# 7

# Modern Human Life History

## *The Evolution of Human Childhood and Fertility*

**Barry Bogin**

**SUMMARY**

*Life history theory needs to account for certain features of human social behavior and physical growth that are unusual compared with other primates. Human infants have a relatively early age for weaning (the cessation of breastfeeding)—on average, by age 36 months—but after weaning, human children are still dependent on older individuals for food and protection, until about age 7 years. Many members of the social group—older siblings, grandmothers, fathers, other kin, even nonkin—take an active role in this provisioning. Also, humans have seven to ten years of relatively slow growth following weaning and then a few years of rapid growth in virtually all skeletal dimensions of the body. No other primate species shares this pattern of skeletal growth.*

*A central question in life history evolution is, did these characteristics evolve as a package or as a mosaic? The evidence suggests a mosaic, with the evolution of a childhood life stage more than two million years ago as perhaps the earliest feature of modern human growth. The evolution of childhood occurred because it provided reproductive advantages to the mother—by weaning early, the mother was free to reproduce again, faster than any ape.*

*As a secondary benefit, the extra time for growth and development afforded by childhood enabled greater investments in physical and social capital of the youngster before maturation. These investments, especially in greater brain growth and behavioral complexity, may be inadvertent and chance consequences of the evolution of childhood. The primary driver of the evolution of human life history was the evolution of childhood and cooperative care of children. These allowed for more rapid reproduction, higher-quality offspring, and lower prereproductive mortality than ever before in mammalian history.*

Consider the following two life histories. Fifi was born near the shores of Lake Tanganyika, Tanzania, probably in 1958. She gave birth for the first time at age 13 years. In the year 2003, at 44 years of age, she became a mother for the ninth time. Her first three births were spaced five years apart, but subsequent births occurred every four years. The exception to this pattern was her eighth birth, which occurred two years after the birth of her seventh infant. Fifi's seventh infant died shortly after its birth, and she became pregnant soon thereafter. Fifi has four living daughters, and the two oldest have blessed her with five grandchildren, of which four are alive. Fifi has four living sons. One of the older two, Frodo, is confirmed as father of three offspring, Fred, Titan, and Sherehe (Morin et al. 1994; Constable et al. 2001). Because of Fifi's involvement with her own offspring, she rarely invests time or resources in her grandchildren.

The second life history concerns Ethel, who was born in 1908 in the village of Gajsin, Ukraine. She gave birth to two daughters, the first at age 22 and the second at age 29. Both survived to adulthood and produced a total of five offspring. Because Ethel had no current children of her own to care for, she was able to invest time, energy, and resources in the care of her grandchildren. All the grandchildren survived to reproductive age and produced ten biological offspring, four of whom are of reproductive age (two males and two females). As of this writing, Ethel (age 97) and her daughters, grandchildren, and great grandchildren are all alive.

Fifi is a chimpanzee, one of the Gombe group studied by Jane Goodall since 1960 (Goodall 2003). Ethel is my maternal grandmother. Both are reproductively successful, though as of this writing, Ethel more so, because she has more confirmed living descendants. Ethel's family will increase further because her oldest grandchild (the present author) and his wife are in the process of adopting a 1-year-old infant. Chimpanzees living in the wild do not adopt the still-nursing infants of other females (Goodall 1983). Ethel's reproductive success is typical of *Homo sapiens* women, but Fifi is "a female that is off the charts in terms of reproductive success!" (Anne Pusey, personal communication 2004). More typically, a female chimpanzee reproduces only two offspring that live to adulthood. Goodall (1983) reports that between the years 1965 and 1980, fifty-one births and forty-nine deaths occurred in one community of wild chimpanzees at the Gombe Stream National Park, Tanzania. During a ten-year period, Nishida, Takasaki, and Takahata (1990) observed "74 births, 74 deaths, 14 immigrations and 13 emigrations" in one community at the Mahale Mountains National Park, Tanzania. Chimpanzee population size in these two communities is, by these data, effectively in equilibrium.

The differences between Fifi's and Ethel's reproductive scheduling, longevity, and family social dynamics (including the behavior of grandmothers toward their grandchildren) illustrate many key features of human life history (see also Hawkes, chapters 3 and 4, Robson, van Schaik, and Hawkes, chapter 2, and Sellen, chapter 6, this volume). The human life cycle sharply contrasts with that of other mammal species, even other primates (van Schaik et al., chapter 5, this volume). Female chimpanzees at Gombe give birth to their first infant at an average age of 14 years; in traditional societies throughout the world today and in the historic past, human women do so at an average age of 19 years. Of course, some chimpanzees and women experience first births at younger and older ages. Chimpanzees usually continue to provide some breast milk to their infant for 4 years or longer and average 5.5 years between successful births. In traditional foraging and horticultural societies, human women can successfully reduce the interval to 3–4 years (Short 1976; Howell 1979; Blurton Jones et al. 1992; Hill and Hurtado 1996; Robson, van Schaik, and Hawkes, chapter 2, this volume), and even to 2.0 years in agricultural and industrial societies (Bogin 2001; Setty-Venugopal and Upadhyay 2002). Human birth intervals can be this short because of the early termination of breastfeeding in traditional societies—by a median age of 30 months (Dettwyler 1995) but as early as 9 months (Lee, Majluf, and Gordon

1991; Sellen, chapter 6, this volume). Another contrast is that chimpanzees continue to reproduce until death but human women stop well before death, usually by their mid-40s, and experience menopause by about age 50. It is possible that chimpanzee females experience menopause after age 50, as documented in one case (Finch and Stanford 2004), but chimpanzees rarely live beyond 50. Human women may live for decades beyond menopause and age 50 (Fedigan and Pavelka 1994).

## THE HUMAN PARADOX

These contrasts between human women and our genetically closest primate cousin present a problem for students of the evolution of life history. Life history theory has to explain an apparent paradox, that humans successfully combine delayed reproduction, births to helpless newborns, and a relatively short duration of breastfeeding with an extended period of offspring dependency, menopause, and great longevity. Life history theory also has to explain the features of human social behavior and physical growth that are unique among primates. In terms of social behavior, after weaning (the cessation of breastfeeding), human children depend on older individuals for food and protection until about age 7 years. Other forms of physical, social, and economic dependency may continue into the third decade of life.

This dependency of human children is due to the immaturity of their dental, motor, cognitive, and linguistic abilities. Children cannot masticate adult-type foods until the first permanent molars and central incisors erupt, which takes place at an average age of 7 years (Smith, Crummett, and Brandt 1994). Children under 7 cannot walk as efficiently as older people; in traditional foraging and horticultural societies, this means that they cannot acquire sufficient amounts of their own food. Nakano and Kimura (1992) and Kramer (1998) find that by age 7 years, on average, humans can walk with almost adult-type efficiency and gait. Children under 7 use more energy per kilogram of body weight when walking than do adults. By 5 to 6 years of age, children are about 85 percent as efficient as adults. At 7 to 8 years of age, youngsters have more than 90 percent the efficiency of adults.

In what has come to be known as the “five to seven year shift” (Sameroff and Haith 1996), new learning and behavioral capabilities emerge, enabling greater social independence. Cognitive and emotional developments permit new levels of self-sufficiency (Tomasello and Call 1997). With little or no supervision, 7-year-olds can perform many basic tasks, including food preparation, infant care, and other domestic activities (Rogoff 1996; Weisner 1996). Finally, the 7-year-old human achieves new competencies in speech production and language usage. One quantitative change involves the relationship between pharynx height and oral cavity length, which changes from birth until 6–8 years of age, when it reaches and stabilizes at the (1:1) ratio that permits adult vowel production (Fitch and Giedd 1999; Lieberman et al. 2001). The 7-year-old also is more adultlike in production phonology, vocabulary, sentence length, and syntax (Locke and Bogin 2005).

Many members of the human social group, including older siblings, grandmothers, fathers, other kin, and nonkin, help provision and protect infants and children. In contrast, weaned chimpanzees and juveniles of other primate species must forage for most of their own food. The weaned young of some species (for instance, marmosets and tamarins) do receive assistance from their mothers and occasionally from the fathers, but much less often from other group members.

Another paradox for life history evolution is the human pattern of physical growth. Most primate species have rapid growth in length and body weight during infancy and then a declining rate of growth from weaning to adulthood (figures 7.1 and 7.2). In terms of physical growth, humans are unusual in having seven to ten years of relatively slow growth following weaning and then a few years of rapid growth in virtually all skeletal dimensions, called the “adolescent growth spurt.” No other primate species, not even chimpanzees, exhibits this pattern of skeletal growth (Bogin 1999a; Hamada and Udono 2002; but see Leigh 2001 for evidence of growth spurts in body weight).

As mentioned before, a central question is whether these characteristics evolved as a package or as a mosaic. In other publications, I explain how the evidence suggests that human life history evolved as a mosaic and may have taken form over more than a million years (Bogin 1999a, 2001). In this chapter, I review the evolution of human childhood, a special life history stage. First, it is necessary to define some key terms, to review the stages of the human life cycle, and to show in more detail how human life history stands in contrast with

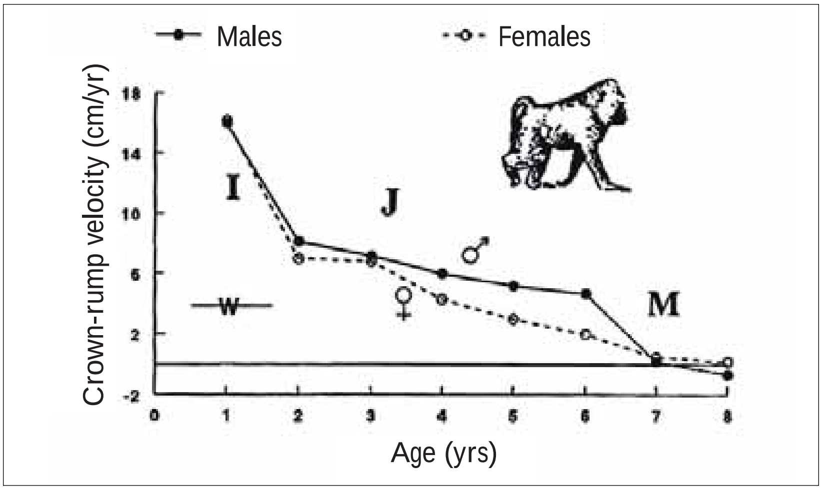

**Figure 7.1**

*Baboon crown-rump-length velocity. Letters indicate the stages of growth:* I, *infancy;* J, *juvenile; and* M, *mature adult. Weaning* (W) *may take place anytime between the ages of 6 and 18 months (from Bogin 1999a, after Coelho 1985).*

other mammals.

## LIFE HISTORY AND LIFE CYCLES

Every species has its own pattern of ontogeny, that is, the process of growth, development, and maturation of the individual organism from conception to death. Every species also has distinct life history traits, that is, major events that occur between the conception and death of an organism. The events of life history "govern natality and mortality" (Cole 1954:103), as well as ontogeny (Charnov 1993, 2001a; Bogin 2001). Stearns (1992:vii) captures the essence of life history theory:

> Consider a zygote that is about to begin its life, and imagine that all opportunities are open to it. At what age and size should it start to reproduce? How many times in its life should it attempt reproduction—once, more than once, continuously, seasonally? When it does reproduce, how much energy and time should it allocate to reproduction as opposed to growth and maintenance? Given a certain allocation, how should it divide those resources up among off-

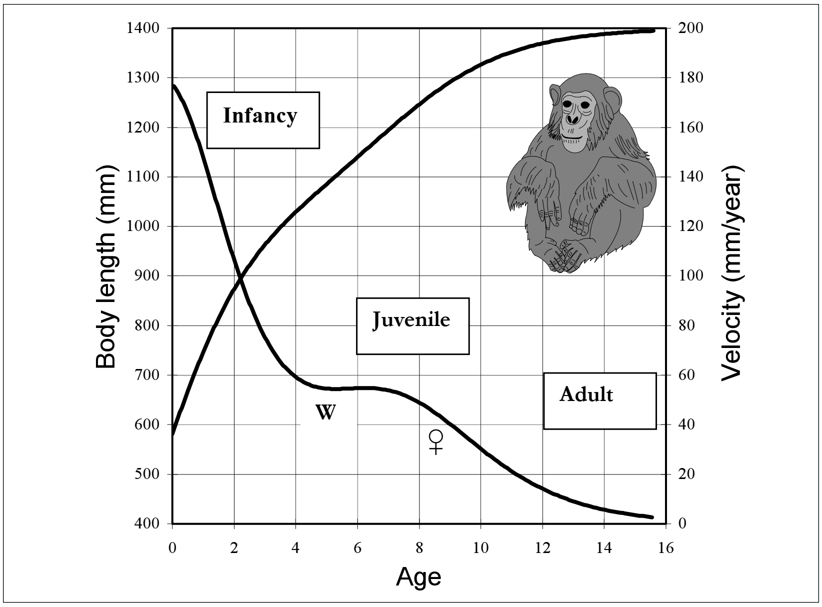

**Figure 7.2**

*A model of distance and velocity curves for chimpanzee growth in body length:* I, *infancy;* J, *juvenile; and* M, *mature adult. This is based on the longitudinal study of captive chimpanzee growth conducted by Hamada and Udono (2002). In the wild, weaning* (W) *usually takes place between 48 and 60 months of age (Pusey 1983).*

> spring? Should they be few in number but high in quality and large in size, or should they be small and numerous and less likely to survive? Should it concentrate its reproduction early in life and have a short life as a consequence, or should it make less reproductive effort in any given attempt and live longer?

Perhaps it is best to conceptualize a species' pattern of life history as a series of trade-offs, or compromises, that an organism makes between principal biological or behavioral traits. Some mammalian life history traits and trade-offs are listed in table 7.1.

The following are principal traits for mammals, including human beings: the timing of birth versus continued fetal development, the length of the lactation stage versus weaning (the cessation of lactation), the size of the brain, the age at first reproduction, and the age

**Table 7.1**

*Life History Principal Traits and Trade-offs for Mammals*

| *Principal Traits* | *Tradeoffs* |
|---|---|
| 1. Size at birth | 1. Current reproduction versus future reproduction |
| 2. Growth patterns<br>• Number of life cycle stages<br>• Duration of each stage | 2. Current reproduction versus survival |
| 3. Brain size at each life stage and at maturity | 3. Number, size, and sex of offspring |
| 4. Age and body size at maturity | 4. Parental reproduction versus growth |
| 5. Sexuality: sexual reproduction, parthenogenesis, no reproduction?<br>• Age at first reproduction | 5. Number versus size of offspring |
| 6. Age-, sex-, and size-specific reproductive investments<br>• Age and size of offspring at weaning | 6. Parental condition versus offspring growth |
| 7. Number, size, and sex ratio of offspring | 7. Offspring growth, condition, and survival |
| 8. Length of life<br>• Reproductive lifespan<br>• Age at last reproduction<br>• Rate of aging/senescence | 8. Parental versus offspring reproduction |

This is a partial list of the most important traits. The bulleted items under each principal trait are examples of specific characteristics of any species. The list is based on the discussion in Cole (1954) and Stearns (1992), who provide additional traits.

at death. The living mammals have greatly varying life history strategies, and examining what shapes these histories is one of the most active areas of research in whole-organism biology.

Bonner (1965) develops the idea that the stages of the life cycle of an individual organism, a colony, or a society are “the basic unit of natural selection.” His focus on life cycle stages follows from the research of several nineteenth- and twentieth-century embryologists who proposed that speciation is often achieved by altering rates of growth of existing life stages and by adding or deleting stages. Bonner (1993:93) proposes that we should not think of organisms as *having* a life cycle but rather *as* life cycles: “The great lesson that comes from thinking of organisms as life cycles is that it is the life cycle, not just the adult, that evolves. In particular, it is the building period of the life cycle—the period of development—that is altered over time by natural selection. It is obvious that the only way to change the character of an adult is to change its development."

My goal in this chapter is to consider the following three topics: (1) the evolution of the childhood stage of modern human life history from the perspective of physical growth and development, (2) the basic trade-offs in growth and fertility that result from life history evolution, and (3) the genetic and hormonal basis of some life history traits.

## HUMAN LIFE HISTORY

Stages in the human life cycle are listed and defined in table 7.2. The focus of this chapter is restricted to human life history from birth to adulthood. During this period, human beings have five life history stages: infant, child, juvenile, adolescent, and adult. These stage names are used here in ways that are biologically definable and meaningful, so their definition may differ considerably from common usage.

The term *childhood* commonly refers to any time before sexual maturation or before legal responsibility is socially recognized in an individual. This usage of *childhood* may cover the ages between birth and 12, 18, or 21 years. In contrast, the childhood stage of human life history in this chapter refers to a period between the ages of 3 and 7 years, on average. The restricted usage of *childhood* and the other life history stage names in this chapter is justified because each stage encompasses a set of biological and behavioral traits that define the stage. These traits have evolved and bestowed on the human species our special nature.

The stages of human life history from birth to adulthood are evident in graphs of body size growth (figure 7.3), showing the growth in height for normal boys and girls (growth in body weight is very similar). The amount of growth from year to year, the distance curve, is labeled on the y-axis on the right side of the graph in figure 7.3. The rate of growth in height during any year, the velocity curve, is labeled on the left side. Growth velocity is more pertinent to the discussion here because the velocity changes mark the division between human life history stages.

The most rapid growth velocity of any postnatal stage occurs in *infancy*, a stage that begins at birth and lasts until about age 3 years. The infant's growth rate is also characterized by a steep decline in velocity, a deceleration. The infant's curve of growth—rapid velocity

**Table 7.2**

*Stages in the Human Life Cycle*

| Stage | Growth Events/Duration (Approximate or Average) |
|---|---|
| *Prenatal Life* | |
| *Fertilization* | |
| First trimester | Fertilization to twelfth week: Embryogenesis |
| Second trimester | Fourth through sixth lunar month: Rapid growth in length |
| Third trimester | Seventh lunar month to birth: Rapid growth in weight and organ maturation |
| *Birth* | |
| *Postnatal Life* | |
| Neonatal period | Birth to 28 days: Extrauterine adaptation, most rapid rate of postnatal growth and maturation |
| Infancy | Second month to end of lactation, usually by 36 months: Rapid growth velocity but with steep deceleration in growth rate, feeding by lactation, deciduous tooth eruption, many developmental milestones in physiology, behavior, and cognition |
| Childhood | Years 3–7: Moderate growth rate, dependency on older people for care and feeding, midgrowth spurt, eruption of first permanent molar and incisor, near completion of brain growth by end of stage |
| Juvenile | Years 7–10 for girls, 7–12 for boys: Slower growth rate, self-feeding capability, cognitive transition leading to learning of economic and social skills |
| Puberty | An event of short duration (days or a few weeks) at the end of the juvenile stage: Reactivation in central nervous system of sexual development, dramatic increase in secretion of sex hormones |
| Adolescence | The stage of development that lasts five to ten years after the onset of puberty: Growth spurt in height and weight, permanent tooth eruption almost complete, development of secondary sexual characteristics, sociosexual maturation, intensification of interest in and practice of adult social, economic, and sexual activities |
| *Adulthood* | |
| Prime and transition | From 20 years old to end of childbearing years: Homeostasis in physiology, behavior, and cognition; menopause for women by age 50 |
| Old age and senescence | From end of childbearing years to death: Decline in the function of many body tissues or systems |
| *Death* | |

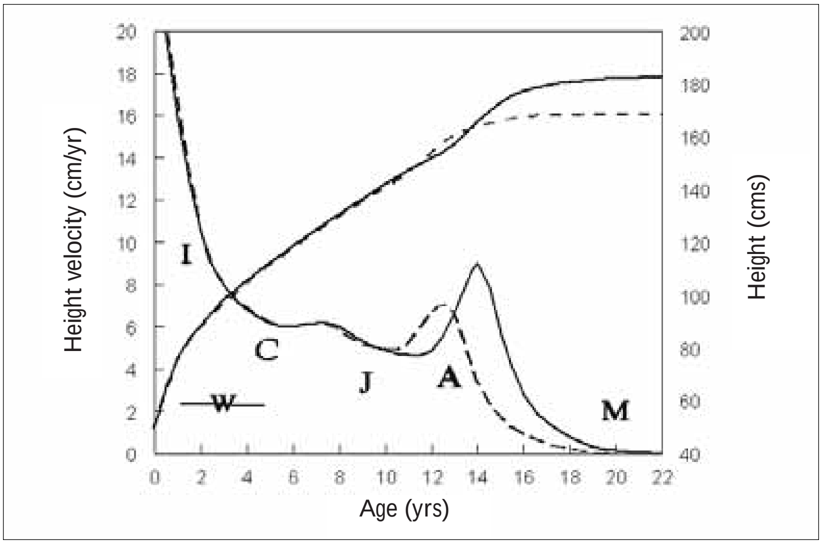

**Figure 7.3**

*Average velocity and distance curves of growth in height for healthy girls (dashed lines) and boys (solid lines), showing the postnatal stages of human growth. In the velocity curves, note the spurts in growth rate at mid-childhood and adolescence for both girls and boys. The postnatal stages:* I, *infancy;* C, *childhood;* J, *juvenile;* A, *adolescence; and* M, *mature adult. In traditional human societies, weaning* (W) *of infants from any breastfeeding occurs at an average age of 30 months, with a range of 6–60 or more months (Dettwyler 1995; Sellen, chapter 5, this volume). The figure is based on original material from Bogin (1999a).*

and deceleration—is a continuation of the fetal pattern, in which the rate of growth in length actually reaches a peak in the second trimester of gestation, and then begins a deceleration that lasts until childhood. The *childhood* stage follows infancy, encompassing the ages of about 3–7 years. The growth deceleration of infancy ends at the beginning of childhood, and the rate of growth levels off at about 6 cm per year. This leveling off in growth rate is unusual for mammals. Virtually all other species continue a pattern of deceleration after infancy that ends with sexual maturation (Bogin 1999a).

Another feature of the childhood growth phase is the modest acceleration in growth velocity that peaks at about 7 years of age (the midgrowth spurt). Some studies note the presence of the midgrowth spurt in the velocity curve of boys but not girls. Others find that up to two-thirds of boys and girls have midgrowth spurts. The midgrowth spurt is often linked with an endocrine event called “adrenarche,” which results in a progressive increase in the secretion of adrenal androgen hormones. However, in a recent study measuring both growth and adrenal hormone production in a group of healthy children (Remer and Manz 2001), the increase in adrenal androgen production occurred one year after the midgrowth spurt. It seems that as-yet-unknown mechanisms are responsible for the midgrowth spurt. Whatever these mechanisms are, they cause the transient increase in growth rate and may also trigger changes in behavior and cognition (described in more detail below). With these changes, the childhood stage ends and the juvenile stage begins.

The human *juvenile* stage begins at about age 7 years and is characterized by the slowest rate of growth since birth. In girls, the juvenile period ends, on average, at about the age of 10, two years before it usually ends in boys; the difference reflects the earlier initiation of puberty and adolescence in girls. Puberty is an event of the neuroendocrine system (Grumbach and Styne 2003). The current understanding of the control of puberty is that one center (or perhaps a few centers) of the brain changes its pattern of neurological activity and its influence on the hypothalamus. The hypothalamus, which is basically inactive in terms of sexual development from about the age of 2 or 3 years, is again stimulated to produce gonadotrophic hormones, which, in turn, stimulate the maturation of the gonads.

Puberty is a relatively short-term event, but adolescence is a lengthy stage of development. During human *adolescence*, most boys and girls experience a rapid acceleration in the growth velocity of virtually all the bones of the body (the adolescent growth spurt). Adolescence is also the stage of life when much social, economic, and sexual maturation takes place. The duration of the adolescent growth spurt covers about eight or nine years, between (on average) ages 10 and 18 in girls and 12 and 20 or 21 in boys. Adolescence ends and early *adulthood* begins with the completion of the growth spurt. In any human population, there is individual variation in the exact ages of each life history stage. However, the modal ages given here do faithfully describe the typical human patterns of growth (see Bogin [1999a, 2001], for discussion of population variation in growth and other life history traits).

Adults achieve full reproductive maturity, meaning that they have the physical, economic, and psychosocial maturity and capacity to care for offspring successfully. Adolescents can bear offspring but usually cannot keep them alive without significant assistance from more competent adults. With the onset of adulthood, growth in height stops because the long bones of the skeleton (the femur, tibia, and humerus) lose their capability to lengthen. In adult humans, a tradeoff is made between investing further time and energy in body growth versus reproduction.

## LIFE HISTORY OF OTHER PRIMATES

The human pattern of growth velocity is distinct from that of other primates (Pereira and Fairbanks 1993). Leigh (1996) published an extensive review of primate growth in body weight. There are fewer studies of skeletal growth velocity. The results of two such studies appear in figures 7.1 and 7.2, for baboons and chimpanzees (see Robson, van Schaik, and Hawkes, chapter 2, and Sellen, chapter 6, in this volume for additional reviews of primate growth and development). Both species have three phases of postnatal growth: an infancy phase of rapid deceleration, a juvenile phase of less rapid or no deceleration, and a sexual maturation phase of steeper deceleration. In no phase are there growth spurts for body length. Both baboons and chimpanzees achieve reproductive maturation during the third phase of growth, and females may become pregnant while still in that third growth phase. The ♀ symbol indicates the average age at first sexual swelling for each species. In contrast with baboons and chimpanzees, human girls achieve menarche (first menstruation) about one year after the peak of the adolescent growth spurt. This is at about age 13 years in reasonably healthy populations (Bogin 2001). First pregnancy does not occur, on average, for about five years after menarche, when all skeletal growth is virtually complete.

## TEETH, FEEDING, AND REPRODUCTION

In addition to changes in growth rate and the timing of first birth, each stage of the human life cycle may be defined by characteristics of dentition, changes in feeding methods, and physical and mental competencies (discussed briefly above and in more detail below). The postpubertal stages may also be characterized by maturation events of the reproductive system and by changes in sexual behavior.

For all mammals, infancy is the stage when the young are fed by maternal lactation. Human infancy requires the mother to provide nourishment to her offspring via lactation or some culturally derived imitation of lactation. During infancy, the deciduous dentition (the so-called "milk teeth") erupts through the gums. Human infancy ends when the child is weaned from the breast, which usually occurs between 24 and 36 months of age in traditional and pre-industrial societies (Dettwyler 1995). By this age, all the deciduous teeth have erupted, even for very late maturing infants (Demirjian 1986), and the young can move on to eating foods specially prepared for children.

One of the important physical developmental milestones of childhood is the replacement of the deciduous teeth with the first permanent teeth. First molar eruption takes place, on average, between the ages of 5.5 and 6.5 years for the majority of human children. Eruption of the central incisor quickly follows, or sometimes precedes, eruption of the first molar. By the end of childhood, usually at the age of 7 years, most children have in place the four first permanent molars and several permanent incisors. Along with growth in size and strength of the jaws and the muscles for chewing, these new teeth provide sufficient capabilities to eat a diet similar to that of adults.

Infancy and childhood are the times of the most rapid postnatal brain growth in human beings. The high rate of brain growth is energetically expensive. The human newborn uses 87 percent of its resting metabolic rate (RMR) for brain growth and function. By the age of 5 years, the percent of RMR usage is still high, at 44 percent, whereas in the adult human the figure is between 20 and 25 percent of RMR. At birth, chimpanzees have smaller brains than do humans, and the difference in size increases rapidly (Leigh 2004). Consequently, the RMR values for the chimpanzee are about 45 percent at birth, 20 percent at age 5 years, and 9 percent at adulthood (Leonard and Robertson 1994).

Table 7.3 lists the key features of human childhood. This suite of traits is not found in any other species of mammal. By the beginning of the juvenile stage (about age 7 years), the growth in weight of the brain is nearly complete (Cabana, Jolicoeur, and Michaud 1993; Robson, van Schaik, and Hawkes, chapter 2, this volume), but much

**Table 7.3**

*The Traits Defining Human Childhood*

- Period of age 3 to 7 years
- Slow and steady rate of growth and relatively small body size
- Large brain; from age 3 to 5 years, a fast-growing brain
- Higher resting metabolic rate than any other mammalian species
- Immature dentition
- Weaned from mother but dependent on older people for care and feeding for about four years
- Sensitive period for maturation of fundamental motor patterns
- Sensitive period for cognitive and language development
- Sensitive period for physical development, with plasticity to the environment

No other mammalian species has this entire suite of features.

physical and cognitive development must still take place. The nutrient requirements for brain growth diminish sharply. Moreover, cognitive and emotional capacities quickly mature to new levels of self-sufficiency during the "5-to-7-years-old transition" (see above). An important consequence of this cognitive transition is that juveniles can conceptualize themselves as independent of older people, something children cannot do. Even when suffering from abuse or neglect, children younger than 6 years old cannot seem to leave their homes. So-called "wolf children" and even "street children," who are sometimes alleged to live on their own, are either myths or not children at all. My search of the literature and personal communication with researchers of street children finds no case of a child (a youngster under the age of 6 years) living alone, either in the wild or on urban streets (see, for example, Panter-Brick, Todd, and Baker 1996). Street children are, in fact, street juveniles and adolescents.

The near completion of brain growth by the start of the juvenile stage enables more energy investment in body growth, but juveniles grow at the slowest rate since birth. A probable explanation for this paradox is that the slow growth of the juvenile body allows for a trade-off between growth, on the one hand, and learning and work, on the other. Studies of juvenile primates in the wild and human juveniles in many cultures indicate that the learning and practice of many food extraction and production skills and much social behavior take place during this stage (Birdsell 1979; J. Altmann 1980; Goodall 1986; Kaplan et al. 2000; van Schaik et al., chapter 5, this volume). Human and nonhuman primate juveniles learn much about important adult activities, including the preparation of food and methods of infant and childcare (Weisner 1987; Pereira and Fairbanks 1993). Because juveniles are prepubertal, they can attend to this kind of social learning without the distractions caused by sexual maturation. As an aside, the start of the human juvenile stage coincides with entry into traditional formal schooling in the industrialized nations. The connection is hardly a coincidence; the juvenile stage is suited for the kinds of learning and socialization found in school environments.

Human juveniles continue their dental maturation and usually have all permanent teeth, except the third molar, by the end of the stage. Indeed, the second permanent molar teeth erupt at a mean age of 10.5–12.0 years in both boys and girls. The eruption of the second molar coincides with the beginning of the adolescent stage, just as the eruption of the first molar marks the end of the childhood stage. No new teeth erupt during human adolescence. Rather, the adolescent stage of life is when social and sexual maturation takes place, largely driven by the hormonal changes of puberty. None of these endocrine changes can be detected directly without sophisticated technology, but the effects of puberty can be noted easily as visible and audible signs of sexual maturation. One such sign is a sudden increase in the density of pubic hair (indeed, the term *puberty* is derived from the Latin *pubescere*, “to grow hairy”). In boys, the deepening of the voice is another sign of puberty (Locke and Bogin 2005). In girls, a visible sign is the development of the breast bud, the first stage of breast development. The pubescent boy or girl, parents, relatives, friends, and sometimes everyone else in the social group can observe these signs of early adolescence.

The adolescent stage also includes development of the external genitalia, sexual dimorphism in body size and composition, and the onset of greater interest and practice of adult patterns of sociosexual and economic behavior. These physical and behavioral changes occur with puberty in many species of mammals, but two important differences distinguish human adolescence. The first is the length of time between the age at puberty and the age at first birth. Humans take, on average, at least ten years for this transition. The average ages for girls are 9 years at puberty (detected by hormonal changes) and 19 years at first birth; for boys, puberty takes place also at about age 9 and fatherhood, no earlier than 21–25, on average. The reasons for delay between puberty and first birth or fatherhood seem to be related to the added value of experience, learning, and physical development provided by the parents (Bogin 1999a, 1999b). The point here is that monkeys and apes take fewer than three years to make the transition from puberty to parenthood.

## WHY DID THE HUMAN LIFE CYCLE EVOLVE? THE REPRODUCTIVE ADVANTAGES OF CHILDHOOD

The life stages of infant, juvenile, and adult are shared by most primates (see figures 7.1 and 7.2) and by many other social mammals (see reviews by Harvey, Martin, and Clutton-Brock 1987; Pereira and Fairbanks 1993; Leigh 1996; Bogin 1999a). The evolution of many details concerning the human stages of infancy, juvenile, adolescence, and adulthood are fascinating, but here I discuss only the evolution of human childhood.

Selection for increased reproductive success is the force that drives much of biological evolution. Reproductive success explains the evolution of childhood. Consider the data shown in figure 7.4, which depicts several hominoid developmental landmarks. Compared with living apes, human beings experience developmental delays in eruption of the first permanent molar, age at menarche, and age at first birth. However, humans have a shorter infancy and a shorter birth interval than apes (Robson, van Schaik, and Hawkes, chapter 2, and Sellen, chapter 6, this volume). Females of all other primate species cannot wean their current infant until two things happen: the first permanent molar (M1) must erupt so that the infant can eat an adult-type diet (B. Smith 1991b), and then the infant must learn to forage for itself.

For chimpanzees, this takes about five years. The chimpanzee infant's M1 erupts at a mean age of 3.1 years (Anemone, Mooney, and Siegel 1996; Smith, Crummett, and Brandt 1994), but the mother continues to nurse for about another two years as the infant learns how to acquire and process foods (Pusey 1983). Because of the infant's dependency on the mother, the average period between successful births in the wild is 5.2–5.6 years at the Gombe Stream and Mahale

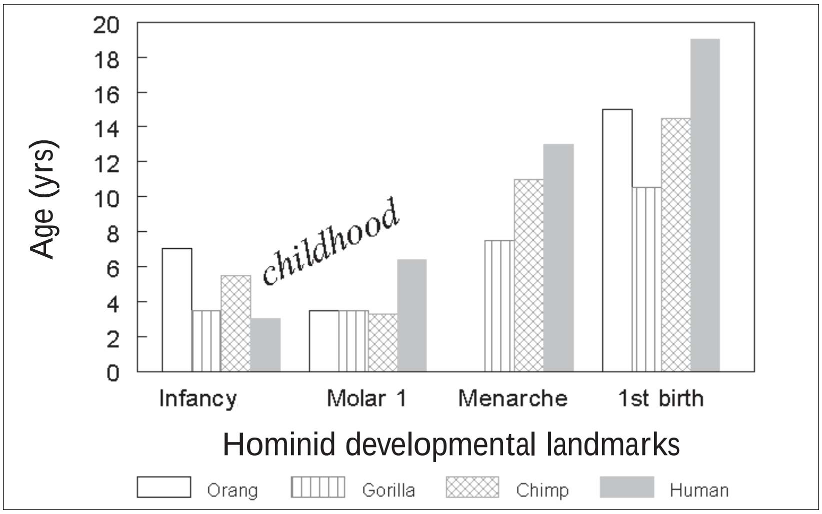

**Figure 7.4**

*Hominoid developmental landmarks. Data based on observations of wild-living individuals or, for humans, healthy individuals from various cultures.* Infancy/B.I. *is the period of dependency on the mother for survival, usually coincident with the mean age at weaning and/or a new birth (*B.I. *means "birth interval");* Molar 1 *is the mean age at eruption of the first permanent molar;* Menarche *is the mean age at first estrus or menstrual bleeding;* First Birth *is the mean age of females at first offspring delivery. Orang,* Pongo pygmaeus*; gorilla,* Gorilla gorilla*; chimp,* Pan troglodytes*; human,* Homo sapiens *(modified from Bogin 1999a).*

Mountain research sites in Tanzania (Teleki, Hunt, and Pfifferling 1976; Goodall 1983; Nishida, Takasaki, and Takahata 1990). At the Kibale Forest research site in Uganda, chimpanzees average 7.0 years between successful births (Pusey 2001). High-ranking females reproduce more rapidly (Fifi's birth interval averages 4.0 years) and have higher offspring survival (Pusey, Williams, and Goodall 1997).

Human women in traditional societies wait, on average, three to four years between births. The human M1 erupts at about 6 years of age, and human offspring have much to learn before they can survive on their own. The relatively early weaning of human infants is therefore quite unexpected when compared with other primates and mammals. However, the short birth interval gives women a distinct advantage over the apes: they can produce and rear two offspring through infancy in the time it takes chimpanzees or orangutans to produce and rear one offspring. The weaned infant, though, must survive to adulthood if the short human birth spacing is to result in a true reproductive advantage. How can human beings trade off early weaning for increased reproductive frequency and still ensure offspring survival?

Short birth intervals entail a life history compromise between maternal investments in a current infant and in a future infant. A mother who stops nursing her current infant leaves the infant in the predicament of how to eat. Human 3-year-olds cannot move on to the feeding semi-independence of the juvenile stage; they cannot forage for themselves. Even if children could get hold of food from others, they cannot process the diet of juveniles, adolescents, or adults because of immature dentition and the small size of the digestive tract (Behar 1977; Smith, Crummett, and Brandt 1994; Sellen, chapter 6, this volume). These children, then, need foods that are specially chosen and prepared, that is, "baby foods." Human mothers, however, do not have to provide 100 percent of nutrition and care directly to their children. Any older individuals in the social group can feed and protect weaned, dependent children. Indeed, traditional societies deal with the problem of childcare by spreading the responsibility among many individuals, including older juveniles, adolescents, grandmothers, and other adults (Blurton Jones, chapter 8, Hawkes, chapters 3 and 4, and Sellen, chapter 6, this volume).

For example, in Hadza society (African hunters and gatherers), grandmothers and great aunts supply a significant amount of food and care to children (Hawkes, O'Connell, and Blurton Jones 1997; Blurton Jones, chapter 8, this volume). In Agta society (Philippine hunter-gatherers), women hunt large game animals but still retain primary responsibility for childcare (Estioko-Griffin 1986). They accomplish this dual task by living in extended family groups—two or three brothers and sisters, their spouses, children, and parents—and sharing the childcare. Among the Maya of Guatemala (horticulturists and agriculturists), many people live together in extended family compounds. Women of all ages work together in food preparation, clothing manufacture, and childcare (Bogin field notes, 1988–1993). In some societies, including the Agta and the Aka pygmies, hunter-gatherers of central Africa (Hewlett 1991b), fathers provide significant childcare. Summarizing the data from many human societies, Lancaster and Lancaster (1983) call this kind of childcare and feeding "the hominid adaptation" because no other primate or mammal does all of this. The evolutionary reward is that by reducing the length of the infancy stage of life (that is, lactation) and by developing the special features of the human childhood stage, humans have the potential for greater lifetime fertility than any ape.

As shown in figure 7.4, the insertion of the human childhood stage "fills the gap" between the maternal dependence of infants and the relative independence of juveniles. The "bottom line," in a biological sense, is that the evolution of human childhood frees the mother from the demands of nursing and the inhibition of ovulation related to continuous nursing. This, in turn, decreases the interbirth interval and increases reproductive fitness. Investments from siblings, fathers, grandmothers, and others explain, in large part, why a greater percentage of human young survive to adulthood than the young of any other mammalian species. Such cooperative breeding behavior to enhance inclusive fitness has evolved in many independent taxonomic groups, such as insects, birds, and mammals (including primates), so finding it in our own species is no surprise (Clutton-Brock 2002).

## BRAIN GROWTH AND LEARNING—A SECONDARY ADVANTAGE OF CHILDHOOD

Human life history—with nearly two decades of postnatal growth and development, including infant dependency and extended childhood, juvenile, and adolescent stages before social and sexual maturation—has long been considered to be advantageous for our species because it provides an extended period ("extra time") for brain development, for the acquisition of technical skills such as tool making and food processing, and for socialization, play, and the development of complex social roles and cultural behavior.

These are common rationalizations for the value of the human growth pattern. They emphasize the value of learning, an idea that Spencer (1886) popularized but which actually goes back to the dawn of written history (Boyd 1980). Learning as the reason for the evolution of several prolonged life stages preceding maturation was nicely summarized by Dobzhansky (1962:58): "Although a prolonged period of juvenile helplessness and dependency would, by itself, be disadvantageous to a species because it endangers the young and handicaps their parents, it is a help to man because the slow development provides time for learning and training, which are far more extensive in man than in any other animal." Allison Jolly (1985:44) also invoked the learning hypothesis for human ontogeny: "Human evolution is a paradox. We have become larger, with long life and immaturity, and few, much loved offspring, and yet we are more, not less adaptable." In an attempt to resolve the paradox of human evolution and our peculiar life history, Jolly (1985:44) concludes in the next sentence that "mental agility buffers environmental change and has replaced reproductive agility."

The reference to reproductive agility means that we are a reproductively frugal species compared with those that lavishly produce dozens, hundreds, or thousands of offspring in each brood or litter. It is fairly easy to argue that humans, with relatively low wastage of offspring, are somehow more "efficient" than other species. But a paradox still remains. The learning hypothesis does not explain how the pattern of human growth evolved. It does not provide a causal mechanism for the evolution of human growth. Rather, it is a tautological argument for the benefits of the simultaneous possession of brains that are large relative to body size, complex technology, and cultural behavior.

Research from hominin paleontology, animal ethology, and archaeology shows that these brain-behavior traits are not causally linked. Extinct hominin species and living primates of various species (and brain sizes) have complex technology and learned behavior (van Schaik et al., chapter 5, and Skinner and Wood, chapter 11, this volume). More to the point, the value of a larger brain, with all the clever learning that the brain can do, is of limited benefit during childhood. Only later in life do the "extra time" and "extra learning" pay off in terms of survival and reproductive success.

Empirical studies of mammalian development show that a childhood stage is not necessary for learning complex skills. Ethological observations of nonhuman primates, elephants, social carnivores, and other mammals show that, during their infant and juvenile stages of life, they can learn and practice all the feeding, social, and reproductive behavior they need. It may be argued that human beings have more to learn than nonhuman primates, such as symbolic language, kinship systems, and the use of technology. Perhaps extra developmental time is necessary to acquire it all. Kaplan and colleagues (2000) suggest that the more complex aspects of human food extraction (such as foraging for hidden foods), hunting animals, and sociosexual behavior may require twenty years or more to master. Maybe human childhood coevolved with these behavioral complexes. Not so, according to several recent reports. A series of ethnographic studies in traditional societies around the world shows that learning the basics of food production does not take extra time (Bogin 1999a; Bock and Sellen 2002, and other papers in that same volume).

Curiously, Bock and Sellen (2002) cite me as the proponent of the learning hypothesis, despite my long-standing disagreement with both the brain growth and learning hypotheses as the primary reasons for the evolution of childhood (Bogin 1988). I contend that the reproductive advantage to adults is what explains the evolution of a prolonged childhood as a new life history stage for humans. The brain growth and learning hypotheses cannot account for the initial selective impetus for the evolution of childhood. Growing a larger (and more complex) brain may be a secondary benefit of childhood. The primary benefit still seems to be the reproductive advantages to the mother and her close genetic kin.

### Maintaining Rapid Brain Growth

R. Martin (1983) and Leigh (2004) demonstrate that the chimpanzee pattern of brain and body growth, even when extended by several years, cannot result in a brain size much greater than 800 cc. This is well below the modern human average of 1,350 cc and below the average for many extinct hominins since the time of *Homo erectus*. Comparing human and chimpanzee brain growth reveals the telling difference (figure 7.5, from Leigh 2004). Before birth (not shown), both chimpanzees and humans have relatively fast *rates* of brain growth, which remain rapid for about eighteen months after birth. However, the total *amount* of growth in human brain mass increases much more rapidly than in chimpanzees. At birth, human brain weight averages 366 g and chimpanzees average 136 g (Robson, van Schaik, and Hawkes, chapter 2, this volume); at 18 months, human brains weigh more than 1,000 g and chimpanzee brains average about 300 g (see figure 7.5). After 18 months of age in both species, the rate of

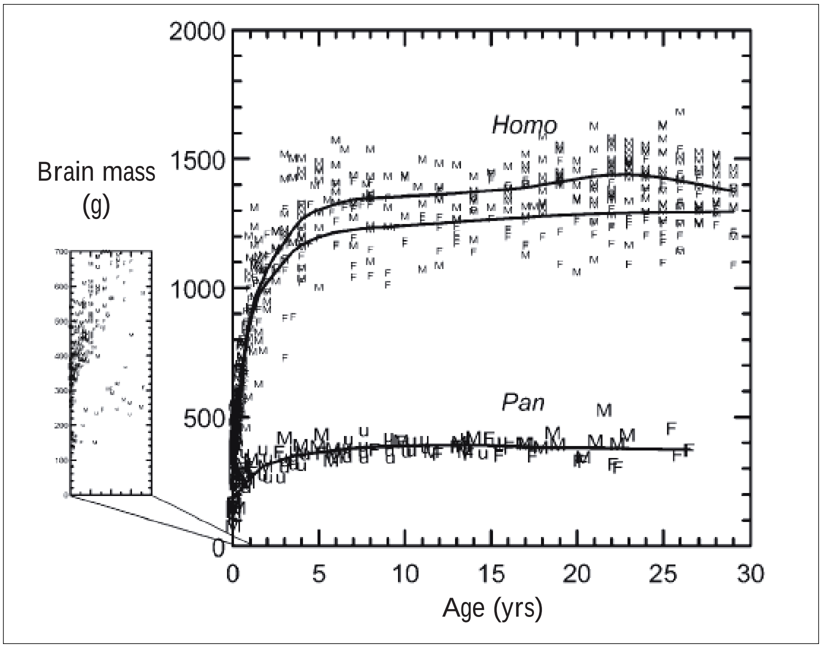

**Figure 7.5**

*Brain-mass growth data for humans* (Homo sapiens) *and chimpanzees* (Pan troglodytes). *Brain mass increases during the postnatal period in both species. Lines represent best-fit lowess regressions through the data points.* M, *males;* F, *females; and* U, *sex unidentified (Vrba 1998). The inset shows brain-mass growth for each species during the first postnatal year (reproduced from Leigh 2004, with kind permission of the author).*

brain growth declines, but more so in the chimpanzee. During the early phase of the human childhood stage (age 3–5 years), the rate and the amount of brain growth exceed those of the chimpanzee (see figure 7.5). Chimpanzee brain growth ends by 5 years of age, whereas human beings continue a slow but significant rate of brain growth for several more years (Vrba 1998; Leigh 2004; see figure 7.5). In sum, the greater amount of human brain growth before and after birth and the prolongation of “fetal-like” rates of brain growth during infancy and early childhood account for the large size of the human brain.

In the light of this, the “extra time” hypothesis for the evolution of childhood and brain growth is much too simplistic. We should no longer consider childhood an extension of the infancy developmental period but rather a distinct stage of life history between the infancy and juvenile stages. Childhood allows the young human being to continue a fast rate of brain growth because of, in large part, the deceleration of body growth during infancy and the slow rate of body growth of childhood. By the start of childhood at age 3 years, the body growth rate levels off at ~6 cm/year. This slow and steady rate of human growth maintains a relatively small-size body during the childhood years, but the child's brain continues a relatively fast rate of growth. In a classic life history trade-off, the child invests energy and material to build a bigger brain while delaying investment in a bigger body. The body will catch up to the brain, but not until the growth spurt during adolescence.

Other trade-offs also result from the insertion of childhood into human life history. The child's brain is relatively large, almost twice the size of an adult chimpanzee's brain. The child's brain is also quite active. As indicated above, at the age of 5 years the child uses, on average, 44 percent of its resting metabolic rate (RMR) for brain growth and function. The child's large, active, and still growing brain requires a diet that is dense in energy, lipids, and proteins. Moreover, the constraints of the child's immature dentition and small digestive system necessitate a diet that is easy to chew and swallow and is low in total volume. Children lack the motor and cognitive skills to prepare such a diet for themselves; they must depend on older individuals for care and feeding.

Fortunately, children are relatively inexpensive to feed. Their slower rate of body growth and smaller body size reduce competition with adults for food resources; slow-growing, small-bodied children require less food than bigger individuals. A 5-year-old child of average body size and activity, for example, requires 22.7 percent less dietary energy per day for maintenance and growth than does a 10-year-old juvenile of average body size (Ulijaszek and Strickland 1993; Guthrie and Picciano 1995). Therefore, provisioning children, though time-consuming, is not as onerous a task of investment as it would be, for instance, if both brain growth and body growth were progressing at the same rapid rate.

## "BABYSITTING" FOR CHILDREN

Directly related to the care and feeding of children is the fact that many older persons can do the job. Because children do not require nursing, any competent member of a social group can provide food and care for them. Early neurological maturity and late sexual maturity enable juveniles and young adolescents to care for themselves and also for children (Bogin 1994). Grandmothers and other postreproductive women provide much childcare (Bogin and Smith 1996; Hawkes et al. 1998; Hawkes, chapter 4, and Blurton Jones, chapter 8, this volume). Again, this frees younger adults, especially the mother, for subsistence activity, adult social behaviors, and further childbearing. Caretaking of this type is rare in other primates, even for apes. Usually, the mother must care for her infant nonhuman primate, or it will die. Adoptions of orphaned infants by females do occur in chimpanzee social groups, but only infants older than 4 years and able to forage for themselves can survive more than a few weeks (Goodall 1983). Goodall noted deterioration in the health and behavior of infant chimpanzees whose mothers had died. The behavioral changes included depression, listlessness, whimpering, and less play. Health changes such as loss of weight were observed. Goodall reported that even those older infants who survived the death of their mothers were affected by delays in physical growth and maturation.

It is well known that human infants and children also show physical and behavioral pathology after the death of one or both parents (Bowlby 1969). However, it seems that the human infant can more easily make new attachments to other caretakers than can the chimpanzee infant (Chisholm 1999). The ability of a variety of human caretakers to attach to one or several human infants may also be an important factor. The psychological and social roots of this difference between human and nonhuman species in attachment behavior are not well understood. The flexibility in attachment behavior evolved by hominin ancestors contributed, in part, to the evolution of childhood and the reproductive efficiency of the human species.

One common pattern of childcare in many traditional cultures is to have juveniles assume caretaking responsibilities for children. This occurs among two well-studied, African hunting-gathering cultures, the !Kung and the Mbuti. Mothers carry their infants with them while foraging. Weaned children (nursing an infant to age 4 years is common in these cultures) must stay “home” at the base camp, for they have neither the strength nor stamina to follow their parents while gathering or hunting (Draper 1976; Konner 1976; Turnbull 1983a, 1983b).

At !Kung camps, children of various ages play together within the camp boundaries, and juveniles assume many caretaking functions for younger children. The children seem to transfer their attachment from parents and other adults to the juveniles, behaving toward them with appropriate deference and obedience. In the age-graded playgroup, older generations transmit cultural behavior, as well as adult parental behavior (Konner 1976), to younger generations. Of course, the children and juveniles are never left entirely on their own. At least one adult is always in camp, though not directly involved in childcare. Rather, he or she is preparing food or tools or is otherwise engaged in adult activity.

The Mbuti (nomadic hunters and gatherers of central African rain forests) have a similar childcare arrangement. After weaning, toddlers enter the world of the *bopi*, the Mbuti term for a children's playground but also a place of age-graded childcare and cultural transmission. Between the ages of 2 or 3 to 8 or 9 years, children and juveniles spend almost all day in the bopi. There they learn physical skills, cultural values, and even sexual behavior. "Little that children [and juveniles] do in the bopi is not of full value in later adult life" (Turnbull 1983b: 43–44).

The age-graded playgroup accomplishes both caretaking and enculturation, freeing the adults to provide food, shelter, and other necessities for all the young at their various stages of development. A woman may be pregnant and simultaneously have a child weaned within the preceding year and one or more older offspring. Thus, adults can increase their net reproductive output in a relatively short time. This benefit, along with the selective advantage of numerous surviving offspring afforded by age-graded caretaking, may partially account for the initial evolution of the prolonged childhood life stage in modern humans. Later in human evolution, the role of the playgroup could have been co-opted to gain more time for brain development and learning. In the protective environment of the home base or camp, the playgroup gives children the freedom to explore and experiment, which has been shown to encourage learning, socialization, and even tool use (Beck 1980; Dolhinow 1999; Bogin 2002a).

## PLASTICITY OF DEVELOPMENT

Another benefit of childhood is a better-adapted body and more behavioral flexibility with that body. The slow rate of body growth between ages 3 and 7 years provides a mechanism that allows more time for developmental plasticity (Lasker 1969). By this, I mean that a slow-growing child can more precisely "track" ecological conditions, with more growth under good conditions and less growth under bad circumstances. The fitness of a given phenotype (the physical features and behavior of an individual) varies across the range of variation in an environment. When phenotypes are fixed early in development, as in mammals that mature sexually soon after weaning (such as rodents), environmental change and high mortality are positively correlated. The human childhood stage adds four years of relatively slow physical growth and allows for physical and behavioral experience that further enhances developmental plasticity.

An example of the role of plasticity in human physical development comes from my research with the children of Guatemala Maya immigrants to the United States (Bogin and Loucky 1997; Bogin et al. 2002). This research began in 1992 with the measurement of body size in a sample of Maya children (n = 174), 6–12 years old, living in Florida and California. In 1999 and 2000 we measured another group of 6–12 year olds (n = 360) living in the same communities. We compared the older and newer samples with a sample of Maya schoolchildren living in rural Guatemala, measured in 1998–1999 (n = 1,297).

Mean values for height for each sample appear in figure 7.6. Reference data for height from the National Health and Nutrition Examination Surveys (*NHANES* in figure 7.6) I and II of the United States are used as a baseline for comparison in each graph. Maya children living in the United States, in both the 1992 (*Maya-USA1992* in figure 7.6) and the 1999 and 2000 (*Maya-USA2000*) samples, are significantly taller than Maya children living in Guatemala (*Maya-Guat*). The average difference in height between the Maya-USA 2000 and the Maya-Guat samples is 10.24 cm. This is possibly the largest difference in mean stature between migrants and *sedentes* (those who remain in the old country) ever recorded.

Further analysis of our data shows that about 70 percent (7 cm) of the increase in stature is due to the longer legs of the Maya living in the United States (Bogin et al. 2002). The children of the immigrants not only are significantly taller but also have significantly altered body proportions.

The greater stature and altered body proportions of the Maya living

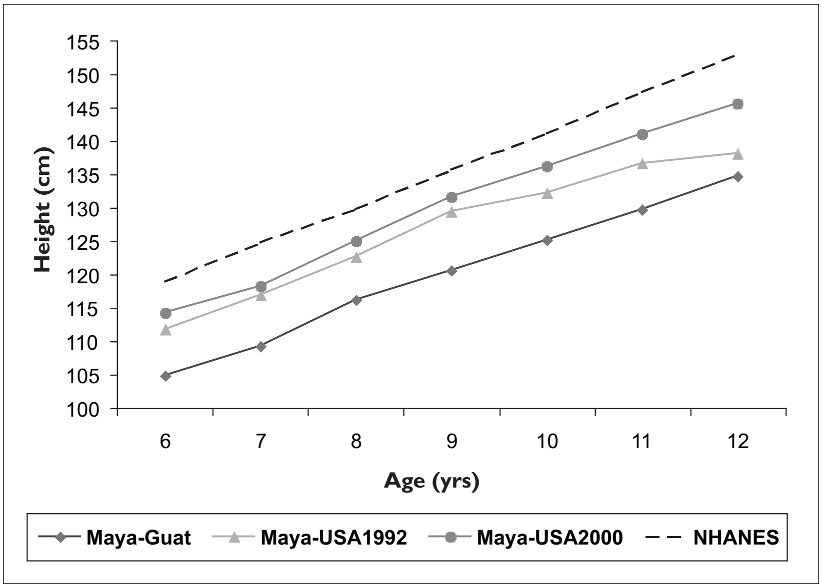

**Figure 7.6**

*Mean height of Maya samples compared with the median height of the NHANES reference data (from Bogin and Varela Silva 2003).*

in the United States are likely due to improvements in the environment for growth. All Maya in the United States have access to clean drinking water, health services, and education, which may not be so in Guatemala. In Florida, we know that almost all the Maya children participate in school breakfast and lunch programs. These health and nutritional changes are known to result in greater stature. Our findings show the extent and rapidity of plastic changes in human biology during the period of growth and development. Because the differences in height are established by age 6, the developmental plasticity must take place during the infant and childhood stages of development.

## WHEN DID CHILDHOOD EVOLVE?

The evolution of new hominin species, such as *Homo habilis*, *H. ergaster*, *H. erectus*, and anatomically modern *H. sapiens*, is accompanied by novel patterns of growth in size and body proportion (Bogin and Rios 2003; Thompson, Krovitz, and Nelson 2003). It is not known to what extent the new fossil hominin species, their patterns of growth, and their life history stages are related. We can directly study the stages of the life cycle only for living species; however, we can postulate on the life cycle of extinct species. Such inferences for the hominins are, of course, hypotheses based on comparative anatomy, comparative physiology, comparative ethology, and archaeology.

I have written at some length about the timing of human life history evolution (Bogin 1999a, 2002b). Here I summarize those discussions by stating that the childhood stage of hominin life history may have appeared by two million years BP. Fossil species such as *Homo habilis, H. rudolfensis, H. ergaster*, or early *H. erectus* may have evolved childhood for the reproductive and adaptive plasticity advantages described above. In early *Homo,* childhood may have lasted only a year or so. Despite its short duration, childhood was inserted into early *Homo* life history at the end of the infancy stage. The reduction of infancy by even one year would offer a significant reproductive advantage to any hominin females whose offspring possessed this new life stage. The new life history adaptation of childhood would be favored by natural selection. Over time, further reduction of infancy and prolongation of childhood would be selected because hominin populations with this pattern of life history would out-reproduce those populations without a childhood stage. By the time of archaic *Homo sapiens*, the duration of childhood expanded to its current span of four years. Additional fossil evidence for the evolution of childhood is presented later in this chapter and in other chapters in this book (Skinner and Wood, chapter 11).

## GENETIC AND HORMONAL REGULATION OF HUMAN LIFE HISTORY TRAITS

There must be a genetic basis for life history traits if such traits are to evolve over time. Indeed, a genetic basis for human life history markers such as the timing of tooth development, puberty, and menarche, as well as rates of growth for stature and body mass, is well established (see reviews by Bogin 1999a; Towne, Demerath, and Czerwinski 2002). The genetics for the timing of other human traits, such as weaning and age at first reproduction, is not established but likely exists, because there is a genetic basis for these types of traits in other species (Stearns 1992; Leips, Travis, and Rodd 2000; Lill 2001).

Genetics, however, is not the whole story. Hormones, as well as their complex interactions with genes and the environment, seem to play the central role in life history regulation and evolution. Finch and colleagues provide excellent reviews of these gene-hormone-environment interactions in life history schedules (Finch and Rose 1995; Finch and Kirkwood 2000; Finch and Ruvkun 2001; Finch 2002). The action of the thyroid hormones is particularly important in life history evolution because thyroid hormones regulate differentiation, development, and metabolism of tissues throughout the body. Gagneux and colleagues (2001) and Crockford (2003) have published original studies and reviews of thyroid research that relate directly to differences between humans and great apes.

The presence of an adolescent growth spurt in humans and its absence in the chimpanzee offer an example of gene-endocrine interaction in the regulation of life history traits. In both boys and girls, the rise of secretion of androgen hormones (such as testosterone), along with low doses of estrogens early in adolescence, seems to increase growth rates. Later in adolescence, the high doses of estrogens seem to decrease growth rates. During the growth acceleration phase, estrogens appear to stimulate the production of growth hormone (GH), and together these hormones result in the growth spurt (P. Ellison 2002; Hindmarsh 2002).

But more is involved. Roughly equivalent amounts of hormone production in both chimpanzees and humans result in strikingly different rates of growth. In the male chimpanzee, the concentration of testosterone in blood serum increases about thirty-one-fold from the prepubertal to pubertal state. In the human male, serum testosterone concentration increases about thirty-eight-fold, or 1.23 times the increase for the chimpanzee (reviewed in Bogin 1999a). Clearly, both chimpanzee males and human boys experience large increases in testosterone production after puberty, but the effects on skeletal growth are not as similar. Chimpanzees have a relatively small increase in the velocity of growth of individual long bones during puberty, “usually less than a centimeter” (Watts and Gavan 1982:58). Hamada and colleagues (1996) report little or no increase in the rate of skeletal growth at the time of puberty for their samples of male and female chimpanzees, despite marked increases in androgen and estrogen levels.

In sharp contrast to the chimpanzee research are the findings for human boys and girls, who show relatively large and easily detectable growth spurts for all the long bones and the vertebrae during adolescence. Cameron, Tanner, and Whitehouse (1982) performed a longitudinal analysis on 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/year for the forearm and 2.44 cm/year for the tibia. Satake, Kirutka, and Ozaki (1993) report that during human adolescence, peak velocity for sitting height (the length of head, neck, and trunk) equals 7.5 cm/year for Japanese boys and 6.2 cm/year for Japanese girls. These two studies show that growth response of the human skeleton to rising endocrine levels is significantly greater than that of the chimpanzee skeleton.

The skeleton's growth potential is likely to be regulated more by the sensitivity of neuroendocrine receptors and post-receptors (biological tissues) to growth stimuli (hormones) than by the rate or amount of production of the stimuli themselves. The differences in bone sensitivity to hormone levels between nonhuman and human primate growth are probably controlled at the genetic level. Given the overall similarity between humans and chimpanzees in structural genes (the DNA that codes for proteins), the variation in growth control likely lies in the regulatory genes (the noncoding DNA that controls the activity of structural genes). These regulatory genes seem to initiate and terminate each of the distinct periods of growth and control their duration (Davidson 2001). Research into the identification and function of regulatory gene domains, such as homeobox gene families (highly conserved sequences of DNA base pairs found in most eukaryotes), is very active at this time. Recent discoveries of homeobox domains for tooth development and skeletal development in mammals show the importance of interactions among regulatory genes, hormones, and growth (Cobourne and Sharpe 2003; Shibaguchi et al. 2003).

## TEETH AND LIFE HISTORY

Long before the discovery of homeobox genes, it was known that the rate of formation of the crown and roots of teeth, as well as their size and shape, is under strong genetic control. The predictability of tooth formation and morphology, even under widely varying conditions for nutrition and health, attests to this strong genetic control (Demirjian 1986; Sullivan 1986; Hlusko, Weiss, and Mahaney 2002). Because of this, dental development schedules provide good correlates of many life history traits and events, as described for humans earlier in this chapter.

The idea of using dental eruption schedules as life history markers for primates originated with Schultz (1924; see Hawkes, chapter 3, this volume). Smith, Crummett, and Brandt (1994) updated Schultz's work with a review of dental eruption data for forty-six species of primates, representing all families. Primates are mammals, and all mammals have two sets of teeth, the deciduous or "milk" teeth and the permanent teeth. Moreover, all the anthropoid primates (Old World monkeys, the apes, and humans) have the same dental formula (the type and number of teeth). Teeth and their development provide a common basis for comparing all species of anthropoids. Smith, Crummett, and Brandt (1994) found that the first few permanent teeth to erupt provide the most information about life history. These authors reported a correlation coefficient of r = 0.72–0.92 for the mean age of first tooth eruption (usually M1) with mean adult body weight (an r = 1.0 would be a perfect relationship). The correlation between M1 eruption and mean adult brain weight is even stronger, r = 0.82–0.97. In another paper, B. Smith (1991b) reports that the correlation between M1 eruption and age at weaning is r = 0.96 (not statistically different from r = 1.0) in thirteen species of primates. Chimpanzees and humans are exceptions. Chimpanzees wean a year or more after eruption of M1, and humans wean several years before M1 eruption (see Robson, van Schaik, and Hawkes, chapter 2, this volume).

These dental comparisons reveal the slower rate of life history progression in apes and people. Smith, Crummett, and Brandt (1994) show that in many species of primates, the newborns have one or more deciduous teeth erupted at birth. The great apes and people, however, are usually toothless for at least a month after birth, and the slow rate of human dental development stands apart from that of the apes. Dean (2000:77) states, "All living great apes are dentally mature by about 11 [years of age], irrespective of their body mass." Humans are not dentally mature until 18–21 years of age. Dean points out that the difference is due mostly to a faster rate of root formation in the great apes than in humans. Formation of tooth crown enamel takes approximately the same time to form in apes and humans. Dean's point is that the dental evidence, as well as much other evidence from growth and development, shows that the evolution of human life history is derived from a general primate substrate.

Dean's conclusion, as well as my own, is that the regulation of tooth development is what separates living primates. And not just tooth development evolved by a change in gene-hormone regulation, but also most of the major features of primate life history. New fossil evidence and the careful analysis of existing fossil material are shedding much light on patterns of regulation in dental development and human evolution. Dean and colleagues (2001) analyzed tooth enamel growth patterns in thirteen fossil hominins. They found that fossils attributed to the australopithecines and early *Homo* (*H. habilis* and *H. erectus* types) are more similar to living African apes than to modern humans. These authors conclude that "truly modern dental development emerged relatively late in human evolution" (Dean et al. 2001:628). Several lines of evidence indicate that a truly modern human life history is no older than 800,000 BP and may be as young as 100,000 years old (Bermúdez de Castro et al. 1999; Thompson, Krovitz, and Nelson 2003).

## CONCLUSION

*The evolution of human childhood occurred because it provided reproductive advantages to the mother and other mature kin of the child.* I have been emphasizing the importance of this reproductive advantage to the mother since the publication of the first edition of my book *Patterns of Human Growth* (Bogin 1988) and in subsequent publications (Bogin 1990, 1993, 1994, 1997, 1999a, 1999b, 2001, 2002b; Bogin and Smith 1996). Unfortunately, some of my readers believe that I favor learning and brain development as the prime movers in human evolution. For this reason, I emphasize here (in italic) the primary reason for childhood.

As a secondary benefit, the evolution of a childhood life history stage may have been co-opted to allow for greater plasticity in growth and for developing new types of investments in physical and social capital of the youngster before maturation. Investments in greater brain growth, symbolic language, and more complex social behavior may be secondary consequences of the evolution of childhood. When this "extra time" became available, human ancestors may have actively exploited childhood for the instruction, learning, and practice of many social and economic skills. But such learning was not the primary driver of human life history evolution. Rather, it was a new type of fertility that made us human—children no longer dependent on breastfeeding and mothers free to resume reproductive cycling more quickly than any other hominoid primate. In addition, cooperative care of children allowed for more rapid reproduction, higher-quality offspring, and lower prereproductive mortality. In sum, childhood and cooperative breeding helped evolve human life history.

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