELOCITY (KG/YR)
AGE (YEARS)
6
5
4
3
2
1
0
−1
0
5
10
15
20


Presbytis (Semnopithecus) entellus
Presbytis obscurus
Colobus guereza
VELOCITY (KG/YR)
AGE (YEARS)
5
4
3
2
1
0
−1
0
5
10
15
20
4
8
12
16


Hylobates lar
Hylobates syndactylus
Pongo pygmaeus
Gorilla gorilla
Pan paniscus
Pan troglodytes
VELOCITY (KG/YR)
AGE (YEARS)

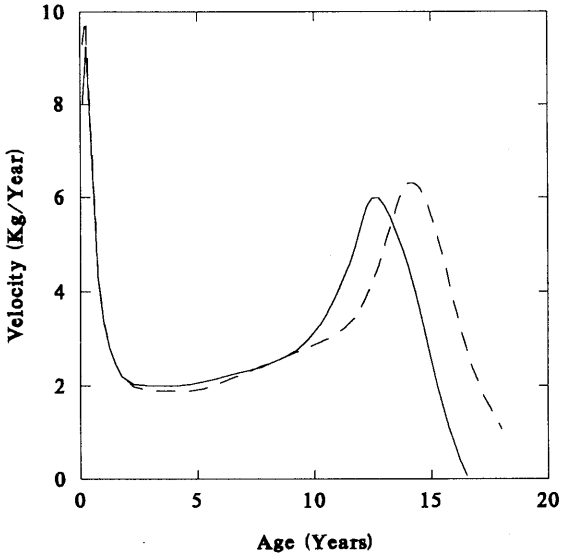


Fig 8

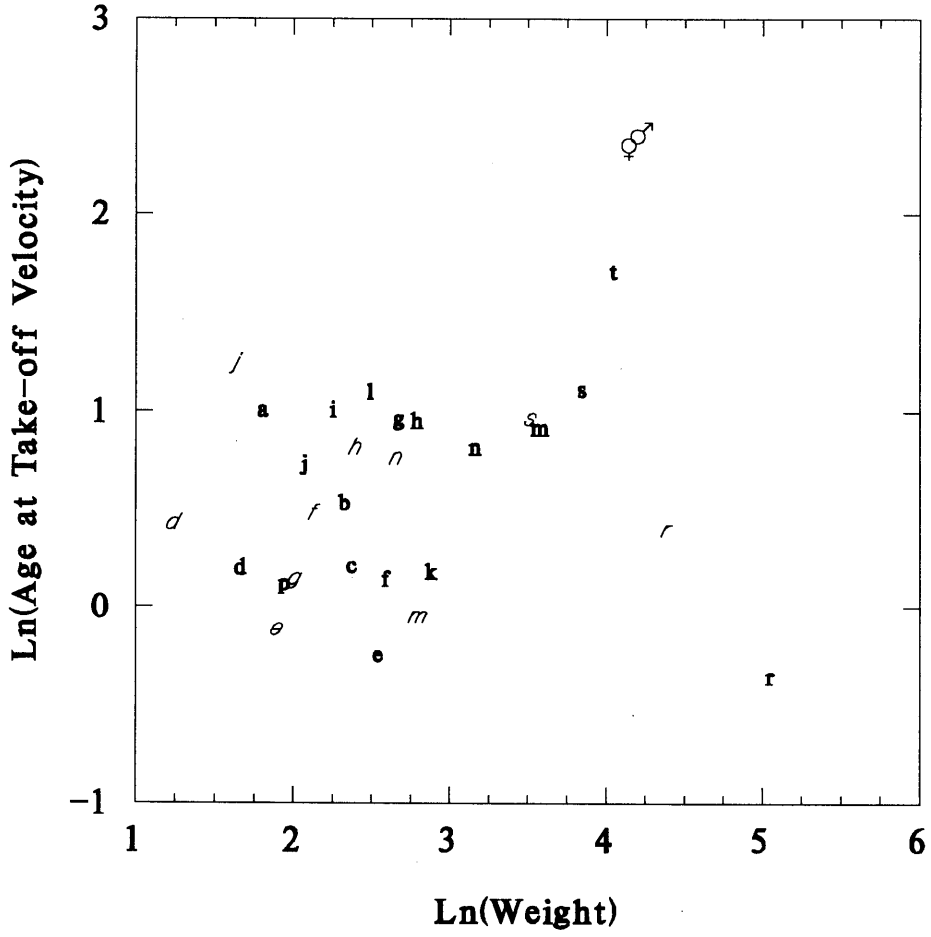
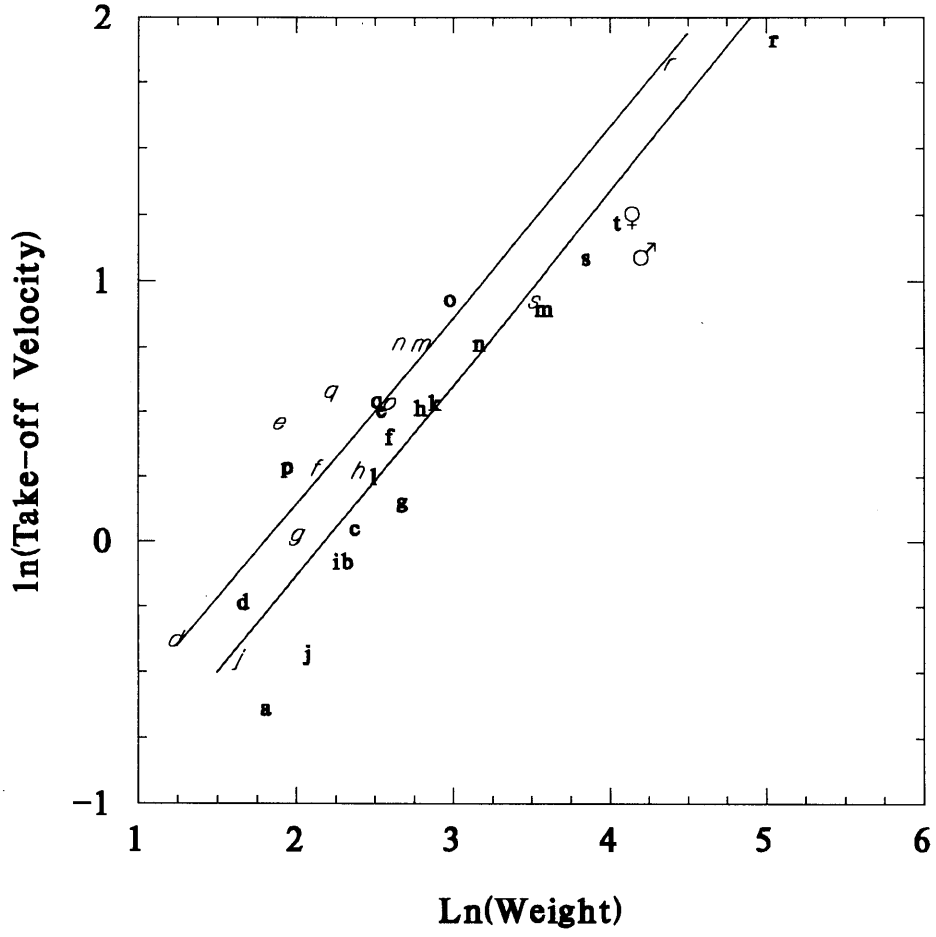
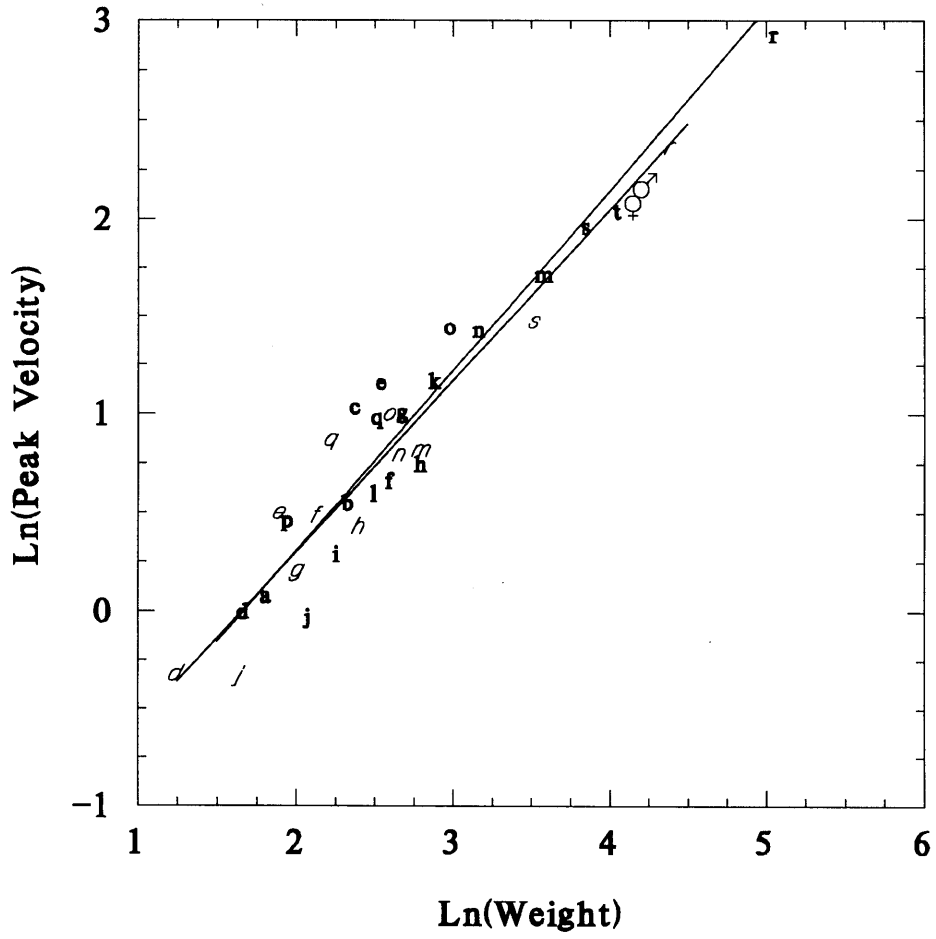
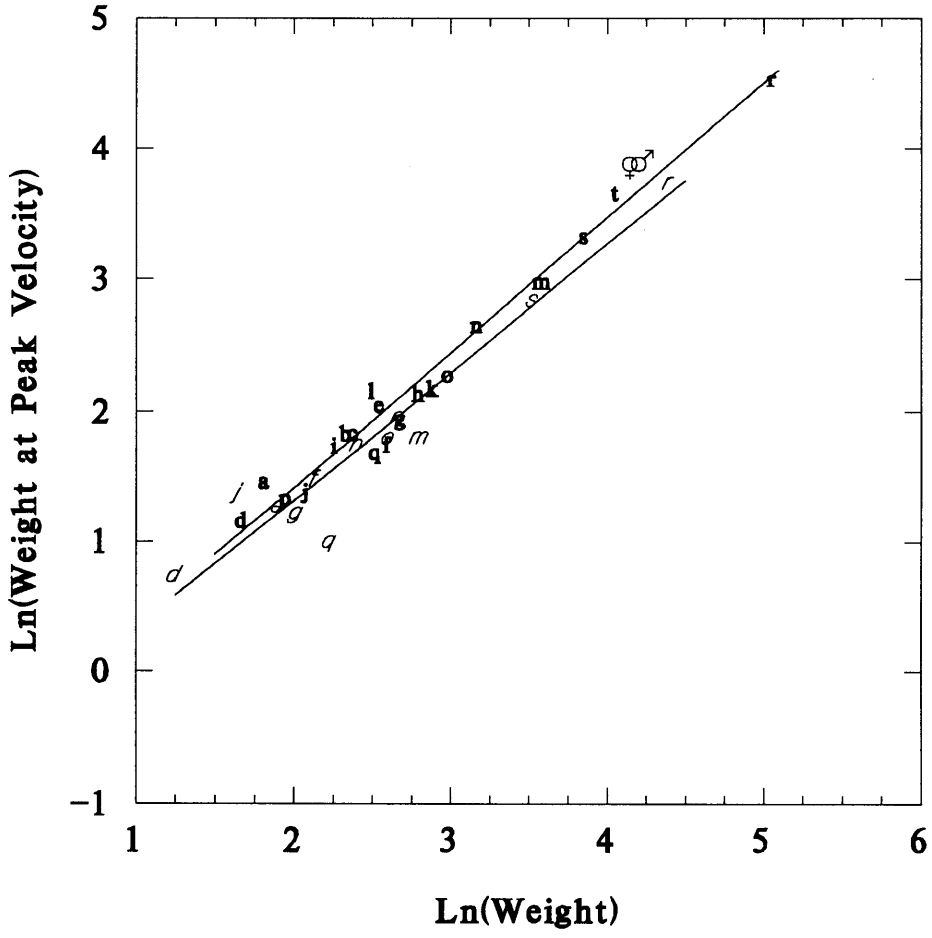


Fig 9


2
1
0
−1
1
2
3
4
5
6
ln(Take-off Velocity)
Ln(Weight)
r
t♀
♂
s
o
m
n
q
e
p
f
h
l
g
c
ib
d
j
a


Ln(Peak Velocity)
Ln(Weight)
3
2
1
0
−1
1
2
3
4
5
6
♀
♂


Ln(Weight at Peak Velocity)
Ln(Weight)
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4
3
2
1
0
−1
1
2
3
4
5
6

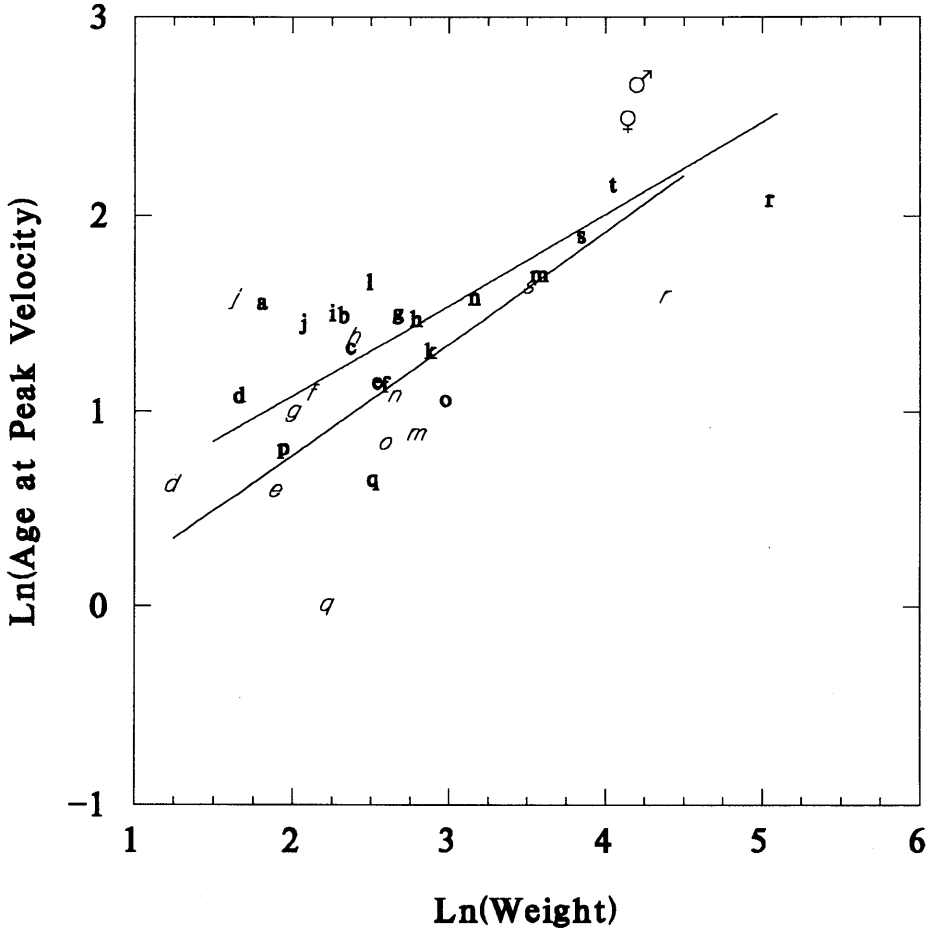


Fig 13

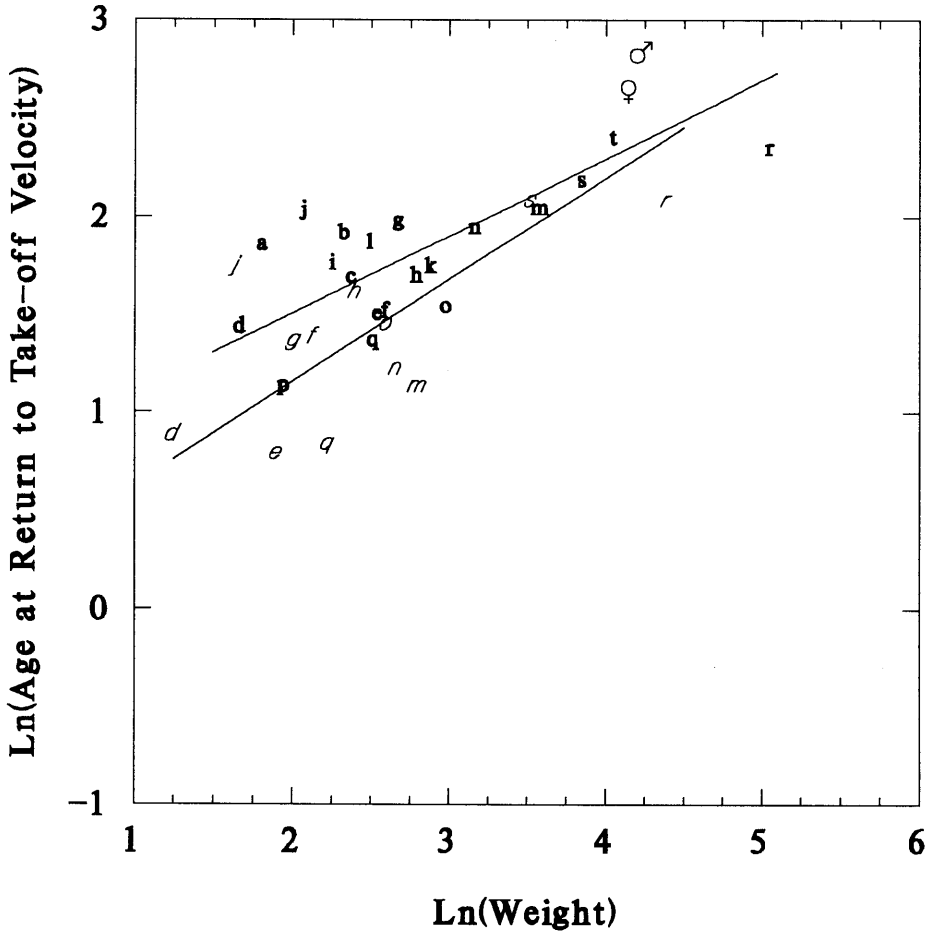


Fig 14

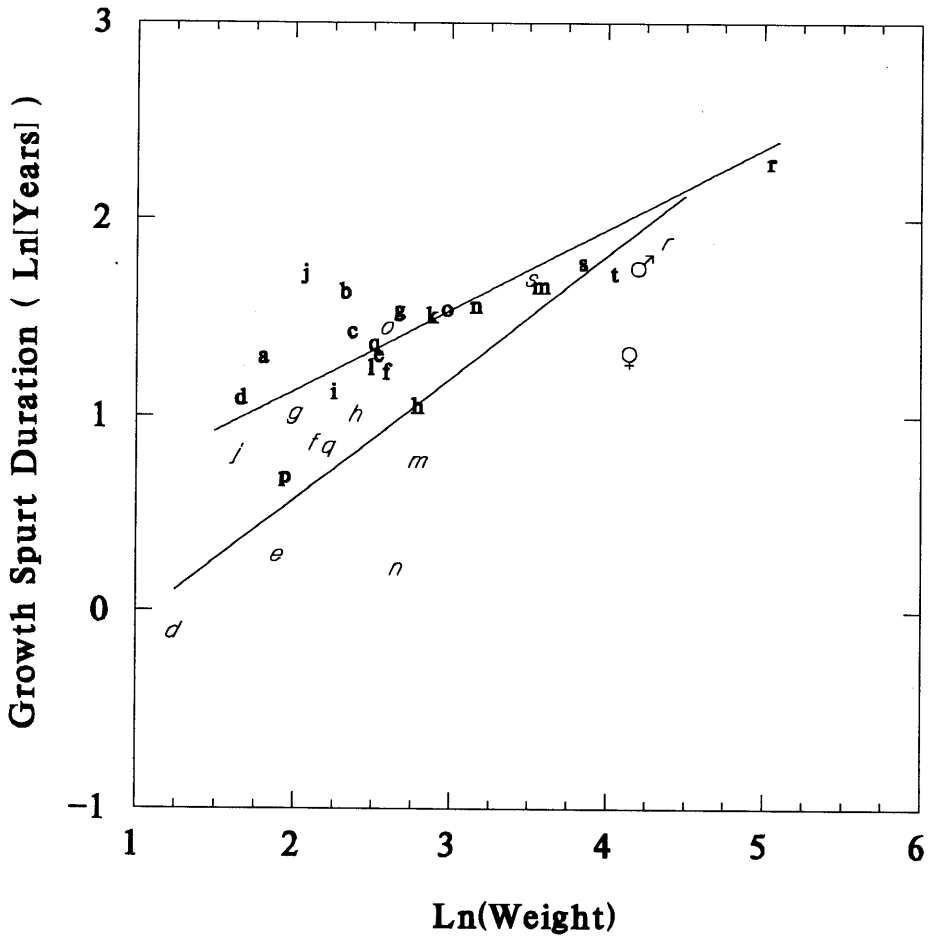
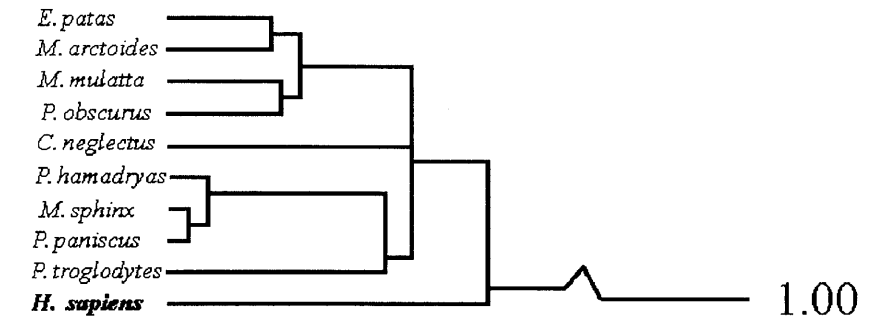
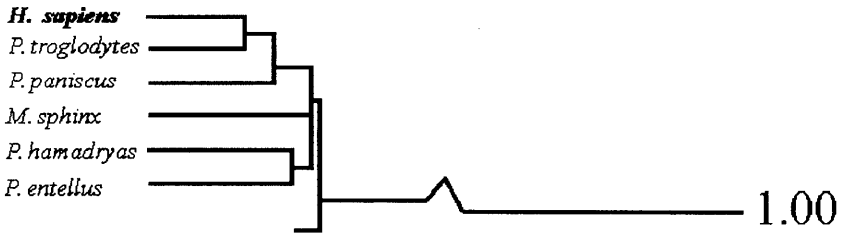


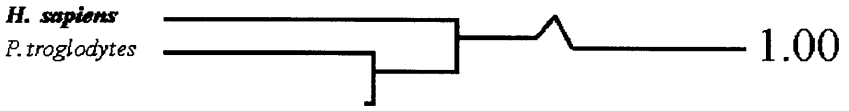
Fig 15



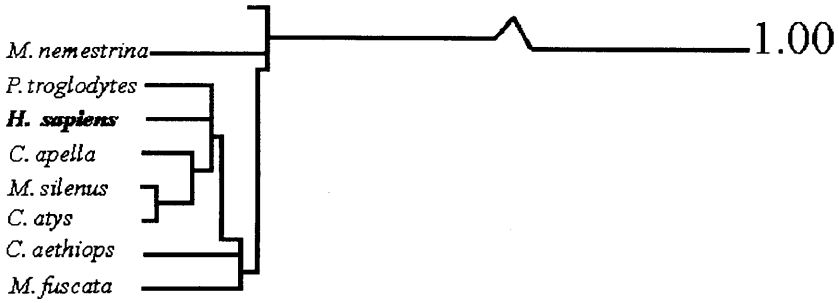
A. All variables, unadjusted



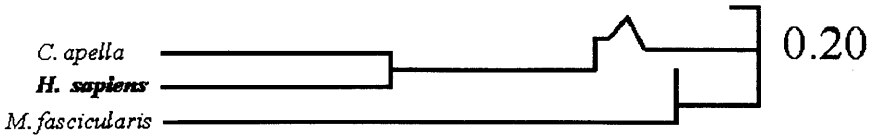
B. Rate variables, unadjusted



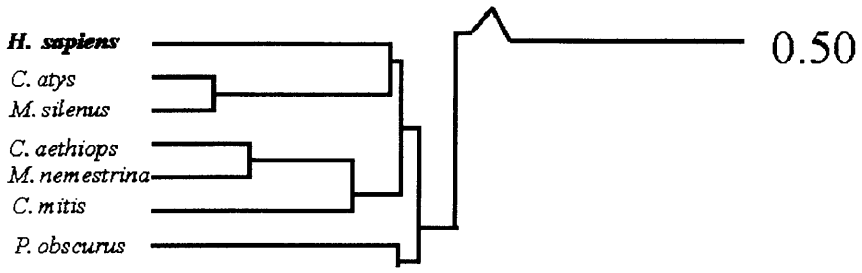
C. Timing variables, unadjusted



D. All variables, adjusted



E. Rate variables, adjusted



F. Timing variables, adjusted

Fig 16

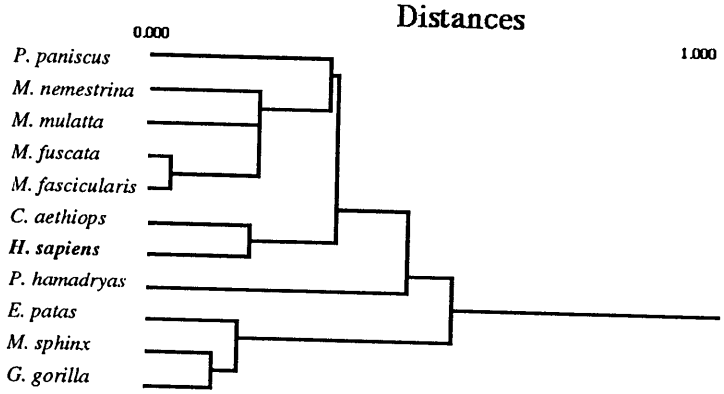

Distances
0.000
1.000
P. paniscus
M. nemestrina
M. mulatta
M. fuscata
M. fascicularis
C. aethiops
H. sapiens
P. hamadryas
E. patas
M. sphinx
G. gorilla

Fig 17