Life History: Evolution of Infancy, Childhood, and Adolescence

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Human life plays out on an extended clock, one with the longest time from newborn to reproducing adult—nineteen years on average—known in the mammalian world. Even mammals with life spans near ours, like the blue whale or the elephant, reach reproductive age in just five or ten years. Only the chimpanzee even approaches us, reaching first birth at fourteen to fifteen in the wild. "Live slow and die old" might be the name of our overall strategy, yet not all features of human lives fit into the "slow" category. Novelties have evolved, including an abbreviated infancy, crowded interbirth intervals, a period of postweaning dependence and growth depression we call "childhood," and an adolescence marked by a novel growth rebound (see Smith and Tompkins 1995).

Recognizing stages in the human life course is ubiquitous. Societies worldwide, traditional and industrial, mark life stages with rites of passage that may introduce a change in name, diet, appearance, residence, association, privilege, and responsibility. Birth, childhood, puberty, adulthood, and pregnancy are often accompanied by ceremony and change of cultural status. In literature, across the 2,000 years from Solon to Shakespeare, Western writers divided human life into sevens (periods of seven years or seven periods), fours, or twelves, influenced by numerology, astrology, or religious text (see Boyd 1980). The English terms we use today derive largely from Latin: *infans* (unable to speak), *adolescere* and *adultus* (to grow up, grown up), *iuniores* (young), *senior* and *senex* (older, old). "Child," however, has Old English roots; it appears as its own stage by the sixteenth century in a progression of infancy–childhood–adolescence. Eighteenth- and nineteenth-century scholars, sometimes for medicolegal purposes, often marked out early life stages by eruption of deciduous and permanent teeth (Boyd 1980).

Recognition of life stages in evolutionary anthropology owes a debt to a long history of human growth studies but also to the field of life history, where a broad "comparative approach" is a central tool. The term "life history" comes from natural history, where it refers to species growth, development, size, life span, and life cycle. As a research field that coalesced after 1950, "life history" combines demography, ethology/ethnography, and natural selection theory to elicit general principles explaining how natural selection has acted on the life cycle, both to produce the diverse array of lifeways we see in the natural world and to enable prediction of future consequences for populations under new selective regimes.

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Examination of life stages begins with a basic question: why have stages evolved? In evolutionary perspective, a life cycle is a solution to a common problem: How can the new generation survive while capturing enough energy to grow to reproductive size, develop reproductive capability, and arrive at reproductive season in the best possible shape? Simply put, animal life stages are a strategy shaped by evolution to (1) negotiate the risky path from egg to reproductive adult, (2) capture sufficient energy to grow and develop, and (3) make the best possible adult.

Many animals transit from egg to adult with a complex life cycle punctuated by metamorphosis. Complexity can extend to change of host, change of sex, alternating sexual and parthenogenic reproduction, and even different morphs present in different generations (e.g., some aphids). Humans, in contrast, like other mammals, have a life cycle that is *simple* and *direct*, without metamorphosis. Simple life cycles tend to occur when young are well provisioned with a rich egg or experience parental care that aids the path to adulthood (Ebenmen 1992). Nursing, the traditional sine qua non of mammals, provides both: provisioning of young and parental care in the association between mother and young. Even though the mammalian life cycle is comparatively simple and direct, however, it is a life with differentiation, one in which hormones turn on and turn off, growth accelerates and slows, organ systems mature, and behaviors, dependencies, and affiliations change.

By convention, mammalogists divide postnatal life into just three stages: the nursing infant, weaned juvenile, and the reproductive adult. Even small, rapidly growing mammals may have transitions that are critical, if brief, especially in transiting from nursing to independence. The tripartite division becomes less satisfactory for the longest-lived mammals, where life stretches out to a point that intermediate stages take on increasing significance, even to the evolution of special features. For humans, the subadult period breaks fairly naturally into more than the classic three stages.

Infancy

2

Both mammalogy and evolutionary anthropology define infancy as the period for which a mother nurses an infant, a period which begins at birth and encompasses early milk-only feeding, mixed feeding, and the weaning process. In humans, pregnancy demands a high degree of investment from the mother in terms of time, energy, and risk. "Birth status," the degree of development of the newborn, shapes the first year of life. Our infants are precocious in comparison to many other mammals, born large for the mother's body weight, with large brains, eyes and ears open, hair through, and well equipped to engage the attention of caregivers. What they are extremely poor at is motor ability, a feature which gave rise to the label "secondarily altricial." Although all primate infants are motor challenged in comparison to other precocial mammals, it will take a human infant about a year to reach a level of motor control a chimpanzee infant exhibits in its early months. Care of human infants is especially costly energetically because they must be carried in arms for many months, whereas primate young cling to mother from their earliest days. Given our lag in motor control at birth, high energy demands of a growing brain, and generally slow growth and development, one might expect the nursing period to be especially long in humans. However, that turns out to be wrong: humans are nursed for relatively short periods of time, leaving a weanling that is less mature than those of other primates.

Across a range of traditional peoples, the average duration of nursing is about two and a half years and, indeed, the World Health Organization now recognizes that infant survival worldwide is greatly enhanced by exclusive breastfeeding for six months and supplementary nursing into the third year. Yet even weaning an infant from the breast at two and a half years comes up short in comparison to our closest relatives. The chimpanzee infant, though smaller and much faster growing than humans, is nursed for four years or more (see Kaplan et al. 2000). For humans, weight at weaning is on the small side as a multiple of birth weight or as a proportion of mother's weight (see Sellen 2007). At two and a half, a human infant has just completed the deciduous dentition whereas great apes are not weaned until all first permanent molars have erupted. The most telling distinction, however, is that *human infants are weaned before they can feed themselves* and young human lives will depend on food sharing for years to come. Although food sharing is not unknown in the wider mammalian world, in general a weaned juvenile mammal feeds independently, whether alone or in a social group with mother.

The key to early weaning with a thriving infant is the frequent offer of high-quality provisions. At two to three years of age, humans have a limited battery of teeth, limited gut surface area, and a sharply increasing demand for energy to support brain growth (see Bogin and Smith 1996). To thrive, weanlings need foods that are energy dense, high in protein and fat, and easily chewed and digested. After breast milk, prechewed meat, brains, and fat are some of the foods hunter-gatherers have been observed to share with infants and young children. Operationally, this spreads the cost of infant feeding away from mother's physiological resources, allowing fathers, grandmothers, or anyone in the social group to share food with the child. Mothers, relieved of the direct drain on their energy, recoup their reserves and return to reproductive cycling more quickly. The early transfer of infant feeding to provisioning appears to be the mechanism behind the relatively short interbirth interval maintained in human societies. With infant provisioning, human hunter-gatherers average three to four years between births whereas chimpanzees manage to give birth only every five or six years, on average (Kaplan et al. 2000).

Childhood

In evolutionary anthropology, "childhood" is a period of postweaning dependence and a decelerating rate of skeletal growth (Bogin and Smith 1996). Although the term "child" is usually reserved for humans, we are not the only mammals with postweaning dependence. In carnivores, weanlings can successfully eat, digest, and grow on the rich carnivorous diet but the young may not be skilled enough to hunt by themselves. Some carnivore parents continue to bring down kills for the young after weaning or regurgitate food back at a den. Renowned primatologist Jane Goodall has also used the term "childhood" for young chimpanzees because they stay in close association with their mothers

3

for about two years after weaning and chimpanzee mothers do engage in some food sharing with infants, even occasionally with older offspring, particularly in response to begging. For humans, however, postweaning dependency continues for many years.

Of course, children do not just have to be fed—they must be kept safe, a challenge if offspring are closely spaced. In foraging groups, the youngest children are held or kept close to an adult a great deal of the time, most often by mother, although fathers and grandmothers also provide direct care. Eventually children may spend a good part of their time in a play group, often a multiage group in foraging peoples (Hewlett and Lamb 2005), although an adult is within earshot. Thus "babysitting" or allocare can be shared across members of a band. Play groups are a locus of learning and all sorts of development, from strength and coordination to foraging skills, sex roles, and social skills. Hunting, in particular, proves to be a skill that will be practiced and improved for decades (Walker et al. 2002).

Middle childhood/juvenility

At about five to six years, human children show several transitions in growth and development, entering a period called "middle childhood" in the human growth literature or the "juvenile period" in the evolutionary literature, to foster comparisons with other mammals. At this point, permanent molars begin to emerge, making the child more able to tackle an adult diet. A small spurt in skeletal growth, more visible in males, peaks around age six. Gait becomes more mature and children become more self-sufficient, more able to carry out tasks and even contribute to food production. In traditional societies, older sisters will play important roles in caring for younger siblings, experience which is important to both parties. Adrenarche, an endocrine event at around ten to eleven years, sets off an increase in androgens that seem to effect body composition, skin, hair, and brain metabolism (Campbell 2011).

In terms of physical growth, the brain nears adult volume in middle childhood, although maturation is ongoing. The juvenile brain has "exuberant" synaptic connectivity; connections will be reinforced under the influence of experience or, if not, pruned throughout adolescence and into the early twenties. Energy demands continue to be high for many years: positron emission tomography (PET) scans find that the developing human brain in three- to eight-year-olds metabolizes glucose at two to three times the adult rate, declining slowly to adult values by the late teens (see Kuzawa et al. 2014).

Concomitant with the brain's peak energy demands, skeletal growth decelerates to its lowest rate since birth, a skeletal pattern not seen in the chimpanzee where juveniles continue at a steadier pace of growth, absolutely and relatively greater than humans (see Bogin and Smith 1996). Throughout this period, energetics of physical growth mirror energetics of the brain—the former reduces while the latter increases (Kuzawa et al. 2014). For humans, the marked slowing of skeletal growth is a life-history novelty that lengthens only the juvenile period without expanding all life stages; furthermore, it frees energy for brain maturation by lowering somatic demands (Kuzawa et al. 2014; Smith and Tompkins 1995). Of note, boys will appear to be juvenile for

5

several more years than girls—one might say that a twelve-year-old boy "pretends" to be younger than he is, which is perhaps related to the special challenges of male competition.

Adolescence

The adolescent stage is one of sexual and social maturation. Change is initiated with a neuroendocrine signal, although adolescence is observed and studied by its later manifestations. Secondary sexual characteristics begin to appear before the distinctive acceleration in growth called the adolescent growth spurt. In the West, peak growth velocity is attained around age twelve for girls and fourteen for boys. Undernutrition will delay it and damp its amplitude but the event appears highly programmed across populations worldwide. Girls reach menarche as growth decelerates again, after the peak in growth velocity (see Bogin and Smith 1996). Onset of menarche seems to be influenced by skeletal growth, energy reserves, and energy flux; intense exercise or high workloads will delay it. For a time, reproductive cycles are frequently anovulatory, producing "adolescent sterility," an adaptation that delays birth until growth is more advanced. Thus, in foraging societies, human females reach menarche at about sixteen or seventeen years but first births are delayed until nineteen or twenty. We know from an American growth series that even well-fed females do not reach full diameters of the pelvic inlet until about eighteen years of age, a factor in labor and birth (see Ellison 2001).

For the average boy, the adolescent growth spurt begins years later and builds to a greater magnitude. The spurt is recognizable all over the skeleton, with increasing shoulder breadth one of the later manifestations (see Dean and Smith 2009). Boys will reach fertility early in adolescence, although few manage to father children until their third decade in traditional societies (Bogin and Smith 1996).

The growth spurt itself provides rapid catch-up from the previous downturn in skeletal growth but why was this innate pattern selected for rather than a more incremental increase? Kuzawa and colleagues (2014) argue that the spurt appears when energy demands of the brain decrease to a crossover point in energy allocation. In social perspective, the growth spurt in size and strength probably alter expectations for behavior and work productivity. By mid-adolescence, work capacity and strength increase greatly, to the point where production and consumption may begin to break even in traditional societies, although peak performance in foraging comes decades later (Walker et al. 2002).

Like other mammals, male chimpanzees bulk up in muscle and weight at sexual maturation, with massive permanent canines also erupting, but do so without a major skeletal growth spurt.

In humans, all the hard tissues are approaching maturation by the average age of first birth for females but this is by no means universal in mammals. The systems are not tightly linked and improvements in nutrition will drop the age of sexual maturation markedly with much less effect on skeletal maturation and less yet on the dentition.

Evolutionary questions

6

One approach to the evolutionary significance of life stages is to ask how each phase contributes to *survival, energy acquisition*, and/or *making the best adult*. The traditional argument is still compelling, that slow development is integral to making the best possible adult (see Smith and Tompkins 1995). "Payback" from extended time for learning or, more specifically, time to acquire a complex repertoire of extractive technology (Walker et al. 2002) have been proposed as the selective force that slowed human development. Recent work on brain development, however, emphasizes that the brain is an organ so costly in energy that growth and maturation must be spread out over a long period, even to the point of sacrificing physical growth of the skeleton and overall body size when energy demand peaks for the brain (Hublin, Neubauer, and Gunz 2015; Kuzawa et al. 2014).

The explanations are not mutually exclusive. Clearly, humans take advantage of the long period of learning to improve cognition. Juvenile brains are "exuberantly connected" with synapses; useful connections will be reinforced by activity for many years while others are pruned away in a process that makes the brain more efficient (see Kuzawa et al. 2014, and references therein).

Our abbreviated infancy makes sense as a means of transferring caloric load from the mother and spreading it flexibly over kin or allies. In turn, mothers intensify production of infants in shorter time intervals, spreading costs and care of a family of multiple dependents among kin (particularly father, grandmother, and older siblings) and the social group. Short interbirth intervals compensate for our late age of sexual maturation, already at an extreme even in the chimpanzee, and a limit of twenty-five years or less of functional fertility for an average human female (Kaplan et al. 2000). A stepped-up birth rate combined with slow maturation, however, sums to multiple dependents for reproducing females. By the age of thirty-five or forty, a mother in a foraging society may have an adolescent, older child, younger child, and infant all dependent to various degrees (Gurven and Walker 2006). Human demography (age and sex structure of groups) as we see it today depends on food sharing to supplement subadults and reproducing females (Kaplan et al. 2000).

When human ecologists follow the flow of calorie production and consumption in foragers, they find that only mature adults are net producers (Gurven and Walker 2006; Walker et al. 2002). Children are net losers, consuming more calories than they produce. Subadults of all ages, it turns out, depend on the hunting skills of males and the gathering skills of mothers and grandmothers. The numbers show starkly the interdependence of family and social group—human females cannot raise multiple dependents alone successfully. Thus, evolution of the human life course is intimately tied to family structure, deserving of the term "cooperative breeding."

Top providers have the skills to produce more than they consume but with only twenty-four hours in a day the practicalities of procuring, distributing, chewing, digesting, and absorbing sufficient calories from a raw plant food diet make such a strategy unworkable (Wrangham 2009). Energy-dense, high-quality yields from hunting and, at some point, from cooking must also underpin human life history. Successful early

7

weaning particularly depends on nutrient-dense foods—such as animal brains, fat, or marrow.

For humans, the two-decade period between birth and reproductive adult produces high-quality young but delay always risks death before reproducing. In the past, prereproductive mortality must have dropped as development slowed and longevity increased (see Kaplan et al. 2000). Foraging people living today have significantly lower mortality of infants and juveniles than monkeys or apes. Something decreased subadult mortality in the genus *Homo*—very likely intensified parental care, perhaps also aspects of feeding strategy, association, or group transfer (e.g., Janson and van Schaik 1993). In broad perspective, the human life cycle seems to be adapted to support a major investment in cognition, a strategy that depends on rich energy resources, low mortality, cooperative childcare, and food sharing, all of which create a path from birth to adult that reduces risk, provides energy for the young, and makes the best possible adult.

The fossil record

Sometime in our evolutionary history, human ancestors evolved to expand the length of juvenile life by an additional 50 percent. Because distinctive features of our life cycle involve an enlarging brain, a delay in dental and skeletal maturation, and altered infant-feeding strategy, and further depend on sophisticated toolkits for foraging and food processing, fossils can reveal points along the way to the modern human life cycle. The fossil record of endocranial capacity (preserved by adult skulls) serves as a proxy for energy investment in brain growth, development, and function; the archaeological record shows the development of technology and, to some extent, behavioral complexity; fossil teeth preserve a record of daily growth that marks the timing of other developmental landmarks.

It is no accident that historic divisions of the human life cycle used markers of tooth eruption. Completion of the deciduous dentition coincides with the typical end of infancy; middle childhood begins with first molar emergence and brain volumes that approach adulthood, and is concurrent with the eruption of most of the permanent dentition, excepting only the last molar or "wisdom" tooth. Our closest relatives differ in revealing aspects of this pattern.

The sample of immature fossils with closely estimated ages at death is small but steadily increasing. Age of emergence of the first permanent molar is the most frequently studied, although a few important skeletons preserve skull, skeleton and tooth development (e.g., the Dikika infant, the *Australopithecus sediba* youth, the Turkana boy, and Le Moustier). Molar eruption itself is tightly integrated into life history across the primate order, probably because molar eruption must pace along with growth and development of the face and skull, a complex which is further integrated with all body growth (see Kelley and Schwartz 2011; Smith and Tompkins 1995).

Estimates of the pace of juvenile development are best known for early hominins from eastern and southern Africa, including the genus *Australopithcus*, known from circa 4–2 million years ago in the Pliocene epoch, and for *Paranthropus robustus*, a genus which persisted into the Pleistocene. All juvenile fossils of these two genera examined show tooth eruption occurring on a much faster time scale than modern humans, with

the first permanent molar erupting at about three to three and a half years, near typical values for great apes and far earlier than the five to six years of age expected for a human child (see Kelley and Schwartz 2011).

The history of increasing adult brain size is well documented in the fossil record, where slow but steady increases are observed over the Pleistocene record of the genus *Homo*. The fast pace of dental development in australopiths matches expectations based on the small brains of these early hominins, in line with the proposal that brain energetics are the key demand that impacts growth rate.

The fossil evidence has brought about general agreement that the origin of the distinctive human life cycle lies within the genus *Homo* and not in its antecedents. The "Turkana boy," or youth from Nariokotome, Kenya, is a skull and skeleton of an adolescent *Homo erectus* male that provides a snapshot growth record from the early Pleistocene, about 1.6 million years ago. Matching tooth development, stature, and bone maturation, the boy is difficult to force onto human growth standards. The combination of his young dental age, large size, and advanced bone age are best explained if the adolescent growth spurt had not yet evolved. There are signs, however, that *Homo erectus* did make slight incremental gains in the length of the developmental period in concert with the expansion of brain size documented for the species (Dean and Smith 2009).

Information remains piecemeal for Middle Pleistocene *Homo* where we lack young juveniles, although the older juveniles we do have display patterns of internal dental development leaning toward a more human condition. Adult pelvises are known in a few instances in the Early and Middle Pleistocene; size of the pelvic inlet has been used to estimate newborn skull size to recover information about infant altriciality. Efforts have been hampered by extrapolation and poor comparative data, although these are improving (DeSilva and Lesnik 2008). In the future, small changes in the location of the "neonatal line" in teeth, a record of growth disruption at birth, could add information about the evolutionary history of neonatal maturity.

With Neanderthals of late Pleistocene Eurasia (Homo neanderthalensis or Homo sapiens neanderthalensis), intentional burial of individual infants and children appears in the archaeological record and fossil immatures can again be counted on more than the fingers of one hand. In-depth study of dental development finds that the timing of the Neanderthal ontogeny is much closer to humans (Smith et al. 2010). For example, if we take a stage of dental development (often first molar emergence but using other events also), Australopithecus hits that mark much sooner than a human child, at about 55 percent the age we expect for a typical human; *Homo erectus* (N = 1) hits the mark at 75 percent, while Neanderthals average about 90 percent of expectations, showing at least an outline of the approach to modernity. Other studies of Neanderthal skull and skeletal growth continue to find unusual features, however, and the adolescent growth spurt has not been confirmed despite a rich archaeological record. Although Neanderthal endocranial volume is at least as large as that of living humans, some argue that shape and substructure of the Neanderthal brain differ enough that volume is an insufficient proxy of metabolic need for close comparison with living humans (Hublin, Neubauer, and Gunz 2015).

At present, the earliest date for which teeth match a pace of growth and development indistinguishable from living humans comes from early *Homo sapiens* from the Jebel

Irhoud site, Morocco, dated at circa 300,000 years ago and from somewhat younger fossils at Qafzeh, Israel (Smith et al. 2010). Nothing, however, is known about skeletal maturation at Jebel Irhoud and the time depth of the distinctive human pattern of growth suppression and growth spurt has not been established.

Sometime in human evolution, hominins abbreviated infancy, dropping it well below the age first permanent molars erupt, shortened the interbirth interval, and began to stack females with multiple dependents. Eventually fossil teeth may point to such changes because dental histology and isotopic analyses have the potential to determine age of weaning and basic growth rate.

In all, the fossil record contains the data needed to map the outline of the evolution of the human life cycle. As that outline is mapped and filled in, evolutionary anthropologists can test hypotheses about the sequence and interdependence of the life cycle in the context of the archaeological record of human behavior.

SEE ALSO: Aging; Behavioral Ecology, Human; Brain Evolution and Energetics of Encephalization; Childbirth and Brain Size, Evolutionary Constraints of; Children and Childhood, Anthropological Study of; Cooperative Child Rearing: Evolution of Alloparenting in Hominins; Demographic Anthropology; Demography, Prehistoric Human; Grandmother Hypothesis, Grandmother Effect, and Residence Patterns; Home; *Homo*: Evolution of the Genus; Hunter-Gatherer Models in Human Evolution; Infanticide; Meat Eating in Apes and Early Hominins; Medical Anthropology Methods: Biocultural Perspectives; Memory; Milk, Breast; Oral Literatures; Parental Effort and Investment; Psychoanalytic Anthropology; Rites of Passage; Self and Selfhood; Skeletal Aging and Sexing Techniques

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