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Chapter 20

Human Growth and Development

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SYNOPSIS

A biocultural approach is taken to the study of the evolution of human growth and development. The biocultural perspective of human development focuses on the constant interaction taking place during all phases of human development, between both genes and hormones within the body, and with the sociocultural environment that surrounds the body. The pattern of human postnatal growth and development—the stages of infancy, childhood, juvenility, and adolescence—is reviewed. Several hypotheses are discussed concerning how the new life stages of the human life cycle represent feeding and reproductive specializations, secondarily allowing for the human style of learning and cultural behavior.

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Growth may be defined as a quantitative increase in size or mass. Measurements of height in centimeters or weight in kilograms indicate how much growth has taken place in a child. Development is defined as a progression of changes, either quantitative or qualitative, that lead from an undifferentiated or immature state to a highly organized, specialized, and mature state. Physical maturation is measured by functional capacity; for example, the maturation of bipedal walking results from changes with age in the skeletal, muscular, and motor skills of the infant and child.

GROWTH AND EVOLUTION

Human growth, development, and maturation have evolved, sometimes as discrete processes but more often as an integrated series of biological events. Biological anthropologists and human biologists have long been interested in how human growth, development, senescence, and aging differ from the corresponding processes in other apes, our closest phylogenic relatives, other nonhuman primates, and mammals. It is easy to document these differences, such as altricial offspring, slow and prolonged growth including childhood and adolescence stages, a late start to reproduction, menopause (see the chapter by Sievert in this volume), survival into the eighth and ninth decades, and a maximum life span of over 122 years (Crews and Bogin, 2010). Determining the evolutionary forces that produced these and other aspects of life history has not been as easy.

The evolution of the human pattern of growth may be understood by the study of growth and development in fossil species and by comparison of growth patterns in living species, especially the Primates. It is now clear that no living species of nonhuman primate has all the characteristics of human growth, in particular the human childhood and adolescent stages of life (these are defined and discussed below). This strongly suggests that the human pattern could only have evolved within the taxonomic group of the hominins, which includes the human species and extinct members of the genera *Homo, Australopithecus*, and perhaps older hominins that evolved by six to seven million years ago in Africa (see chapters by Hunt, Ward, and Simpson).

HUMAN VERSUS CHIMPANZEE GROWTH

Stages in the human life cycle are outlined in Table 1. In this entry, the focus is on human postnatal growth and development prior to adulthood, which may be divided into the stages of infancy, childhood, juvenility puberty, and adolescence (a more detailed explanation for the entire life cycle is found in Bogin, 2010; Bogin and Smith, 2012). Each stage may be defined by characteristics of dentition, changes related to methods of feeding, physical and mental competencies, and maturation of the reproductive system and sexual behavior. The most visually direct characteristic of each stage is its rate of growth. Shown in Figure 1 are rates and amounts of growth in height that take place between birth and adulthood for normal boys and girls. Growth in weight follows very similar curves. In Figure 1, the distance curve of growth—that is, the amount of growth achieved from year to year—is labeled on the right *y*-axis. The velocity curve, which represents the rate of growth during any one year, is labeled on the left *y*-axis. Below the velocity curve are symbols for each postnatal stage.

Presented in Figure 2 are the distance and velocity curves of body length growth for the chimpanzee. The figure is based on the longitudinal study of captive chimpanzee growth conducted by Hamada and Udono (2002). Postnatal growth of the chimpanzee has only two stages, infancy and juvenility prior to adulthood. The chimpanzees of this study were raised at two research institutes in Japan. As infants, five were nursed by their mothers and seven were bottle fed by human caregivers. After the nursing or bottle-feeding period, all were transferred to social groups with age peers, except for one infant chimp who remained with his mother. During their juvenile growth stage some of the chimpanzees were housed in social groups and some in individual cages. All chimpanzees were measured serially from infancy until adulthood. The measurements and routine medical examinations were performed at three-month or six-month intervals, with the chimpanzees anesthetized. These chimpanzees were given good care, but their captivity and treatment may have influenced their physical growth.

Infancy for both human beings and chimpanzees is characterized by the most rapid velocity of body growth of any of the postnatal stages, but also by a steep decline in velocity, or deceleration. Infancy of humans, chimpanzees, and other mammalian species is comparable in many other respects, such as feeding by maternal lactation and the appearance of deciduous teeth. However, in most mammals, including chimpanzees, infancy and lactation end with eruption of the first permanent molars. This occurs between the age of 48 and 60 months in chimpanzees, as indicated by the "W" (weaning, defined as cessation of nursing) in Figure 2. Note the change in chimpanzee growth velocity at the time of weaning. At this point the chimpanzee enters the juvenile growth stage. Juvenile mammals are largely responsible for their own care and feeding, but are still sexually immature.

In humans, by contrast, there is an interval of about three years between weaning, which takes place at a median age of 30–36 months in preindustrial societies, and eruption of the first permanent molars at about six years of age. This interval is the stage of life described here as childhood. The biological constraints of childhood, which include an immature dentition, a small digestive system, and a calorie-demanding brain that is both relatively large and growing rapidly, necessitate care and feeding that older individuals must provide.

TABLE 1 Stages in the Human Life Cycle and Life History

Stage	Growth Events/Duration (Approximate or Average)
Prenatal Development	
Fertilization	
First trimester	Fertilization to 12th 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 Development	
Neonatal period	Birth to 28 days: extrauterine adaptation, most rapid 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 to six months of age and then lactation with gradual introduction of complementary foods, deciduous tooth eruption, many developmental milestones in physiology, behavior, and cognition
Childhood	Years 3.0–6.9: moderate growth rate, dependency on older people for care and feeding, midgrowth spurt, eruption of first permanent molar and incisor, virtual completion of brain growth by end of stage
Juvenility	Years 7–10 for girls, 7–12 for boys: slower growth rate, capable of self-feeding, cognitive transition leading to learning of economic and social skills
Puberty	An event of short duration (days or a few weeks) at end of juvenility stage: reactivation in the hypothalamus of the GnRH pulse generator, dramatic increase in secretion of sex hormones from the ovaries/testes
Adolescence	The stage of development that lasts for 5–10 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 18–20 years of age for women to 45 years (end of childbearing) and from 21 to 25 years of age for men to about 55 years of age: commences with completion of skeletal growth, homeostasis in physiology, behavior, and cognition; loss of fecundity and menopause for women by age 50; fecundity for men may decline with age, but does not drop to zero at any age.
Old age and senescence	From end of childbearing years to death: decline in the function and repair ability of many body tissues or systems
Death	

The rate of body growth during childhood proceeds at a steady 5–6 cm per year. These growth rates are typical for healthy, well-nourished children. Indeed, the pattern of growth velocity from birth to adulthood is highly similar in all human populations, but growth rates and the total amount of growth will vary in relation to health and nutritional status. Many children experience a transient and small "spurt" in growth rate as they transition into the juvenile period. In many traditional human societies (such as hunter-gatherers, horticulturalists, and pastoralists), juveniles perform important work including food production and the care of children (i.e., "babysitting"). Juvenile growth rates decline until puberty. Here we define puberty as an event that takes place within the central nervous system resulting in a change in the regulation of hormone production and secretion, and initiating sexual maturation and the adolescent life stage (Bogin, 2010, 2011). The hormones responsible for sexual maturation also cause the adolescent growth spurt in stature and other skeletal dimensions. Growth of the skeleton ends at about 18–19 years for girls and 20–22 years for boys, and with this the adulthood or reproductive stage of life history begins.

Significant changes in motor control, cognitive function, and emotions are associated with infant, child, juvenile, and adolescent development—and are related to brain growth and maturation. Infancy and childhood are the times of most rapid postnatal brain growth in human beings. At birth, human brain size is about three times that of the chimpanzee—384 g versus 128 g. At adulthood, the difference increases to about 3.3 times—1352 versus grams 410 (Bogin

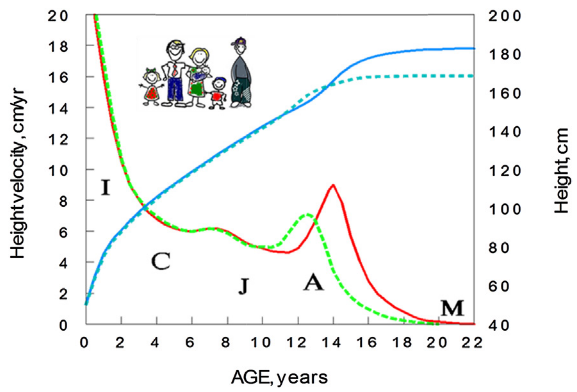

FIGURE 1 Distance and velocity curves of growth for healthy, well-nourished human beings. Boys, solid line; girls, dashed line. These are modal curves based on height data for Western European and North American populations. The stages of postnatal growth are abbreviated as follows: I, infancy; C, childhood; J, juvenility A, adolescence; M, mature adult. Weaning takes place at a mean age of 30–36 months—at the transition from infancy to childhood. *(Modified from Bogin, 1999.)* The distance curve (right *y*-axis) indicates the amount of height achieved at a given age. The velocity curve (left *y*-axis) indicates the rate of growth at a given age. Growth velocity during infancy is rapid with a steep deceleration. Childhood growth is relatively constant at about 6 cm per year. Growth rate slows during the juvenility stage and then accelerates during the first phase of adolescence—the adolescent growth spurt. Growth rates decline during the second phase until all growth in height stops at the onset of the adult stage. The image of the "family" is not meant to promote any particular type of family as desirable or normal; rather, the cartoon figures illustrate the stages of human life history between birth and adulthood from left to right—juvenile, adult male, adult female with infant, child, and adolescent. (See color plate section).

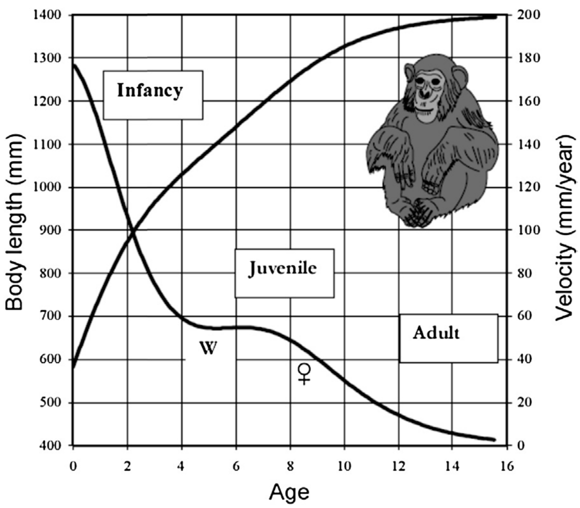

FIGURE 2 Distance and velocity curves for chimpanzee growth in body length (Hamada and Udono, 2002). In the wild, weaning (W) usually takes place between 48 and 60 months of age (Pusey, 1983).

and Smith, 2012). Most of the adult difference is achieved by the end of the human childhood growth stage, which has led to hypotheses that the evolution of childhood was to provide additional time for increased embodied capital, meaning larger brain size, greater learning, higher quality bodies, more complex social networks, and generally, human cultural behavior (Kaplan et al., 2000). An alternative hypothesis is that the primary selective pressure for a childhood stage was the reproductive advantages that accrued to the mother.

Chimpanzee and human mothers have very different reproductive patterns. Chimp mothers must feed and care for their infants for almost five years. No other chimpanzee helps, and the death of the mother usually results in the death of the infant. At five years of age, the young chimpanzee becomes a juvenile and must forage for food on its own and protect itself from dangers. Chimpanzee females must space their births at five-year intervals, as they cannot care for two infants simultaneously. This places constraints on chimpanzee reproductive success. In the wild, chimpanzee females are just able to produce and raise two offspring to adulthood. As a consequence, chimpanzee populations are stable, with equal numbers of births and deaths.

Human women in premodern and modern societies are almost never the sole caretakers of their infants. Other family members, including siblings, parents, husbands, and other children of the mother provide significant amounts of care to mothers and their infants (Hrdy, 2009). The major exceptions are the WEIRD societies—Western, Educated, Industrialized, Rich, and Democratic (Henrich et al., 2010). The social segregation, and often isolation, of mothers, children, adolescents, and the elderly from each other and working adults that is commonplace in North America, much of Western Europe, Japan, Australia, and other WEIRD nations is of very recent origin in human history. The typical human social condition for infant care for 99% of human evolutionary history (at least the past 125,000 years and maybe much longer) was cooperative breeding that eventually evolved into biocultural reproduction.

Cooperative breeding is found in some species of birds and mammals, such as wolves and hyenas, and it works to increase net reproductive output. Only two nonhuman primate groups are cooperative breeders, the marmosets and tamarins of South America. In those species, and in some but not all human groups, the cooperative breeders are close genetic relatives of the mother. By assisting the mother to care for her offspring, rather than selfishly caring only for themselves and their own offspring, the helpers increase their own inclusive fitness, meaning that they help to ensure that their genetic kin survive to reproductive age. Biologists define "fitness" of a species by the number of offspring produced that reach their own reproductive maturity.

Unlike the other cooperative breeding species, human societies define behavioral roles related to infant and child care on the basis of marriage and kinship categories. These often have greater social than genetic foundations. Hill et al. (2011) surveyed 32 present-day foraging societies, including the !Kung (Ju/'hoansi), Hadza, and Ache, and reported that human hunter-gatherer societies have a social structure that is unique among all primates. Hill and colleagues found that most individuals in residential groups were genetically unrelated, or at least not genetically related by descent from common parents or grandparents. This is due to the practice by both men and women of either dispersing from or remaining within their natal group for marriage. Migration to new groups dilutes genetic relationships and requires social kinship designations to structure relationships among people.

Human reproductive cooperation does more than increase biological fitness—it also enhances the technological, social, economic, and political "fitness" of the group. For this reason, the phrase biocultural reproduction seems to best describe the human practice (Bogin et al., 2014). The result of the human type of biocultural reproduction is that a human woman can successfully produce two or more infants in the time it takes a chimpanzee to produce one. It also means that 60%–97% of human infants survive to adulthood. Even in the traditional societies of hunters and gatherers, 50%–60% of live-born infants survived to adulthood. Chimpanzees, in contrast, successfully raise only 36% of their offspring to adulthood. In Darwinian evolutionary terms, these are significant biological advantages and explain, in part, why chimpanzee populations number in the thousands while humans number more than seven billion.

ADOLESCENCE

Puberty resets the central nervous system to resume positive feedback within the hypothalamic–pituitary–gonadal (HPG) axis. During fetal development and until about two to three years after birth, production of gonadotropin-releasing hormone by cells in the hypothalamus promotes the release of luteinizing hormone and follicle-stimulating hormone from cells in the anterior lobe of the pituitary gland (Bogin, 2011; Savage et al., 2011). These hormones stimulate the growth and development of the testes or ovaries, the release of androgens and estrogens, and sexual maturation of the fetus and infant. This process is paused in middle to late infancy when the HPG axis switches to negative feedback, by which circulating androgens and estrogens, as well as pituitary hormones, inhibit the hypothalamus (Ellison et al., 2012).

The change in regulation of the HPG axis from positive to negative feedback by the onset of the childhood growth stage, and the return to positive feedback at puberty, is common to many species of African monkeys, all apes, and human beings (Plant, 2008). Unique to humans is the shift from decelerating to accelerating skeletal growth that follows puberty (Bogin, 2010, 2011). Monkeys and apes have localized accelerations in growth, for example in the jaws, to accommodate projecting canine teeth in some species. Many nonhuman primate species have accelerations in body mass at puberty, especially those with male muscle development. Examples are gorillas and orangutans, as in these species adult males come to weigh more than twice as much as adult females. Nonhuman primates, however, do not have the human body-wide acceleration in the growth, development, and maturation of all long bones of the skeleton (such as the tibia, femur, and humerus), as well as the vertebrae, jaws, and other small bones. This systemic acceleration of skeletal biology following puberty is the human adolescent growth spurt. The spurt is clearly depicted in Figure 1. The spurt is absent in the chimpanzee (Figure 2) and other nonhuman primates (Bogin, 2010; Bogin and Smith, 2012).

There is more to human adolescence than just the skeletal growth spurt. In most species of primates, puberty is followed within a few months or a year by first reproduction. In humans, the delay between puberty and first reproduction is greater, usually on the order of 5–10 years. This interval is the human adolescent growth stage. In humans, the gonadal hormones responsible for the growth spurt also promote sexual maturation. In both sexes there is a sudden increase in the density of pubic hair and often other body hair. In boys, there may be an increased density and darkening of facial hair. The deepening of the voice (voice "cracking") is another sign of male puberty. In girls, a visible sign is the development of the breast bud, the first stage of breast development, which often precedes the appearance of dense pubic hair. The pubescent boy or girl, his or her parents, and relatives, friends, and sometimes everyone else in the social group can observe one or more of these signs of early adolescence.

Another notable feature of adolescence is the completion of permanent tooth eruption; the second permanent molar erupts at about 12 years of age, and the third molar at about 18–21 years. In addition, the years of the adolescence stage include the development of secondary sexual characteristics such as fat patterning and muscularity typical of each sex. At all ages from birth onward, girls on average have more body fat than boys. Just before the onset of puberty, at about nine years of age, the differences between the sexes are relatively small. Girls in the United States average about 30% body fat and 65% soft lean tissue (e.g., muscle and connective tissue) for total weight and boys average 25% body fat and 70% soft lean tissue. In both the girls and the boys the remaining 5% of body weight is made up of hard lean tissue such as bone. By 20 years of age, the differences become greater. Young women average 38% body fat and 60% soft lean tissue, and young men average 22% body fat and 71% soft lean tissue (Borrud et al., 2010). During adolescence, women tend to add body fat to breasts, buttocks, and thighs, while men tend to add muscle over the entire body. Another feature of adolescent development, common to both girls and boys, is the intensification of interest in and practice of adult social, economic, and sexual activities leading to sociosexual maturation in early adulthood.

EVOLUTION OF HUMAN ADOLESCENCE

Some theorists hypothesize that the adolescent stage of human growth evolved to provide the time to learn and practice the complex economic, social, and sexual skills required for effective food production, reproduction, and parenting. In this perspective, adolescence is a time for apprenticeship, working and learning alongside older and more experienced members of the social group. The benefits of skills acquired during adolescence are lower mortality of both first-time mothers and their offspring.

However, apprenticeship cannot be the primary cause for the evolution of adolescence. Learning for child care is an example. In most species of social mammals, the juveniles are often segregated from adults and infants. The ethnographic literature, however, documents that in human societies juvenile girls often are expected to provide significant amounts of child care for their younger siblings. Human girls enter adolescence with considerable knowledge of the needs of young children. Learning about child care, then, is not the reason why human girls experience adolescence. A similar case may be made for boys' learning of most skills needed for successful adulthood. More to the point, the additional 5–10 years of lack of fecundability associated with adolescence could not evolve by natural selection, since those individuals who "cheated" by terminating growth and reproductively maturing at an earlier age would begin reproducing sooner and would be at a reproductive advantage. All other primates do, in fact, begin reproducing at earlier ages than humans, and none of the nonhuman primates has a humanlike adolescent growth spurt or many of the other biological and behavioral features of human adolescence. Clearly, a juvenile primate does not need to pass through a lengthy period of adolescence, with apprenticeship-type learning, just to be reproductively successful (Bogin and Smith, 2012). As was the case for the evolution of human childhood, the evolution of human adolescence may be due in large part to the human style of biocultural reproduction. A multilevel model of selection for mating and parenting has been proposed for the evolution of human adolescence (Bogin, 2009). Multilevel models in evolutionary biology include selection at the level of the individual and at the level of the social group. Such models allow for time lags between the stage of life when selection takes place and the accrual of reproductive benefits later in life. The complex pattern of human individual growth and development, combined with equally complex human social and cultural behavior, seems to be better explained by multilevel evolutionary models than by simpler models, for example those focusing only on fertility or mortality of the adolescent.

Human mating and parenting are of course related, but they are not identical. Charles Darwin identified two types of biological selection—natural selection and sexual selection (see Futuyma)—and both are likely to be involved in the evolution of human adolescence. Sexual selection is all about opportunities for mating, while natural selection is in part about parenting (Darwin, 1871; see the chapter by Flinn, and chapter by Gangestad and Grebe). Darwin wrote of the many structures and instincts developed through sexual selection, including biological weaponry for offense and defense, often used to drive away rivals for mating opportunities; and ornaments, vocalizations, and glands to emit odors and attract mates. Some human examples are the waist-to-hip ratio and childlike voice pitch of women that may be alluring to men, and verbal skills for gossip and attack that may be used to drive away mating rivals (Locke and Bogin, 2006).

GIRLS AND BOYS: SEPARATE PATHS THROUGH ADOLESCENCE

The multilevel nature of the evolution of human adolescence may be seen by considering the trade-offs related to biocultural reproduction and the different sequence of biological and behavioral events experienced by adolescent girls and boys. The differences allow each sex to improve opportunities for mating and parenting. Mating will eventually lead to the birth of offspring, but producing offspring is only a small part of reproductive fitness. Rearing the young to their own reproductive maturity is a surer indicator of success. The developmental paths of girls and boys during adolescence may be key in helping each sex to both produce and rear its own young successfully.

The path that girls take gives them the outward appearance of sexual maturity many years before they are, in fact, fecund. In contrast, the path that boys take gives them an outward appearance of immaturity for several years after they are, in fact, fecund.

The order in which adolescent events occur in girls and boys may be expressed in terms of time before and after peak height velocity (PHV); that is, the maximum velocity during the adolescent growth spurt. The velocity curves for girls and boys depicted in Figure 1 are aligned on chronological age, and PHV takes place about two years earlier in girls than in boys. If the curves for girls and boys are aligned at PHV, the timing of events before and after PHV becomes easier to appreciate. The following analysis will use the Tanner Maturation Staging System for the development of secondary sexual characteristics (Tanner, 1962). This system is based on five stages. Prepubertal maturation is denoted as B1and PH1 for girls—the absence of breast development and pubic hair—or G1 and PH1 for boys—the absence of gonadal (testes or penis) enlargement and absence of pubic hair. The adult appearance is stage B5, PH5, or G5.

In both girls and boys, puberty begins with changes in the activity of the central nervous system, the HPG axis as described above. These events begin at the same relative age in both girls and boys—that is, three years before PHV. This is also the time when growth rates change from decelerating to accelerating. In girls, the order of events is:

1. The first outward sign of puberty is the development of the breast bud (B2) and wisps of pubic hair (PH2) between −2 and −1 years PHV;
2. A rise in serum levels of estradiol that leads to the laying down of fat on the hip buttocks, and thighs, at −1.5 to −1.0 years PHV;
3. Increased velocity of the adolescent growth spurt, noticeable between −2 and −1 years PHV;
4. Further growth of the breast and body hair (B3 and PH3) at about +3 months PHV. At this stage the adolescent girl has the outward appearance of fecundity.
5. Menarche (first menstruation) at about +1 to +1.3 years PHV;
6. Completion of breast and body hair development (B5 and PH5) between +2 and +3 years PHV;
7. Attainment of adult levels of ovulation frequency at about +4.5 years PHV. At this stage the adolescent girl is fecund;
8. About +6 years PHV, growth in height ends and adulthood begins.

The path of adolescent development in boys starts with:

1. A rise in serum levels of luteinizing hormone, and the enlargement of the testes and then penis (G2) at about −3 years PHV;
2. A rise in serum testosterone levels (T) that is closely followed by the appearance of pubic hair (PH2) at about −2 years PHV;
3. About a year later (−1 year PHV) motile spermatozoa may be detected in urine, stages G3 to G4 and PH3 to PH4. At this stage, the adolescent boy is fecund;
4. About +0.5 years PHV there is a deepening of the voice, and stages G5 and PH5 are achieved;
5. At about +2.5 years PHV boys undergo a spurt in muscular development and strength. At this stage the adolescent boy has the appearance of fecundity;
6. Between +4 and +9 years PHV, growth in height ends and adulthood begins.

The sex-specific order of adolescent events tends not to vary between early and late maturers. The normal age ranges for puberty are 8–13 years in girls and 9–14 years in boys (Tanner, 1962). The sequence of adolescent events is also essentially identical between well-nourished girls and boys and those who suffered from severe malnutrition in early life, between rural and urban dwellers, and between major geographic and ethnic groups (e.g., European, Asian, and African, Bogin and Smith, 2012).

The different paths of sexual development may allow girls and boys to best learn the physical, social, and emotional skills to be successful at mating (sexual selection) and parenting (natural selection). In human societies, adolescent girls gain knowledge of sexuality and reproduction because they look mature sexually and are treated as such several years before they actually become fecund. The dramatic changes of adolescence stimulate both girls and the adults around them to participate in adult social, sexual, and economic behavior. For the postmenarcheal adolescent girl, this participation may be "low risk" in terms of pregnancy. Even so, some may become pregnant, and there are other social and psychological risks to adolescent sexual behavior. Teenage mothers and their infants are at risk because of the reproductive and emotional immaturity of the mother (Cunnington, 2001). This often leads to a low-birth-weight infant, premature birth, and high blood pressure in the mother. The likelihood of these risks declines and the chance of successful pregnancy and birth increases markedly after 15 years of age, and reaches its nadir after 18 years of age (Bogin and Smith, 2012). Due to these biological and social risks, most human societies carefully regulate, according to age and sex, the onset and type of sexual behavior that is permitted by adolescent girls.

The adolescent development of boys is quite different from that of girls. Boys become fecund well before they assume the size and physical characteristics of men. Analysis of urine samples from boys 11–16 years old show that they begin producing sperm at a median age of 13.4 years. Yet, cross-cultural evidence indicates that few boys successfully father children until they are into their third decade of life. The explanation for the lag between sperm production and fatherhood is not likely to be a simple one of sperm performance, such as not having the endurance to swim to an egg cell in the woman's fallopian tubes. More likely is the fact that the average boy of 13.4 years is only beginning his adolescent growth spurt (Figure 1). Growth researchers have documented that in terms of physical appearance, physiological status, psychosocial development, and economic productivity, a 13-year-old boy is still more a juvenile than an adult.

The delay between sperm production and reproductive maturity is not wasted time in either a biological or a social sense. The obvious and the subtle psychophysiological effects of testosterone and other androgen hormones that are released after gonadal maturation may "prime" boys to be receptive to their future roles as men. Early in adolescence, sociosexual feelings including guilt, anxiety, pleasure, and pride intensify. At the same time, adolescent boys become more interested in adult activities, adjust their attitudes toward parental figures, and think and act more independently (Sisk and Zehr, 2005). In short, they begin to behave like men. Because their adolescent growth spurt occurs late in sexual development, young males can practice behaving like adults before they are actually the size of an adult and perceived as mature by other adults. The sociosexual antics of young adolescent boys are often considered to be more humorous than serious. Yet, they provide the experience to fine-tune their sexual and social roles before their lives or those of their offspring depend on them.

ADOLESCENT CONTRIBUTIONS TO THE REPRODUCTIVE SUCCESS OF ADULTS

Another aspect of the multilevel nature of human adolescence may be contributions that adolescents make to the reproductive success of older social group members. Adolescence delays the onset of reproduction for the adolescent, and allows the adolescent to channel food and work toward others. Human juveniles may hunt, gather, or produce some of their own food intake, but overall they require provisioning to achieve energy balance. In contrast, human adolescents are capable of producing sufficient quantities of food to exceed their own energy requirements. Some of the food that adolescents produce may be used to fuel their own growth and development, creating larger, stronger, and healthier bodies. Another portion of their production is shared with other members of the social group, including younger siblings, parents, and other immediate family members (defining families in the broad anthropological sense, Bogin, 2010; Bogin and Smith, 2012). Adolescent contributions enhance the fertility of adults and the survival of infants, children, and juveniles. The biological trade-off is the delay of years between puberty and first birth for adolescents. For their valuable services in food production, the adolescents receive care and protection to safeguard their health and survival. This is important because adolescents are immature in terms of sociocultural knowledge and experience.

RISKS OF CHILDHOOD AND ADOLESCENCE

The evolution of any new structure, function, or stage of development may bring about many biosocial benefits; however, it also incurs risks. Human childhood and adolescence come with their own set of specific risks. Children are dependent on older people for feeding, care, and protection. Neglect and abuse of children are common today and have been throughout recorded history. Predation on children by large carnivores and birds of prey was a real threat in the human past and still is today in some parts of the world. Childhood immaturity of the immune system means that viral and bacterial predators may also pose risks (Bogin and Smith, 2012). Immaturity and inexperience also mean that children are prone to accidents and other physical trauma.

Among the most common and serious threats to adolescents are psychiatric and behavioral disorders. The onset of such problems tends to peak during adolescence. Most mammalian species terminate all brain growth well before sexual maturation, but human adolescents show enlargement and pruning of some brain regions leading to structural changes in the cerebral cortex well into their third decade. Some scholars hypothesize that the increase in brain-related disorders may derive from these cortical changes, which affect the adolescent brain's sensitivity to reward. The reward system of the brain may lead adolescents toward risk-taking behavior. Whether risk taking is inherently biological or shaped by social stimuli is debated. What is clear is that adolescence is a time of life with a higher level of risk for certain diseases of the mind and body, and greater mortality, than was the case for the juvenility stage. Adolescent mortality often is associated with ritualized violence, such as serving as combatants in warfare, or being exposed to inherently dangerous but socially normative behaviors such as automobile driving, alcohol consumption, cigarette smoking, and sex, without appropriate instruction and regulation by society.

CONCLUSIONS

In this article, a biocultural approach is taken to the study of the evolution of human growth and development. The patterns of human postnatal growth and development—the stages of infancy, childhood, juvenility and adolescence—were reviewed. Several hypotheses were discussed concerning how the new life stages of the human life cycle represent feeding and reproductive specializations, secondarily allowing for the human style of learning and cultural behavior.

The biocultural perspective of human development focuses on the constant interaction taking place during all phases of human development, between both genes and hormones within the body, and with the sociocultural environment that surrounds the body. Research from anthropology, developmental psychology, endocrinology, primate behavior, and human biology shows how the biocultural perspective enhances our understanding of human development.

REFERENCES

Bogin, B., 1999. Patterns of Human Growth, second ed. Cambridge University Press, Cambridge.

Bogin, B., 2009. Childhood, adolescence, and longevity: a multilevel model of the evolution of reserve capacity in human life history. American Journal of Human Biology 21, 567–577.

Bogin, B., 2010. Evolution of human growth. In: Muehlenbein, M. (Ed.), Human Evolutionary Biology. Cambridge University Press, Cambridge, pp. 379–404.

Bogin, B., 2011. Puberty and adolescence: an evolutionary perspective. In: Brown, B.B., Prinstein, M.J. (Eds.), Encyclopedia of Adolescence, vol. 1. Academic Press, San Diego, pp. 275–286.

Bogin, B., Bragg, J., Kuzawa, C., 2014. Humans are not cooperative breeders but practice biocultural reproduction. Annals of Human Biology 41, 368–380.

Bogin, B., Smith, B.H., 2012. Evolution of the human life cycle. In: Stinson, S., Bogin, B., O'Rourke, D. (Eds.), Human Biology: An Evolutionary and Biocultural Perspective, second ed. Wiley-Blackwell, New York, pp. 515–586.

Borrud, L.G., Flegal, K.M., Looker, A.C., Everhart, J.E., et al., 2010. Body composition data for individuals 8 years of age and older: U.S. population, 1999–2004. Vital Health Statistics 11 (250). National Center for Health Statistics, Hyattsville, Maryland.

Crews, D.E., Bogin, B., 2010. Growth, development, senescence, and aging: a life history perspective. In: Larsen, C. (Ed.), A Companion to Biological Anthropology. Wiley-Blackwell, New York, pp. 124–152.

Cunnington, A.J., 2001. What's so bad about teenage pregnancy? Journal of Family Planning and Reproductive Health Care 27 (1), 36–41.

Darwin, C., 1871. The Descent of Man and Selection in Relation to Sex. John Murray, London.

Ellison, P.T., Reiches, M.W., Shattuck-Faegre, H., Breakey, A., Konecna, M., Urlacher, S., Wobber, V., 2012. Puberty as a life history transition. Annals of Human Biology 39 (5), 352–360.

Hamada, Y., Udono, T., 2002. Longitudinal analysis of length growth in the chimpanzee (*Pan troglodytes*). American Journal of Physical Anthropology 118, 268–284.

Henrich, J., Heine, S.J., Norenzayan, A., 2010. The weirdest people in the world? Behavioral and Brain Sciences 33, 61–83.

Hill, K.R., Walker, R.S., Bozicević, M., Eder, J., Headland, T., Hewlett, B., Hurtado, A.M., Marlowe, F., Wiessner, P., Wood, B., 2011. Co-residence patterns in Hunter-Gatherer societies show unique human social structure. Science 331, 1286–1289.

Hrdy, S., 2009. Mothers and Others: The Evolutionary Origins of Mutual Understanding. The Belknap Press of Harvard University Press, Cambridge.

Kaplan, H., Hill, K., Lancaster, J.B., Hurtado, A.M., 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evolutionary Anthropology 9, 156–185.

Locke, J.L., Bogin, B., 2006. Language and life history: a new perspective on the development and evolution of human language. Behavioral and Brain Sciences 29, 259–325.

Plant, T.M., 2008. Hypothalamic control of the pituitary–gonadal axis in higher, primates: key advances over the last two decades. Journal of Neuroendocrinolgy 20, 719–726.

Pusey, A. 1983. Mother–offspring relationships in chimpanzees after weaning. Animal Behavior 31, 363–377.

Savage, M.O., Hwa, V., David, A., Rosenfeld, R.G., Metherell, L.A., December 12, 2011. Genetic defects in the growth hormone-IGF-I axis causing growth hormone insensitivity and impaired linear growth. Frontiers of Endocrinology (Lausanne) 2 (95). http://dx.doi.org/10.3389/fendo.2011.00095.

Sisk, C.L., Zehr, J.L., 2005. Pubertal hormones organize the adolescent brain and behavior. Frontiers of Neuroendocrinology 26 (3–4), 163–174.

Tanner, J.M., 1962. Growth at Adolescence, second ed. Blackwell, Oxford.