EVOLUTIONARY PERSPECTIVE ON HUMAN GROWTH

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Abstract To better understand both the shared and special features of human growth, this article explores the evolution of growth patterns of mammals in general and primates in particular. Special attention is paid to several competing hypotheses concerning the adaptive value of the juvenile stage to the life history of the social mammals. One hypothesis claims that all social mammals have a juvenile stage of life, but although most primate species are social, not all primates show a juvenile stage of life history. There is also controversy over whether the adolescent growth spurt is a uniquely human feature. On the basis of empirical observations and evolutionary considerations, I conclude that the human adolescent growth spurt in stature and skeletal maturation is species specific, not found in any other primate species. Finally, data and theory are used to advance a philosophy of human growth. An acceptable philosophy must acknowledge the mammalian and primate foundations for the human pattern of growth. But a robust philosophy of human growth must also account for the ecology to which the human species, indeed any species, is adapted. Accordingly, a philosophy of human growth must allow for the evolution of variations on common themes and of new stages of growth that may be unique to the human species.

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INTRODUCTION

Biologists and anthropologists have proposed a number of taxonomic schemes for classifying Homo sapiens. Lovejoy (1981) suggested five characteristics of humans as defining features: bipedality, a large neocortex, reduced anterior dentition with molar dominance, material culture, and unusual sexual and reproductive behavior. The development of each characteristic can be seen in the ontogenetic unfolding of the human pattern of growth and development. For instance, bipedality is made possible by differential growth of the legs and pelvis, including the bone, muscle, tendons, and ligaments, versus the arms and shoulder girdle (Simpson et al 1996). Our unusual reproductive behavior results, in part, from a prolonged childhood, delayed maturation, and species-specific neuroendocrine physiology. The human pattern of endocrine physiology results in the menstrual cycle of women, continuous sexual receptivity of both sexes, development of our secondary sexual characteristics, e.g. hair patches on the groin and armpits, and menopause in women. These are only some of the features of H. sapiens and human growth.

Although these characteristics set us apart from all other species, they have their origins in evolutionary history. Thus, we share many basic growth patterns with other species, but we differ in other ways because of special evolutionary developments. To better understand the shared and special features of human growth, this article reviews the phylogeny of growth of mammals and primates—the group that includes monkeys, apes, and humans. Material for this article is taken from a broad survey of the relevant literature, including historically important work, my research findings and interpretation of data (Bogin 1988, 1991, 1993, 1994a,b, 1995, 1996, 1997, 1999), and new research published in the last year.

THE BASIC CURVE OF GROWTH

The growth and development of any organism may be viewed as movement through space or time (Thompson 1917, 1942). They move through time in two ways: in days, months, and years; and in development and maturation from earlier
to later stages of life. Both ways can be represented in mathematical form. Most nonhuman organisms share the same basic curve of growth, an S-shaped, or sigmoid, curve (Figure 1A). Chickens, rats, and cattle follow this growth curve (Brody 1945, von Bertalanffy 1960, Laird 1967, Timiras 1972). The growth of parts of organisms and colonies of cells, such as bacteria and tumors in animals, also conform to this sigmoid curve. Figure 1B and C illustrate some other mathematical features of the general growth curve. The velocity, or rate of growth, is given in Figure 1B; only a single peak, or maximum rate, of growth occurs, indicating an initial acceleration followed by a period of deceleration in growth rate. In Figure 1C, the changes in acceleration are clearer: Point zero acceleration corresponds to the inflection point in the velocity curve where the rate of growth stops increasing and begins to slow. Growth rate at any subsequent point on the curve decreases with time.

In mathematical terms, parts B and C of Figure 1 are related to A as its first and second derivatives, respectively. That the curve of general growth is completely differentiable means, mathematically, that the growth process represented by this curve is smooth and continuous. That continuity means that we can predict changes in amounts and rates of growth during the course of development with precision. Such predictions allow us to make quantitative and qualitative assessments of the growth of any individual organism and to make comparisons between different individuals, groups of individuals, and even different species of animals in terms of the mathematical properties of their growth curves.

STAGES OF MAMMALIAN GROWTH

All placental mammals share the basic skeletal and reproductive adaptations related to rapid and flexible locomotion and to efficient feeding of both the fetus, via a placenta, and the infant, via lactation. They also share the neurological systems, especially the brain, which allow for intense parental investment and high levels of learning by the offspring. In contrast to these universals of mammalian biology and behavior, mammals can also be grouped by patterns of postnatal growth. The velocity growth curve of the mouse (Figure 2) and of the Holstein cow (Figure 3) show the pattern that is typical for most mammals.

The shapes of these velocity curves are fundamentally different from human growth curves (Figures 4 and 5) in several ways. First, humans achieve their maximum rate of growth in length and weight during gestation, and postnatal growth rates decelerate during infancy. Humans achieve such rapid growth during gestation because they have both only one fetus per pregnancy (the most common case) and the most efficient placentation of all mammals. Mice and cows reach their maximum rate of growth after birth, during the infancy stage. For mice this is probably because of competition among multiple fetuses for placental resources (litters are the norm). For both mice and cows, lactation provides improved nutrition over that provided via the placenta, which may promote a surge in growth rate: and for both, growth rates begin to decline soon after weaning.
Figure 1  General growth curves: (A) weight versus time, (B) rate of growth (velocity) versus time, and (C) acceleration of growth rate versus time. The units of time (X axis) and growth (Y axis) are arbitrary. (From Medawar 1945.)
The second difference is that for mice and cows, sexual maturation occurs relatively soon after weaning and just after the maximal rate of growth. Within a few days of weaning, vaginal opening occurs in female mice and they can become pregnant. About two weeks after weaning, male mice produce sperm. Human growth and maturation contrast sharply with that of mice and cows because humans delay puberty and sexual maturation for many years after the end of infancy, i.e. after weaning. Weaning is defined here as the cessation of feeding by lactation; for most mammals, the infant stage of life history ends with weaning. Life history stages are periods of time that an organism devotes to growth, maintenance, reproduction, raising offspring to independence, and death. In the broad course of mammalian evolution, several different life history strategies have emerged.

The human delay in puberty and sexual maturation is even longer if measured from the time of maximal rate of growth after conception. Mice and cows achieve peak growth rate velocity after birth, but because human peak velocity occurs before birth, humans experience an average delay of more than a decade between gestation and puberty.

A third difference is that for mice and cows, puberty occurs while growth rates are in decline but still near the maximal rate. Human puberty occurs when the postnatal rate of growth in height and weight are at their lowest points since birth. The fourth difference is that human puberty initiates a series of changes in endocrine function that leads to the adolescent growth spurt. In contrast, growth rates of mice and cows continue to decline after puberty. The fifth, and last, difference

![Figure 2](image.png)

**Figure 2** Velocity curves for weight growth in the mouse. Weaning (W) takes place between days 15 and 20. In both sexes, puberty (*P), meaning vaginal opening for females or spermatocytes in testes of males, occurs just after weaning and maximal growth rate. [From data reported by Tanner (1962).]
is that soon after puberty, mice are fertile and begin to reproduce, but for humans there is a delay of years between puberty and the onset of the adult reproductive stage of life.

Many of these differences between human and nonhuman mammalian growth were recognized previously. In a classic analysis of mammalian growth, Brody (1945) demonstrated that most mammals have a pattern of growth similar to that of mice. Brody's analysis was confirmed by von Bertalanffy (1960) and Tanner (1962). Tanner presents many growth curves for mice, rats, rabbits, sheep, and cattle, showing that size makes little difference in the pattern of growth. The growth curve of Holstein cattle, animals with a mean adult weight of 2640 kg and a shoulder height of 135 cm (Figure 3), is virtually identical to that of mice (Figure 2).

![Graph showing growth curves for different cow breeds.]

**Figure 3** Monthly gains in height at the withers for the several varieties of cows. (Data from Brody 1945.) Monthly values for height as the mean value for many animals (sample size varies from 67 to 239 at each age) measured monthly from birth to 24 months.
Figure 4  Distance and velocity curves for growth in body length during human prenatal and postnatal life. The figure is diagrammatic, based on several sources of data. (Dotted lines) The predicted curve of growth if no uterine restriction takes place. In fact, such restrictions do take place toward the end of pregnancy and may impede the flow of oxygen or nutrients to the fetus. Consequently growth rate slows but rebounds after birth and returns the infant to the size she or he would be without any restriction. (From Tanner 1990.)
Figure 5  Idealized mean distance curves (A) and velocity curves of growth (B) in height for healthy girls (dashed lines) and boys (solid lines) showing the postnatal stages of the pattern of human growth. (B) Note the spurts in growth rate at mid-childhood and adolescence for both girls and boys. The stages of human postnatal growth are abbreviated as follows: I, infancy; C, childhood; J, juvenile; A, adolescence; M, mature adult. [Data used to construct the curves come from Prader (1984) and Bock & Thissen (1980).]
These three researchers are in agreement that the majority of mammals progress from infancy to adulthood seamlessly, without intervening stages of development. In contrast, the path from conception to maturity is different for human beings. Brody states that his analysis "demonstrates the close similarity between the age curves of different animal species. The human age curve, however, differs from the others in having a very long juvenile period, a long interval between weaning and puberty (approximately 3 to 13 years); this period is almost absent in laboratory and farm animals. In these animals, weaning merges into adolescence without the intervention of the juvenile phase found in man" (1945:495).

By today's standards, however, this terminology is out of date. For example, no distinction is made between puberty and adolescence, and both are equated with sexual maturation. We know now that puberty is an event of the neuroendocrine systems in the brain that control sexual maturation. In humans this event occurs at the end of the juvenile period and before the start of the adolescent growth spurt and life stage. We also know that only humans, and perhaps some apes, have an adolescent stage of growth and of life history. Nevertheless, Brody correctly notes that of the animals he studied, only humans and chimpanzees have a juvenile growth period. Despite this important discovery, Brody still tried to show that in essence all animals, parts of animals, colonies of cells, and even populations of animals follow a common pattern of growth. "The general similarity between the curves of growth of individuals and of populations is not surprising, since ultimately both are collections of individuals. Our bodies are made of cells, and our bodies, in turn, are cells in a social body. Individuals are organisms and also units of a larger organism, an epiorganism" (Brody 1945:495).

Brody was searching for a type of grand unification theory of growth. His specific hypothesis was that all growing organisms and populations or organisms could be modeled with one curve of growth. He aligned the maximum rate of growth after birth for many species, including mice, cows, and humans, and then showed that all have two phases of growth velocity. The first is a self-accelerating phase, from birth to peak velocity, and the second is a self-inhibiting phase, from peak velocity to adult size. Humans, even with their juvenile growth period and adolescent growth spurt, would have to fit into this unification of growth curves. Accordingly, Brody equated the adolescent growth spurt of humans with the velocity curve of growth for animals such as mice, rats, and many domesticated farm animals (cows, pigs, sheep). In this hypothesis, all mammals followed the same curve of growth, but some mammals had their growth spurt soon after birth (e.g. mice and Holstein cows), whereas for others (e.g. humans), the spurt was delayed until later in life.

In many ways, Brody's methodology and speculative ideas are ingenious and stimulating. His analyses and findings apply to the laboratory and farm animals in his database, but they do not apply to humans. The main problem with the unification hypothesis is that some animals, especially humans, have more than one phase of self-acceleration and self-inhibition of growth rate. In fact, humans have three such phases: The first occurs during gestation, the second is the midgrowth spurt, and the third is the adolescent growth spurt. Brody knew only about the
adolescent growth spurt and incorrectly equated it with the solitary growth spurt of his laboratory and farm animals.

Brody's work is mentioned here because it had a strong influence on the study of human growth for many years. Even today, it is common to read about adolescent growth spurts or an adolescent phase in animals, such as rodents or farm animals, but it is not like human adolescence. Although these ideas seem preposterous today, bear in mind that during the first third of the twentieth century, when Brody carried out most of his original research, the nature of the human postnatal growth curve, even the existence of the adolescent growth spurt, was still being debated (Bogin 1999:Ch. 1). The human postnatal stages of childhood and juvenile growth, as well as the human prenatal curve of growth (Figures 4 and 5), were unknown to most researchers at that time. Moreover, the neuroendocrine control of growth and of puberty were poorly understood.

**Juvenile Mammals**

Brody's discovery of the human juvenile growth period is one of his lasting contributions to the field. Since that time, juvenile growth stages have been discovered for several other mammalian species. Highly social mammals, such as the social carnivores (wolves, lions, hyenas), elephants, many cetaceans (porpoises, whales), and most primates, all evolved a new stage of development between infancy and adulthood—the juvenile stage (Bekoff & Byers 1985, Pereira & Fairbanks 1993). Juveniles may be defined as offspring who are weaned, i.e. no longer dependent on maternal lactation for feeding, but who are still prepubertal. Juveniles are largely responsible for their own care and feeding. They must find their own food, avoid predators on their own, and compete with adults for food and space. Juveniles may even compete with their own mothers, who may be encumbered with another pregnancy or a nursing infant. Clearly, the juvenile stage adds several new risks along the path toward reproductive maturity. In fact, the highest rates of postneonatal mortality (i.e. deaths after the first month following births) for social mammals occur during the juvenile stage (Pereira & Fairbanks 1993).

**Hypotheses for the Evolution of the Juvenile Growth Stage**

The juvenile growth stage must have evolved because it added some benefits to the life of social mammals, but there is some debate as to its function. A stimulating review and analysis of the evolution of this stage is offered by Janson & van Schaik (1993). They propose two benefits. The first is that the juvenile period provides the extended period of brain growth and learning time necessary for reproductive success in various species of social mammals (the traditional learning hypothesis explanation). Social carnivores, elephants, and primates must all learn how to live within the social hierarchy of the group. They must also acquire complex feeding skills required for hunting animal prey, opening fruits or seeds with protective coverings, and discerning where and when food can be found. Reproductive skills must also be learned, including how to compete for mates and care for offspring. Johnson (1982) and Lancaster (1985) show that the selective bene-
fit of learning is that it permits adaptation to unpredictable ecological changes. Included are common problems faced by all extant and extinct hunting and gathering societies, such as seasonal variability in climate, plant growth, and animal migrations. The unique capacity for learning in humans is also brought to the forefront in rare crises, such as the 1943 drought in Central Australia. Birdsell (1979) relates that during this time, an old Aborigine man, by the name of Paralji, led a band of people on a 600-km trek in search of water. After passing 25 dry waterholes, he finally led them to a fallback well. The old man had not visited that place for more than 50 years. The well was also dry, though, and so Paralji was forced to trek 350 km more on ancient trails, seeking to locate water holes by place names learned from initiation rites and ceremonial songs he had memorized as a juvenile.

Even the way humans forage for food requires extensive learning gained during the childhood and juvenile growth periods. Much of the food humans utilize is hidden from view or is encased in protective coatings; tools are usually needed to extract and process these foods. The costs of tool manufacture, however, and the time and energy required to find and process raw materials are outweighed by the benefits. Tool-using human gatherers extract twice as many calories from savanna/woodland environments as do non–tool-using primates. Other foods are poisonous before processing by washing, leaching, drying, or cooking. For example, acorns and horse chestnuts, eaten by many North American Indians, and manioc, a staple food for many extant cultures in the tropics, are toxic if eaten raw and must be leached by boiling in water and dried before consumption. Furthermore, one must acquire knowledge of the location and methods of processing these foods, as well as the location of the necessary raw materials and their manufacture into tools. One example is provided by the hunting and gathering Arunta of Central Australia. They are compelled to live in self-sufficient nuclear families because in their habitat food resources are widely dispersed (Service 1978). The children, once able, follow their mothers and fathers on the daily rounds of food collection and preparation. Elkin (1964) observed that boys and girls as young as 5 years were taken by their fathers on hunting trips and shown how to collect and prepare raw materials for use in spears, points, and other tools. Because it takes more than a decade to become proficient in the manufacture and use of these tools, early learning, slow growth, and delayed maturation during the juvenile stage are all mutually beneficial.

Learning seems like a great idea, but the learning hypothesis does not take into consideration the high mortality associated with the juvenile stage. After all, evolution works by differential mortality and reproductive success, and high levels of mortality during the prereproductive juvenile stage will not lead to evolutionary success. The second benefit of juvenility, and a complement to the learning hypothesis, is the ecological risk aversion hypothesis. Janson & van Schaik (1993) developed this hypothesis to deal with the issue of juvenile mortality risk: When the risk of predation is high for the individuals of a species, natural selection often favors the formation of social groups—there is relative safety in numbers. The formation of social groups comes at a cost, however, and that cost is an
increase in competition for food within the group—there are more mouths to feed. According to Janson & van Schaik, newly weaned individuals are most likely to be adversely affected by this competition because they have less-developed foraging skills than adults do. The young must develop and grow to mature size to reproduce, and there are two basic ways to get from infancy to adulthood. One is to develop quickly and minimize the duration of the nonreproductive period between weaning and sexual maturation. This is the strategy followed by mice, bison, and most mammals. Because there is little time to learn, it places a premium on reproductive quantity rather than quality. The other strategy is to develop toward adulthood slowly, increase the time for learning, and produce higher-quality adults. A corollary of each strategy for mammals of medium-to-large body size is that fast development requires fast growth, but slower development allows for slow growth. Janson & van Schaik hypothesize that slow juvenile growth reduces the risk of death and simultaneously provides the time for juveniles to learn.

The risk of death during competition for food is an example. Juveniles must forage for their own food, a skill that must be practiced until mature levels of success are achieved. Much of their foraging is in competition with adults. This competition becomes clearest during times of food scarcity, when juvenile primates die in greater numbers than infants or adults. But not all juveniles die, and there is a relationship between growth and mortality. A small, slow-growing juvenile requires less food than a larger, fast-growing individual and may survive periods of food scarcity; there is evidence for this from studies of both primates (Janson & van Schaik 1993) and elephants (Lee & Moss 1995). Moreover, slow growth and smaller size allow juveniles to practice feeding skills with less risk of starvation during all seasons. According to this risk-aversion hypothesis, the juvenile stage evolved when the rate of growth was slowed and the duration of growth prolonged.

An example of the juvenile pattern of growth is given for elephants (Figure 6). The distance curves are based on cross-sectional means of shoulder height, a common measure of skeletal growth for elephants [see Lee & Moss (1995) for details of the methodology of measurement]. The original means were plotted and fit with a distance-weighted, least-squares regression. The curve produced by this statistical technique represents the main trend, or average growth pattern. The distance curve for both male and female elephants shows the typical juvenile pattern: many decades of prolonged and relatively slow growth. The increments in growth between successive data points were calculated, and as was done for the distance curves, the increments between means were plotted and fit with a distance-weighted least-squares regression. The shape of this fitted increment curve reveals the stages of postnatal growth more clearly than the distance curves. The approximate durations of infancy, juvenile, and mature adult stages are indicated.

The increment curves must be interpreted with a great deal of caution because they are calculated from means rather than from individual data. Increments are presented only to provide a rough approximation of growth velocity. Overall, the fitted curve shows a fairly rapid decline in rate of growth during the first decade of
Figure 6  Growth curves for elephants illustrating the pattern of growth in social mammals with infant (I), juvenile (J), and mature adult (M) stages of growth. (A) Distance curves. (B) Increment curves. Weaning (W) takes place at a mean age of 40 months. Puberty (P) occurs at approximately age 9 in females, with first birth at approximately 10 years. Males do not reproduce until after 25 years of age. [The mean values of shoulder height were kindly supplied by Dr. PC Lee, Department of Biological Anthropology, University of Cambridge, and published by Lee & Moss (1995).]
life and then a slower, prolonged, decline to age 25 years for females and age 50 for males. The difference seen in the distance curve in shoulder height between the sexes is explained by the additional 25 years of growth for males. The increment estimates fluctuate widely, and some are even negative. This is due to the cross-sectional nature of the data, i.e. to the adjacent measurements from different individual elephants, and to the unequal spacing between increments for each individual. The fluctuations also may be due to different ecological conditions for growth during the life of these individuals. It is possible that negative increments represent the difference in size between individuals in good ecological conditions and those who grew up under harsh conditions. Notice that the negative increments, and most of the fluctuations, are confined to the first 20 years of life. That time includes the infancy and juvenile stages. The fluctuations in these increment data, despite their limitations, do add some support, as an explanation for the juvenile stage of growth, to the ecological risk-aversion hypothesis. In other words, the environment in which these elephants live is unpredictable, and a strategy of slow growth to adulthood may well provide the best chance for avoidance of starvation during bad years.

The dominance hypothesis is another possible explanation for the existence of a juvenile stage for social mammals. Research using wild and captive primates, including elephants and social carnivores (wolves, lions, hyenas), shows that high-ranking individuals in the social hierarchy can suppress and inhibit the reproductive maturation of low-ranking individuals (Pereira & Fairbanks 1993). The inhibition may be due to the stress of social intimidation acting directly on the endocrine system, or it may be secondary to inadequate nutrition because of competition for food. Juveniles are almost always low-ranking members of primate social systems. In the past, individuals with slow growth and delayed postinfancy reproductive maturation may have survived to adulthood more often than individuals with rapid growth and maturation, and in this context, the juvenile stage may have evolved. Whatever the roots of the juvenile growth stage, learning, risk aversion, or social inhibition, one scholar points out that in a broad perspective, "...juvenile life has two main functions: to get to the adult stage without dying and to become the best possible adult" (Alexander 1990). Adding a juvenile stage must have served these functions well for it to have evolved independently in so many social mammals.

PRIMATE GROWTH PATTERNS

Most primates are highly social mammals and, as would be expected, have a juvenile stage of growth and development. The primates, however, are a highly diverse group that includes the prosimians (such as lemurs, lorises, and tarsiers), New World monkeys (ranging from marmosets and tamarins to cacaos and howlers), Old World monkeys (such as baboons, rhesus, and colobus), apes (gibbons and siamangs, orangutans, gorillas, common chimpanzee, and bonobo), and humans. In all, there are more than 50 genera and more than 200 species of living primates (Napier & Napier 1967). Primates live in environments that range from
Figure 7  Three primate species showing different patterns of postnatal growth in weight. Abbreviations: I, infancy; J, juvenile; A, adult. Marmosets are weaned at 63 days and can breed at 1 year of age (Harvey et al 1987). Marmoset growth rate shows no postnatal growth spurt and no change in growth rate typical of a juvenile growth stage. Baboons are weaned by 18 months and begin puberty at about 3.5 years for females and 4.5 years for males (Harvey et al 1987). Baboons have a juvenile growth stage for both males and females, but only males have clear weight growth spurt. Colobus monkeys are weaned at about 13 months and females have their first birth at about 4.6 years of age. Colobus monkeys show a postnatal spurt for both sexes, but it is not clear if there is a juvenile growth stage. (Velocity curves) Fit to cross-sectional data collected from captive animals using the statistical estimates based on lowess regression. See the text for further details. (From Leigh 1994b.)

Semiarid scrub, to savanna, to woodland, to rain forest, and from sea level to more than 2000 meters above sea level. Adult sizes range from that of male gorillas, 160 kg, to that of mouse lemuris (Microcebus murinus), 0.08 kg. Maximum life span ranges from 8.8 years for dwarf lemurs (Cheirogaleous major) to approximately 120 years for humans (Harvey et al 1987). Given this variation in local ecologies, world distribution, general environments, adult body size, and life span, it is reasonable to expect that primates have a variety of patterns of growth and development, and indeed they do.

Three patterns of primate postnatal growth in weight (Figure 7) are based on the work of Leigh (1992, 1994a,b). There are differences in growth patterns between the three species (marmoset, baboon, colobus) and between males and females within species. Furthermore, none of these species follows a pattern of weight growth similar to that of the human species. The marmoset seems to follow the type of growth curve Brody described for most mammals, i.e. an acceleration phase followed immediately by a deceleration phase. The switch between phases seems to occur just before the time of birth, and the infancy stage merges seamlessly into the reproductively mature stage. Based on the velocity curves of weight growth, there is no evidence of a juvenile stage. The lack of a juvenile
growth stage may relate to marmoset social behavior. Marmosets, and the closely
related tamarins, live in a type of family group in which females form a social
bond with one or a few males. These polyandrous families establish feeding and
breeding territories and exclude other marmosets. The young, usually born in
pairs or triplets, are raised cooperatively by the mothers and her male consorts
(young of the same litter may be sired by different males). After weaning, which
takes place as early as 6 months for some species and by 12 months for others,
the young are protected and provisioned with food by both adult males and
the mother (Goldizen 1987) until they reach sexual maturity, approximately
15–24 months. Following the risk aversion hypothesis of Janson & van Schaik, a
juvenile stage of growth would not be needed in this type of territorial family
social group [see Garber & Leigh (1997) for an alternative interpretation]. Leigh
(1996) analyzed growth data for five other species of marmosets or tamarins, and
all these follow a pattern of growth essentially the same as that for the common
marmoset.

The baboon velocity curves show evidence for infant, juvenile, and adult
stages of growth. Baboon infants are weaned within approximately 18 months of
birth, but growth rates remain fairly stable until approximately 4 years of age—
clearly a juvenile pattern of growth. Baboons reach a peak in growth rate before
birth, just as humans do, but by the time of birth, baboons are already growing at
the slower, steady rate that characterizes late infancy for humans. Both male and
female baboons follow this pattern during infancy, but during the juvenile phase
males show a pronounced acceleration in weight growth—a spurt. Baboons live
in large social groups composed of males and females of all ages, and therefore
their growth pattern conforms to the prediction that they will have a juvenile
growth stage. Why males and not females have a juvenile growth spurt in weight
is not known. It is known that the spurt is due mostly to an increase in muscle
mass, which in males is used in competition for scarce resources such as food and
mates.

Colobus monkeys show yet a third pattern of postnatal growth. Weight growth
after birth has a clear acceleration in both males and females. What is not clear is
whether these accelerations can be classified as juvenile growth spurts. It is possi-
ble that colobus monkeys grow more like marmosets than like baboons. Like the
marmoset, the colobus may also have only a single peak rate of growth but one
that is reached soon after birth. The colobus, then, would be following a growth
pattern like that for mice and cows (Figures 2 and 3). Colobus social behavior and
diet do not provide a clear case for the prediction of a juvenile stage. Colobus
monkeys live in troops of 3–15 animals, with a troop typically composed of a sin-
gle adult male, three to four adult females, and their offspring. These troops are
highly social, there is little evidence for a female dominance hierarchy or female
aggression, and infants seem to be groomed and cared for by troop members other
than the mother. This shared infant care, as well as the intense allo-grooming
between adult females, is believed to maintain a highly cohesive social group
(Struhsaker & Leyland 1987). Colobus monkeys eat mostly young leaves from
the hackberry tree (Celtis durandii) and two other tree species, which together
comprise 69% of their total diet. Colobus, and related leaf-eating monkeys of the subfamily *Colobinae*, digest this large quantity of leaves in a specialized stomach composed of three or four subcompartments. Their digestive system is similar to the ruminant digestive system of cows. Given the wide distribution and availability of their food, and given their cohesive and non-competitive social organization, it is possible that young colobus monkeys have a low risk for mortality. If so, then the risk aversion hypothesis would predict the absence of a juvenile growth stage, or the presence of a very brief stage. There is some empirical support in favor of this prediction. In an analysis of 42 primate species, Leigh (1994a) found a significant correlation between diet and rate of growth. *Folivores*, such as colobus monkeys, have faster rates of growth than do species of non-folivore monkeys and apes, such as rhesus monkeys and gibbons. So, perhaps it is not so far-fetched to state that colobus have both cow-like stomachs and cow-like patterns of growth.

Some Historical Background

A more detailed discussion of primate juvenile growth, especially of postnatal growth spurts, is presented below. Before that review, some of the history and findings of research into primate growth are discussed so as to provide a better appreciation of what primates share with other mammals and what is special about primate growth. Comparative studies of primate growth began with the work of Schultz (1924). From inception, his studies were aimed at "...the relation of the growth of primates to man's evolution...(1924:163). Perhaps Schultz's most lasting contributions were summarized in his 1960 illustration of the approximate ages of some life periods of the primates (Figure 8). Despite the grandeur and vision of Schultz's research on primate growth and primate evolution, few primate species were actually studied in detail by 1960. In fact, until the 1980s, details of skeletal, dental, and somatic growth were known from only three species, rhesus monkeys (*Macaca mulatta*), chimpanzees (*Pan troglodytes*), and humans.

Laird continued Schultz's interest in evolution of the human growth curve. In a 1967 paper, she reviewed studies of the growth of the three well-studied species: rhesus monkeys, chimpanzees, and humans (Laird 1967). She took a mathematical approach to the study of growth. By fitting mathematical functions to the growth data, Laird hoped to reveal more precisely the stages in the evolutionary development of the human growth curve. The curves were fitted to the monthly weight data points by the method of least squares regression. Essentially, this method minimizes the sum of the squared deviations of each data point from the fitted curve, i.e. it produces an average line between the data points.

Laird found that monthly weight increases in rhesus monkeys and chimpanzees followed two separate growth curves. For male rhesus, the first curve fit the data from birth to 22 months, and the second from 23 months onward. A change in growth rate that occurred between months 22 and 23 necessitated the use of different mathematical curves to model growth in the two periods. Sexual development in male rhesus takes place during the second growth phase, after month 40. The deviations of weight growth above the fitted curve between months 48 and 54.
Figure 8  Schultz's diagram of the proportional increase in the length of life stages across the *scala naturae* of living primates. Schultz used eruption of the permanent teeth to mark the boundary between life periods. Note that Schultz did not recognize the childhood or adolescent stages for modern humans. Indeed, all primate species have the same life stages, but they increase in length from prosimian to human. The estimates for total length of life are based on average expectations rather than theoretical maximums. (From Schultz 1969.)
corresponded to the time of reproductive maturation and the beginning of adult levels of gonadal hormone secretions. The curves of growth for female rhesus were similar to those of male, except that the time of onset of sexual maturation was earlier, occurring at about 42 months. For chimpanzees, the first curve fit the early phase of growth, from birth to 6 years. This early phase is essentially the infancy period, which lasts until 5 years of age in chimpanzees (Teleki et al 1976, Goodall 1983, Nishida et al 1990). The second curve was fit to what Laird called the adolescent phase. Male and female chimpanzees followed the same curve of growth from birth to 6 years. During the adolescent phase males grew in weight at a faster rate than did females, and this required separate mathematical functions for each sex. Because of the different rates of weight growth, sexual dimorphism in weight became well marked. The sexual dimorphism reached its greatest level at the age when male chimpanzees begin to sire offspring. Laird, in her analysis, confirmed the work of Tanner (1962), who had shown that the sexual dimorphism in the weight of adult chimpanzees was largely due to a weight growth spurt for the males (a more recent example is shown in Figure 11).

Laird (1967) found that the velocity curve of human growth (Figure 5B) required three mathematical functions to model its course. This conclusion was confirmed independently (Bock & Thissen 1976, Bogin 1980, Karlberg 1987). The need for the third function is one aspect of human growth that makes it different from that of other primates. Laird described the similarities of growth between rhesus monkeys and chimpanzees and the distinct pattern of human growth as follows: “[T]he curvilinear growth by which the body weight of an organism approaches its mature value and during which sexual maturation characteristically occurs, starts at birth in sub-primate mammals and birds, but is deferred in monkeys ... the preliminary growth occupying about 1/3 and the adolescent growth about 2/3 of the time required to reach fully mature size. In the chimpanzee, adolescent growth is deferred to the last 1/2 of the total period... In the human a further delay has occurred so that adolescent growth with its concomitant development of sexual maturity occupies only the last 1/3 of a prolonged growth period. The delay in the human can be interpreted as being due to the insertion, between birth and adolescence, of two growth phases, rather than the single phase identifiable in the monkey and the chimpanzee....” (1967:351–52).

It seems that Laird considered all three primates to be alike in having a juvenile phase between infancy and what she refers to as adolescence. The second growth phase for humans between infancy and puberty is childhood (Figure 5B). I define childhood as a life history stage in the human life cycle that occurs between the end of infancy and the start of the juvenile growth period (from approximately 3 to 7 years of age). Children are weaned from breast feeding (or bottle feeding) but must be provided especially prepared foods and require intensive care by older individuals. In contrast, juvenile primates provide for their own feeding and care. Human childhood is characterized by relatively rapid neurological development and slow physical growth and development.

Based on the mathematical analysis by Laird, I conclude that in terms of anatomy, physiology, and behavior only humans have a childhood life history stage.
The insertion of childhood into the human life cycle not only requires a third mathematical function to model growth, but, more important, changes the biological and social ecology of the human species. These biosocial changes are discussed in detail in other publications (Bogin 1996, 1997, 1999).

**Of Brains and Bodies**

Another key difference between nonprimate and primate growth involves the relative rates of growth of the body, the brain, and the reproductive system. Most mammals, including rats (Figure 9) and the social mammals, show an advancement of brain growth relative to body growth. In rats, reproductive maturation occurs before the brain or the body achieve final adult size (Donaldson 1895). Primates delay body growth and reproductive development but do not delay brain growth. These relationships in humans are illustrated in Figure 10. The weight of the human brain reaches 80% of adult size by age 4 and almost 100% of adult size by age 7. Yet body growth continues until age 18 and beyond. Even more to the point, brain growth is finished before reproductive maturity even reaches 10% of the adult value. This pattern of relative growth of the brain, body, and reproductive system is also found in rhesus monkeys and chimpanzees (Laird 1967). Other organs of primate bodies (e.g. heart, lungs, liver) follow the body growth curve. Primate brain, then, is most unusual in its pattern of accelerated growth in comparison to other organs and to the body as a whole.

In an obvious way, this pattern of growth relates the fact that primates are learning creatures par excellence. There are other consequences of the primate
pattern of growth that are not as obvious. It is worth noting that rapid brain growth, deferred body growth, and progressively delayed sexual maturation greatly enhance the quality and quantity of reproductive efficiency in primates. Not only is a given offspring endowed with great flexibility of learned behavior, but also as an older prereproductive juvenile, this individual can help its mother provide care for new infants. In humans, reproductive efficiency is further enhanced with our childhood and adolescent periods of growth. These advantages resulted in selection at the genetic level of primate biology to develop and to maintain these patterns of growth.

**IS THE HUMAN ADOLESCENT GROWTH SPURT UNIQUE?**

One of the hallmarks of human growth is the adolescent growth spurt, the post-juvenile acceleration in rate of growth in height and weight. Many individual organs and most body dimensions experience the adolescent spurt (Shock 1966, Cameron et al 1982, Satake et al 1993, Dasgupta & Das 1997, Greil 1997). Moreover, the adolescent spurt is detectable in both boys and girls, and in every human population so far examined. The adolescent spurt (Figure 5B) is a regular and normal feature of human growth. Only chronic and severe illness, malnutrition, or physiological stress can obliterate the growth spurt. For instance, Quechua Indian boys and girls living at the high altitudes of the Peruvian Andes have a late and poorly defined adolescent growth spurt. The reason for this is that
these children suffer from the combined stress of hypoxia (insufficient delivery of oxygen to the tissues of the body), energy malnutrition, heavy workloads, and cold temperatures. Instead of a clear spurt, the Quechua experience a prolonged adolescent growth period, lasting until age 22 and beyond (Frisancho 1977).

There is some controversy as to whether the adolescent growth spurt is a uniquely human feature. On the basis of empirical observations and evolutionary considerations, I conclude that the human adolescent growth spurt in stature is a species-specific characteristic; that is, a skeletal growth spurt of the human type is not found in any other primate species (Bogin 1993, 1994a, 1999; Bogin & Smith 1996). This conclusion stands in contrast to previous research. As discussed above, Brody (1945) believed that the human adolescent growth spurt, both for height and weight, was homologous with the peak velocity of growth shown just after birth by most laboratory and farm animals. von Bertalanffy (1960) and Laird (1967) also believed this to be the case. For these researchers, the special features of primate growth were the prolongation of the juvenile period, found in all haplorhine primates, and the evolution of the childhood period, found only in humans. The addition of the juvenile, and then the childhood, growth phases simply delayed the ubiquitous postnatal growth spurt of all animals to the adolescent phase of humans. As shown above, this interpretation is incorrect.

Perhaps Tanner (1962) was the first to reject the grand unification hypothesis proposed by Brody. A pediatrician and a human biologist, Tanner was able to understand that primates follow a pattern of growth that is different in many ways from that of other mammals. According to his analysis, one such difference is that Old World monkeys, apes, and humans show two growth spurts: the universal spurt shared by all mammals that occurs just before or after birth, and a spurt at the time of puberty. Although Tanner's analysis sufficiently clarifies this point, confirmation and further clarification of this unusual pattern has since been provided (Laird 1967, Timiras & Valcana 1972). Tanner analyzed growth curves for male and female rhesus monkeys and chimpanzees. Their weight velocity curves show that rates peak at or just before birth and then decline after birth. The period lasts for more than a year for rhesus monkeys and for more than 3 years for chimpanzees. Both species then show an acceleration in weight velocity that has all of the characteristics of the human adolescent spurt in weight, including the earlier onset of the spurt in females and the greater intensity of the spurt in males. Tanner presents velocity curves for crown-rump length for rhesus monkeys and concludes, again, that both males and females have an adolescent spurt. This skeletal spurt, however, is much smaller than the spurt in weight and of much shorter duration. The rhesus weight spurt spans almost 3 years in males, but the skeletal spurt lasts at most 6 months. Based on other skeletal measurements, Tanner concludes that a rhesus growth spurt is "...largely one of shoulder breadth and, above all, of muscle mass" (1962:235).

A Survey of Weight Growth in Primates

Based on the evidence available today, there is no question that some monkeys and apes have pubertal growth spurts in weight. To date, Leigh (1996) has pro-
vided the most comprehensive study directed at the question of the primate growth spurts in weight. Some of Leigh’s findings are presented (Figure 7). Leigh collected chronological age and body weight data for 2395 captive primates, housed at both zoos and primate laboratories. There are 35 nonhuman species in his sample, including representatives of New World monkeys, Old World monkeys, and apes. He also included a data set for healthy humans (English boys and girls measured in the 1970s and 1980s). Although there are many longitudinal records for individual animals in the database, the data are analyzed in a cross-sectional fashion. Leigh explains that cross-sectional analysis “...leads to artificially depressed estimates of growth spurt magnitudes...[and] should lead to a conservative diagnosis of the presence of growth spurts” (1996:457). He also used the nonparametric mathematical technique called lowess regression to fit smoothed curves to the growth data for each primate species. There are many advantages and disadvantages to the use of mathematical curve-fitting. Interested readers should consult books on the theory and application of regression for details. Leigh’s decision to use the mathematical smoothing technique of lowess regression is useful, because it helps to reduce the unimportant variability (often called noise) in time-series data sets and helps to reveal the important main trends that occur over time. Lowess curves were fit to the distance data, and then the first derivative of the distance curve was estimated to produce a velocity curve. This follows exactly the procedure used to construct Figure 1.

A summary of Leigh’s results for the 35 nonhuman species he analyzed is given in Table 1. Only one species of New World monkey, Cebus apella, shows a spurt, and only for males. All studies of Old World monkeys show a spurt for males, and for many species they also show a spurt for females. Among ape species, gibbons (Hylobates spp.) show no spurt, orangutans (Pongo) show a possible male spurt, common chimpanzees (Pan troglodytes) shows a male spurt but no female spurt, and both bonobos (Pan paniscus) and gorillas (Gorilla) have male and female weight spurts. The variation in presence or absence of a postnatal weight spurt among primate species, and between sexes within a species, is in keeping with the diversity of primate biology and ecology. Leigh’s data show clearly that a postnatal weight spurt is not a primate characteristic; rather, it is a variable trait found in one, or both, sexes of some species.

The velocity curves for the apes are illustrated in Figure 11. The rate of weight growth of the gibbon generally decelerates from birth to sexual maturity in a manner similar to marmosets (Figure 7). Gibbons are also socially somewhat like marmosets in that both species live in family groups. But unlike the marmosets, gibbons have a juvenile stage of growth. Gibbon infants are weaned at approximately 3 years of age, and the age when females first give birth is approximately 9 years, which means that gibbons spend about 6 years as juveniles. The gibbon data show that postnatal growth spurts, especially spurts around the time of puberty, and the juvenile growth stage are not causally associated with each other. Great apes, including orangutans, gorillas, bonobos, and chimpanzees, all have infant, juvenile, and adult stages of growth but show varying patterns of stage duration and varying patterns of growth spurts. Weaning takes place by 4 years of
### TABLE 1  Summary results of Leigh’s (1996) analysis of weight growth in primate

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample size (Male/Female)</th>
<th>Growth spurt (by sex)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cebioidea (New World monkeys)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cebuela pygmaea</td>
<td>36/51</td>
<td>None</td>
</tr>
<tr>
<td>Callithrix jacchus</td>
<td>48/71</td>
<td>None</td>
</tr>
<tr>
<td>Callirino goeldi</td>
<td>42/27</td>
<td>None</td>
</tr>
<tr>
<td>Saguinus fuscicolli</td>
<td>18/19</td>
<td>None</td>
</tr>
<tr>
<td>Saguinus geoffroyi</td>
<td>9/10</td>
<td>None</td>
</tr>
<tr>
<td>Saguinus imperator</td>
<td>11/14</td>
<td>None</td>
</tr>
<tr>
<td>Saguinus oedipus</td>
<td>46/18</td>
<td>None</td>
</tr>
<tr>
<td>Leontopithecus rosalia rosalia</td>
<td>26/31</td>
<td>None</td>
</tr>
<tr>
<td>Saimiri sciureus</td>
<td>32/28</td>
<td>None</td>
</tr>
<tr>
<td>Cebus apella</td>
<td>26/28</td>
<td>Male</td>
</tr>
<tr>
<td>Callicebus moloch</td>
<td>30/23</td>
<td>None</td>
</tr>
<tr>
<td>Aotus trivirgatus</td>
<td>25/23</td>
<td>None</td>
</tr>
<tr>
<td>Cercopithecoidea (Old World monkeys)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cercopithecus aethiops</td>
<td>30/30</td>
<td>Both</td>
</tr>
<tr>
<td>Cercopithecus mitis</td>
<td>27/37</td>
<td>Male</td>
</tr>
<tr>
<td>Cercopithecus neglectus</td>
<td>29/23</td>
<td>Male</td>
</tr>
<tr>
<td>Erythrocebus patas</td>
<td>41/52</td>
<td>Both</td>
</tr>
<tr>
<td>Cerocebus atys</td>
<td>38/71</td>
<td>Male</td>
</tr>
<tr>
<td>Macaca arctoides</td>
<td>52/58</td>
<td>Male</td>
</tr>
</tbody>
</table>

(continued on next page)

age for gorillas, by 5 years for chimpanzees and bonobos, and by approximately age 6 for orangutans. Adult females first give birth at age 10 for gorillas, age 12 for orangutans, and between 13 to 15 years for chimpanzees and bonobos. Each species, then, varies in amounts of time spent in the juvenile stage. Even though gorillas have the shortest infancy and juvenile stages, they achieve the largest body weights of all the apes. This is because, at any age, gorillas are always growing faster than any of the other great ape species (Figure 11).

**Skeletal Growth in Primates**

In contrast to Leigh’s comprehensive survey of primate weight growth, there are only a few studies of skeletal growth. Coelho (1985) measured gains in crown-rump length (CRL) and weight in a mixed-longitudinal sample of 250 male and 452 female olive baboons (*Papio cynocephalus anubis*). The animals were part of a laboratory colony living under nature-like conditions in terms of physical envi-
TABLE 1 (continued)  Summary results of Leigh's (1996) analysis of weight growth in primatesa

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample size (Male/Female)</th>
<th>Growth spurt (by sex)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macaca fascicularis</td>
<td>13/13</td>
<td>Both</td>
</tr>
<tr>
<td>Macaca fuscata</td>
<td>64/71</td>
<td>Both</td>
</tr>
<tr>
<td>Macaca mulatta</td>
<td>52/58</td>
<td>Both</td>
</tr>
<tr>
<td>Macaca nemestrina</td>
<td>39/64</td>
<td>Both</td>
</tr>
<tr>
<td>Macaca silenus</td>
<td>39/41</td>
<td>Male</td>
</tr>
<tr>
<td>Papio hamadryas</td>
<td>33/53</td>
<td>Male</td>
</tr>
<tr>
<td>Mandrillus sphinx</td>
<td>49/59</td>
<td>Both</td>
</tr>
<tr>
<td>Colobus guereza</td>
<td>46/49</td>
<td>Both</td>
</tr>
<tr>
<td>Presbytis entellus</td>
<td>29/24</td>
<td>Both</td>
</tr>
<tr>
<td>Presbutis obscura</td>
<td>19/17</td>
<td>Male</td>
</tr>
<tr>
<td>Hominoidea (apes and humans)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hylobates lar</td>
<td>25/25</td>
<td>None</td>
</tr>
<tr>
<td>Hylobates syndactylus</td>
<td>19/21</td>
<td>None</td>
</tr>
<tr>
<td>Pongo pygmaeus</td>
<td>42/42</td>
<td>Maleb</td>
</tr>
<tr>
<td>Gorilla gorilla</td>
<td>77/64</td>
<td>Both</td>
</tr>
<tr>
<td>Pan paniscus</td>
<td>13/23</td>
<td>Both</td>
</tr>
<tr>
<td>Pan troglodytes</td>
<td>22/23</td>
<td>Male</td>
</tr>
<tr>
<td>Homo sapiens</td>
<td>Literature Data</td>
<td>Both</td>
</tr>
</tbody>
</table>

aSpecies evaluated, sample sizes, and presence or absence of a postnatal growth spurt by sex.
bPresence of spurt is uncertain.
anni et al (1982), and Macaca sinica (Cheverud et al 1992). Based on these studies, there is no evidence for the presence of human-like adolescent growth spurs in the skeleton of any of these species of Old World monkeys. Another mixed-longitudinal study of growth in weight and CRL with baboons suggests a pubertal spurt in skeletal growth. The authors of this study report "the presence of a pubertal growth spurt in body weight, and possibly CRL, in male but not in female baboons" (Crawford et al 1997). The male CRL spurt amounts to about a 2-cm increase in growth rate from prepubertal values. But the analysis of the spurt is based on a varying number of individual baboons, with as few as two and as many as eight individuals measured on different occasions. It is difficult, if not impossible, to derive an accurate and reliable estimate of growth velocity from data of this type.

Cross-sectional studies of both weight and skeletal growth (e.g. limb lengths, trunk length, etc) in Japanese macaques (Macaca fuscata) and chimpanzees (Pan troglodytes) have been published by Hamada (1994) and Hamada et al (1996). The macaque group consisted of both laboratory colonies and seminatural colonies reared in monkey parks in Japan. The data are cross sectional, representing 2886 animals (1288 males, 1598 females) between the age of birth to 15 years. The chimpanzee data, which are also cross sectional, came from animals reared at a primate park owned by a Japanese corporation. There were a total of 172 chim-
panzees (81 male, 91 female) between the ages of birth and 15 years, Hamada and colleagues analyzed the data by fitting spline curves to the median values of growth for each age class, e.g. 3 months, 6 months, 12 months, 2 years, etc. The first derivative of these distance curves was used to produce a velocity curve. The spline curve method is similar to the lowest regression method used by Leigh in that both are designed to fit a smooth, continuous curve to a set of data points. One difference between the methods is that spline curves are forced to pass through each data point, whereas lowest curves may pass between data points.

Hamada found that the postnatal growth of the Japanese macaque, in terms of both distance and velocity, had, in general, three distinct phases: "...[1] from birth to two years when the growth velocity decreases rapidly; [2] from two to three and a half (in females) or four and a half (in males) years of age when the velocity stays constant or growth accelerates; [3] from those ages to eight years of age when velocity decreases again to zero". This overall pattern is a textbook case of an animal with infant, juvenile, and adult growth stages. Note that during the juvenile stage the growth rate stays constant or accelerates (Hamada's phase 2). Weight growth for Hamada's male and female monkeys provides an example of both juvenile patterns. Male monkeys show a clear spurt in weight, but female monkeys show no spurt (similar to the baboons in Figure 7). The analysis of the macaques also includes the calculation of distance and velocity curves of growth for 15 different body segments or cranial dimensions, such as trunk length, tail length, upper arm and forearm length, thigh length, and head breadth. Some of these dimensions show what might be a growth spurt, for example in hand and leg length, but other dimensions, such as forearm length and head breadth, do not. Generally, male monkeys show spurts more often in these 15 dimensions than do female monkeys.
Chimpanzee data analyzed by Hamada et al (1996) included measurements of body weight and trunk length (measured from the cranial end of the sternum to the cranial end of the pubic symphysis). Velocity curves for these two measurements show that the chimpanzees have three stages of growth: infancy, juvenile, and adult. During the juvenile stage male chimpanzees experience a clear spurt in weight but not in trunk length. Female chimpanzees do not show a postnatal growth spurt in either weight or length.

In another study, Hamada et al (1998) analyzed the pattern of bone maturation for a group of 65 male and female chimpanzees from the same primate park colony used in the somatic growth study. The authors employed the Tanner-Whitehouse 2 method (Tanner et al 1975) to assess the stages of bone maturation. From these bone stages, Hamada et al computed RUS scores for the 13 epiphyses of the radius (R), ulna (U), and short bones (S) (metacarpals and the first, third, and fifth phalanges). The RUS scores are calculated as points, with zero points meaning that no epiphyses are present and 1000 points indicating full maturity of the 13 epiphyses. The Tanner-Whitehouse 2 and RUS methods are widely used to assess bone maturation in human boys and girls. The findings of Hamada et al for chimpanzees are shown in Figure 13 as increments in RUS points between successive measurements. The chimpanzee data are compared with similar data from human boys and girls. The human RUS point increments are taken from the 50th percentile curve published by Tanner et al (1975); in other words, from the sample used to develop the RUS scoring system.

Chimpanzees and humans have distinctly different patterns of skeletal development. Boys and girls show the typical human curve of growth, with a deceleration in bone maturation during infancy, a steady rate of bone maturation during the childhood and juvenile stages, and an adolescent spurt in bone maturation. Note that the human adolescent spurt has but a single peak. Both male and female chimpanzees also show a deceleration during their infancy stage but, in contrast to humans, show an immediate acceleration in the rate of bone maturation, then another deceleration, and then a secondary acceleration. Hamada et al call these last two phase of bone maturation the midadolescent trough and the postadolescent peak. I would substitute the word juvenile for adolescent, but whatever one calls these changes in rate of bone maturation, they have no parallel in the human condition.

The studies by Leigh and by Hamada and colleagues are valuable because they include large samples of nonhuman primates and many species of primates. Taken together, these studies show that some primate species have postnatal growth spurts in weight, linear dimensions, and bone maturation that occur around the time of sexual maturation. About half of the species studied show a weight spurt for males only, and when a female weight spurt is present it is always smaller than the male spurt. These accelerations in weight growth are the result of an increase in size of several tissues, particularly in muscle mass and body fat. Behavioral studies of free-ranging animals show that adult males use this muscle mass in reproductive competition with each other. Female primates may also choose to mate with larger males, who may be healthier and socially more suc-
cessful than smaller males. The absence or reduced size of a female growth spurt allows females to maintain smaller adult body size compared with males. This may be advantageous during pregnancy and lactation because smaller bodies require less energy and other nutrients and therefore would permit the mother to divert more of the food she eats to her developing offspring. Within this context of reproductive strategies, one may begin to understand how evolutionary pressures and natural selection have shaped the type and intensity of growth spurts that non-human and human primates experience. Human boys and girls experience a growth spurt in weight and in height during adolescence, and the male spurts are more intense than the female spurts. Discussions of the types of evolutionary pressures that may have shaped human growth at adolescence can be found elsewhere (Bogin 1993, 1994a, 1999). Here, attention is focused on a more detailed consideration of skeletal growth spurts, for it is in the growth of the skeleton that we see the clearest difference between the patterns of growth for human and non-human primates.

SKELETAL GROWTH SPURTS IN PRIMATES

A serious limitation of the otherwise excellent studies by Leigh and by Hamada et al is that the growth velocity curves were computed from cross-sectional data, which tends to minimize the size of any actual growth spurt. But cross-sectional data analysis may also produce a growth spurt when none is really present. Differences in the care, feeding, or health of animals from which information is gath-
ered for adjacent data points may result in discordant patterns of growth that produce spurious growth spurts. Only a pure longitudinal analysis can faithfully represent the growth of a primate, or group of primates, over time. One of the first longitudinal analyses of nonhuman primate growth was published by Gavan (1953), who analyzed the skeletal growth of nine male and seven female chimpanzees. The data were collected at the Yerkes Primate Laboratories beginning in 1939. The chimpanzees were measured once a year from birth to age 12. Influenced by Brody’s speculations, and using mathematical methods and devices (i.e. adding machines) available at that time, Gavan concluded that chimpanzees have a human-like skeletal growth spurt at the time of puberty. In 1971, however, Gavan reanalyzed his chimpanzee data based on newer mathematical methods and the use of a computer and found that no spurt in linear growth could be detected. “After all, a smoothly decelerating curve gave the best fit to most of my data with a very small residual variance” (Gavan 1982:3).

Watts & Gavan (1982) reanalyzed the same chimpanzee data and new growth data for the rhesus monkey. The rhesus data were collected by Gavan between 1960 and 1967 from a laboratory colony. Longitudinal assessments of growth were made at least once a year from birth to 5 years of age. They found that simple plots of height or weight for age did not reveal a growth spurt in either the rhesus monkey or the chimpanzee. This stands in contrast to the human case where simple graphical methods of analysis reveal the adolescent growth spurt in most individuals. To search for nonhuman primate growth spurts, the longitudinal data for each chimpanzee or rhesus was fit with an exponential regression formula. “This model depicts growth as a process that is gradually and constantly decelerating as size increases. Its use, therefore, assumes that an adolescent spurt does not exist” (Watts & Gavan 1982:56). This is the same model Gavan (1971) used when he concluded that the chimpanzee had no growth spurt in trunk length or in other linear dimensions.

Watts & Gavan (1982) found that deviations in skeletal growth from the regression model followed a consistent pattern in all 16 chimpanzees and in all the rhesus monkeys. An example is depicted in Figure 14 for growth of the thigh of one chimpanzee. Deviations are positive, above the curve, in early infancy, negative in later infancy and just prior to puberty, and positive again following puberty. The authors noted that the differences between the observed and predicted values at each age are small, less than a centimeter, and often only a few millimeters. It was impossible for them to depict these differences graphically as two distinct curves. “Therefore, to exaggerate the differences for drawing this figure the actual deviations were multiplied by a factor of three...” (Figure 14; Watts & Gavan 1982:58). Watts & Gavan emphasized their consistent finding of growth deviations from the predicted curve as evidence for the presence of adolescent growth spurts in nonhuman primates. No statistical test of the mathematical significance of the deviations was made. Watts does make the following qualitative assessment: “...the magnitude of the change is very small” (1985b:56).

Tanner et al (1990) published a longitudinal analysis of skeletal growth in female rhesus monkeys (Macaca mulatta) and found evidence for “clear pubertal
growth spurts” (1990:101) for tibia length, CRL, and weight. Their data consist of measurements taken every three months on nine monkeys housed indoors and six monkeys housed outdoors at the Yerkes Regional Primate Center in Atlanta, Georgia. The original figures from the article are reproduced here (Figure 15) because they are essential to the analysis by Tanner et al. The velocity curves shown in Figure 15 are mean values that were calculated by combining the data from all nine indoor-housed monkeys. This was done by aligning their curves on their age at maximum velocity to produce peak length velocity curves. This method is identical to the procedure invented by Boas in 1930 to study human adolescent curves and is “...an exact copy of Shuttleworth’s (1937) famous analysis of human growth and produces essentially a mean-constant velocity curve” (Tanner et al. 1990:102).

According to Tanner et al, these figures of rhesus monkey growth “...establish the occurrence of a pubertal growth spurt beyond any reasonable doubt, at least for this species” (1990:101). The mean curve for tibia length certainly seems to support this, as there is a single peak velocity of about 2.25 cm/3 month (on an annual basis this peak velocity equals about 0.6 cm/year). The mean curves for CRL and weight are less easily interpreted. Both CRL and weight show two or three spurts, albeit the one that precedes menarche is the largest. Tanner and colleagues offer only these figures as evidence for the primacy of the premenarchial

![Figure 14](image)

**Figure 14** Observed and predicted growth curves for thigh length in a male chimpanzee. (From Watts & Gavan 1982.)
Figure 15  Mean-constant velocity curves for growth of female rhesus monkeys. Tibia length, crown-rump length (CRL), and weight. (From Tanner et al 1990.)
spurt. They do not carry out any statistical analysis to demonstrate that this spurt represents a significant increase in growth rate compared with any other period of growth. Nor do they analyze the duration of the spurt, which is important if we want to understand the contribution of this spurt to the total pattern of growth for these monkeys. Another complication arises because the pattern of growth and growth spurts seen for the nine monkeys housed indoors differs significantly from that of the six outdoor-housed monkeys. Both the outdoor- and indoor-housed groups show a tibia-length spurt that occurs just before menarche. The outdoor-housed females show either no spurt for CRL, or a small postmenarchial spurt, and two spurts for weight (Wilson et al 1988). Their first weight spurt occurs before menarche and the second well after menarche, unlike the situation for the indoor-housed monkeys.

Tanner et al provide illustrations of the velocity curves for the tibia and CRL for "...three individual indoor-housed monkeys...selected at random from the total group" (1990:103). That illustration is reproduced here as Figure 16. The data show much variability, with skeletal growth rates oscillating between 0.00 cm/3 months and more than 2.5 cm/3 months for adjacent measurements. Maximum individual peak velocities occur both before and after menarche (CRL for monkey no. 1 and 4, respectively), and smaller spurts occur both before and after first ovulation (CRL for monkeys no. 4 and 7; note also the variation in spurts for tibia length for all three monkeys).

The Human Adolescent Growth Spurt

Longitudinal data for primate skeletal growth are rare, and it is even less common to see these data analyzed in a proper longitudinal fashion. The 1990 work of Tanner et al is valuable because it presents and analyzes such longitudinal data. The quality of their data is unquestionable, and their analysis meticulous. Nevertheless, human adolescents do not follow the patterns of growth seen in rhesus monkeys. Figure 17 is a mean-constant curve of human velocity growth in height and weight produced from the longitudinal growth records of 12 Guatemalan girls. The data are derived from a study of children, juveniles, and adolescents at a private school in Guatemala City (Bogin et al 1992). The girls are from families of high socioeconomic status, and all were healthy and well nourished at the times of measurement—once per year. The same methods were used to construct Figure 17 as were used by Tanner et al (1990) to construct the mean-constant velocity curves for the nine rhesus monkey females of Figure 16. One indicator of human puberty is the decreasing to increasing change of growth velocity that marks the transition from the juvenile stage to adolescent stage. That point is labeled on Figure 16. The mean age at peak height velocity and peak weight velocity for these 12 girls is 12.5 ± 1.07 years, and the standard error of the mean is 0.31 year.

Human–Rhesus Difference in Growth Velocity

There are at least five differences between humans and rhesus monkeys in the pattern of velocity growth: (a) Humans have one relatively large and unambiguous growth spurt for both height and weight during adolescence, (b) the magnitude of
Figure 16  Velocity curves for tibia length and crown-rump length velocity for three individual rhesus monkeys chosen at random from the sample used to construct the curves in Figure 15. (From Tanner et al 1990.)
the human adolescent spurt in the rate of skeletal growth is absolutely large compared with that of the nonhuman primates, (c) human growth velocities do not oscillate from near-maximum velocity to near-minimum velocity between adjacent measurements, (d) the human adolescent spurt lasts for years and the rhesus
spurts last for only a few months, which is a relatively short amount of time even when considering that the life span of a monkey is only one third that of a human being, and (e) that the human adolescent growth spurt is found in all human populations, including those housed indoors and those housed outdoors (that is, in societies ranging from the urban/industrialized to the rural hunting and gathering groups). Exceptions to each of these six points are reflected in the rhesus data.

Because the Guatemalan girls were measured only once per year, it was not possible, with that data set, to show that humans maintain a fairly smooth trajectory of adolescent growth even over shorter time periods. At monthly intervals there is a good deal of variation in stature increments for boys and girls (Bogin 1977, 1978; Togo & Togo 1982). Even so, during the duration of the adolescent spurt in stature, human growth increments never approach zero, as they do for the rhesus monkey. At 6-month intervals between measurements, most of this human variability disappears. A 6-month interval for humans would be a fair comparison with the rhesus monkey 3-month interval, as humans take more than twice the time to grow up. One famous example of human growth measured every 6 months was provided by the growth data gathered by the Count Philibert Guénée du Montbeillard of France. He measured the stature of his son every 6 months from the boy’s birth in 1759 to his 18th birthday. George-Louis Leclerc de Buffon included the measurements, and his commentary on them, in a supplement to his Histoire Naturelle published in 1777. These data are usually considered as the first longitudinal study of human growth, and because of Buffon’s commentary, the most famous. Togo (1995) analyzed this French boy’s growth based on the full data set gathered at 6-month intervals between measurements and showed that during his adolescent growth spurt in height, the boy increased smoothly to peak height velocity and then decreased smoothly for the next year. Togo did not find any of the oscillations that typify rhesus monkey growth after puberty.

PATTERNS OF GROWTH FOR HUMANS VERSUS OTHER PRIMATES

There is no doubt that some nonhuman primates have increases in the rate of skeletal growth for some body dimensions at the time of puberty. Considerable evidence shows that these small increases in skeletal growth represent real and important biological processes. Most likely, the perturbations in growth around the time of puberty are due to the onset of adult levels of gonadal hormone secretions. It has been well established that testosterone in male primates and estrogens, such as estriol, in female primates can increase growth rates (Martin et al 1977, Bercu et al 1983. Prader 1984). But there is more involved: Roughly equivalent amounts of hormone production in both chimpanzees and in humans result in strikingly different rates of growth. In male chimpanzees, the concentration of testosterone in blood serum prior to puberty (from 1 to 6 years of age) averages 13 ng per dl (Martin et al 1977). For human males, the prepubertal serum testosterone concentration (from ages 1 to 12 years) averages 9 ng/dl (Winter 1978). The peak velocity in long bone growth of the eight male chimpanzees stud-
ied by Watts & Gavan (1982) occurred at a mean age of 10.96 years, with a standard deviation of 1.31 years. At this age, serum testosterone averages about 400 ng/dl (Martin et al 1977). Peak height velocity in human boys from western Europe occurs at a mean age of 14.06 years, with a standard deviation of 0.92 years (Marshall & Tanner 1986) when serum testosterone levels average about 340 ng/dl (Winter 1978). Based on these data, the serum testosterone concentration of chimpanzees increases about 31-fold from the prepubertal to pubertal state. In human males, serum testosterone concentration increases about 38-fold, or 1.23 times the increase for chimpanzees.

Clearly, both chimpanzee males and human boys have large increases in testosterone production after puberty, but the effects on skeletal growth are not so similar. According to Watts & Gavan (1982), chimpanzees have a relatively small increase in the velocity of growth of individual long bones during puberty "...usually less than a centimeter" (1982:58). Similar findings are reported by Copeland et al (1985), who analyzed growth in weight and CRL in 86 male and female chimpanzees. These researchers found that in males there was a marked increase in serum testosterone between the ages of 6 and 8 years. This was followed by a slight increase in the rate of weight gain but no detectable spurt in CRL. Females also showed a rise in serum testosterone between the ages of 6 and 8 years and rise in estradiol after 10 years of age. In contrast to males, female chimpanzees had a much smaller increase in the rate of weight gain in relation to testosterone levels. Females had no detectable spurt in CRL at any age. Hamada et al (1996) confirm these findings when they report no increase in the rate of skeletal growth at the time of puberty for their samples of male or female chimpanzees.

In sharp contrast to the chimpanzee research are the findings for human boys and girls that show relatively large and easily detectable growth spurts for both height and weight during adolescence. Because chimpanzees are not bipedal, it is not possible to take a measurement that is exactly equivalent to human height. It is therefore more appropriate to compare chimpanzee and human growth in terms of body segments. Cameron et al (1982) performed a longitudinal analysis of the growth of individual limb segments in British boys. They found that the peak value in velocity during the adolescent growth spurt ranged between 1.34 cm per year for the forearm and 2.44 cm per year for the tibia. Satake et al (1993) report that during human adolescence, peak velocity for sitting height (roughly equivalent to CRL) equals 7.5 cm per year for Japanese boys and 6.2 cm per year for Japanese girls. Based on these findings, one may propose that there are differences in the effect of testosterone and estrogen on the skeletal growth of chimpanzees and human beings. The growth response of the human skeleton to rising testosterone levels is greater than the response of the chimpanzee skeleton. The change in the serum hormone levels for males of the two species differs by a factor of about 1.23, but the change in the velocity of growth of various body segments is two to four times greater for the human arm or leg, and more than 10 times greater for human sitting height.

The velocity of growth in weight of male chimpanzees (and, presumably, of male baboons and some female primates) is better correlated with endocrine
changes at puberty (Figures 7, 11). This observation suggests that there are differences in the growth response of skeletal and nonskeletal tissue, such as muscle and adipose tissue. There are also differences in the effect of hormones on tissue growth between males and females within the same species. Female chimpanzees experience a much smaller weight spurt than males, and female baboons show no weight spurt at all. It is important to contrast this to the human case; most girls experience significant growth spurts in both height and weight. Thus, the growth effects of pubertal endocrine changes differ between individuals of the same sex but of different species (e.g. male chimpanzees and human boys), and between the sexes within the same species (e.g. male and female chimpanzees).

Three major differences between human and nonhuman primate growth may be highlighted at this point. These are (a) the residual growth potential of the nonhuman versus the human primate at adolescence, (b) the sensitivity of different body tissues to growth-promoting stimuli, and (c) sex differences in the expression of growth spurts at adolescence. Monkeys, apes, and humans all experience a prolongation in the time for growth and a delay in the onset of sexual maturation. As noted by Brody (1945) more than 50 years ago, the delay is relatively and absolutely greater in humans than in nonhuman primates, and in addition to this, humans also have a markedly increased potential over apes and monkeys for growth in height and weight during adolescence. This growth potential is more likely to be regulated by the sensitivity of neuroendocrine receptors and postreceptors (i.e. biological tissues) to growth stimuli than by the rate or amount of production of the stimuli (hormones) themselves. The lack of linear associations between testosterone concentrations and growth velocities in skeletal and nonskeletal tissue of chimpanzees and humans show this. The differences in cellular sensitivity to growth stimuli between nonhuman and human primate growth are probably controlled at the genetic level. Although it is possible that the different patterns of growth in the various primate species are the result of the evolution of new structural genes (genes that code for specific proteins), it is more likely that the variation in growth control lies in the regulatory genes that initiate, terminate, and control the duration of each of the distinct periods of growth (Britten & Davidson 1969, King & Wilson 1975, Bogin 1999:Ch. 7).

A PHILOSOPHY OF HUMAN GROWTH

Nonhuman primate models are used in studies of human growth because of the similarities in anatomy and physiology between the species. When Schultz started his studies, he explicitly assumed that there was an evolutionary continuum between the living primate species. His illustration of primate life history (Figure 8) shows this assumed continuum very nicely. There is an evolutionary connection relating all primate species, but living monkeys, apes, and humans have separate evolutionary histories. A separation between Cercopithecoids (Old World monkeys) and hominoids (apes) occurred some 20 million years ago and the hominoid-hominid (ape-human) split occurred approximately 5–6 million years ago. There is no evolutionary reason to expect that the patterns of growth for
these three divergent and ecologically distinct species should be identical or even similar. As Gavan (1971:54) observed, chimpanzee postnatal growth begins "...with an initially high rate which decelerates smoothly as size increases, but it is well known that human growth is characterized by a growth spurt.... Some change must have occurred in human growth since we and the chimpanzee have had a common ancestor."

The notion of an evolutionary continuum is one legacy of the philosophy of a Great Chain of Being (Lovejoy 1936). This is a popular cultural construct in western society that has historical roots going back at least to ancient Greek writers. In biology, the Great Chain takes the form of the scala naturae. In its original usage it erroneously implies that all living creatures, from the amoebae to the human, form a living evolutionary sequence from the simplest to the most complex creature. We now understand that humans are not the culmination or the goal of evolutionary history. We are just one of more than 2 million species of animal alive today, each the end product of its own history and with its own unique place in nature. Yet, the scala naturae is sometimes misapplied to the connection between human and nonhuman primates.

Some observers tend to see monkeys and apes more as models for human biology and behavior than as creatures in their own right. This point was cogently argued by Scott (1967:72): "Subhuman primates are not small human beings with fur coats and (sometimes) tails. Rather they are a group which has diversified in many ways, so that they are as different from each other [and humans] as are bears, dogs and raccoons in the order Carnivora." Although Scott referred specifically to psychological attributes of species within the orders Carnivora and Primates, his cautionary remarks apply equally to morphology, physiology, and, in the present context, patterns of growth. As mentioned above, within the Carnivora, certain social species (dogs, wolves, lions) experience a prolonged period of relatively slow growth between infancy and adulthood that corresponds to the juvenile growth phase. Nonsocial species of carnivores mature from infancy to adulthood without a juvenile stage of growth. There is no reason to expect, a priori, that the primates, as an order of mammals, would be any more uniform in growth patterns than the Carnivora. Newell-Morris & Fahrenbach (1985) reviewed the use of nonhuman primates as models for human development and growth and concluded that "...there are problems with the extrapolation from the nonhuman primate model to the human condition because of intergeneric differences in size, growth and development rates, and timing. Although investigators justify direct extrapolation of their findings on the basis of the close genetic relationships of all primates, this assumption in many cases may be little more than absolute faith in the evolutionary argument from which it stems" (1985:35).

Watts (1990) points out that the patterns of growth of the New World monkey Cebus. Old World rhesus monkeys, chimpanzees, and humans, are all derived from an ancestor or ancestors. Each of the living species is likely to be derived from its ancestor in ways that are independent and unequal due to "different ecological and adaptive circumstances" (1990:99). Watts argues that rhesus monkeys make poor models for human growth because of their advanced state of skeletal
development at birth and early onset of puberty and menarche compared with humans. The rhesus is also a seasonal breeder in nature; ovulation takes place in the fall or winter months and birth occurs in the spring or summer. Female rhesus monkeys raised outdoors may reach menarche in any season but have their first ovulation only in the fall (Wilson et al 1988). When housed in artificial conditions, such as for the indoor-housed monkeys studied by Tanner et al (1990), sexual maturation for female rhesus is very much altered because they can reach first ovulation in any season. Several studies show that when animals, including primates, are housed indoors and exposed to 12 h of light followed by 12 h of darkness (a standard procedure), many of their normal endocrine system functions are disturbed, or even obliterated (Bogin 1977). Because both sexual maturation and body growth are influenced by many of the same hormones, it seems unreasonable to expect nonhuman primates reared indoors to serve as models for human growth and development.

One colleague, Leigh, offered the following comment after reading a draft of this review: “The presence of a spurt in tibia or in other anatomical units certainly does not, as your review indicates, imply homology with the human statural spurt.” In biology, the term homology is used to describe anatomical structures, physiological processes, or behaviors that are found in different species because of a common evolutionary origin. The five fingers and toes and the intimate mother-infant relationship characteristic of almost all primate species are due to homology. Leigh’s point is that growth spurts for various parts of the body of different species of primates are not necessarily homologous. He continues: “For example, my recent studies of baboons demonstrate unambiguous growth spurts in the snout, probably comparable in magnitude to tibial spurs observed by Tanner et al in macaques...The presence of these spurts, however, does not imply homology with human growth spurts in stature. CRL and sitting height would be the closest homologues, but even then, locomotor differences among these primates would greatly complicate assessments of homology. What I derive from the ideas you are presenting here, and in the last section, is that it might be best to think of growth spurts as modular and highly evolvable features of ontogeny. Natural selection (or sexual selection) can effectively ‘put’ spurts where (anatomically) and when they are needed to increase fitness. I think that the field has labored a little too long under Brody’s desire to find a universal pattern. What may be happening here is more akin to a universal process. Perhaps we could propose that the universal process is modularity and evolvability of growth spurts (or decelerations), and that this process need not produce a uniform pattern between any two species or within a particular clade” (S Leigh, personal communication).

An acceptable philosophy of human growth must acknowledge the mammalian and primate foundations for the human pattern of growth. But that philosophy must account for the ecology to which the human species—indeed any species—is adapted. A recent evolutionary perspective on the ecology of human growth and development is available (Bogin 1999:Ch. 4). Grounded in evolutionary ecology, a robust philosophy of human growth ought to allow for the evolution of variations on common themes. One variation may be the evolution of new
stages of life history, such as human childhood (Bogin 1997). Another variation is new patterns of growth in body segments, such as the pubertal growth spurts in a baboon snout or a rhesus monkey tibia. A final variation may be the coevolution of both new stages and new patterns of growth, such as human adolescence and the human adolescent growth spurt.

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