Reconstructing Life History of Hominids and Humans

Douglas E. Crews[1] and Linda M. Gerber[2]

[1] Department of Anthropology and School of Public Health, The Ohio State University, Columbus, Ohio, USA

[2] Department of Public Health and Medicine, Weill Medical College of Cornell University, New York, USA

A B S T R A C T

Aspects of life history, such as processes and timing of development, age at maturation, and life span are consistently associated with one another across the animal kingdom. Species that develop rapidly tend to mature and reproduce early, have many offspring, and exhibit shorter life spans (r-selection) than those that develop slowly, have extended periods of premature growth, mature later in life, reproduce later and less frequently, have few offspring and/or single births, and exhibit extended life spans (K-selection). In general, primates are among the most K-selected of species. A suite of highly derived life history traits characterizes humans. Among these are physically immature neonates, slowed somatic development both in utero and post-natally, late attainment of reproductive maturity and first birth, and extended post-mature survival. Exactly when, why, and through what types of evolutionary interactions this suite arose is currently the subject of much conjecture and debate. Humankind's biocultural adaptations have helped to structure human life history evolution in unique ways not seen in other animal species. Among all species, life history traits may respond rapidly to alterations in selective pressures through hormonal processes. Selective pressures on life history likely varied widely among hominids and humans over their evolutionary history. This suggests that current patterns of human growth, development, maturation, reproduction, and post-mature survival may be of recent genesis, rather then long-standing adaptations. Thus, life history patterns observed among contemporary human and chimpanzee populations may provide little insight to those that existed earlier in hominid/human evolution.

Key words: *biocultural adaptations, evolution, growth and development, senescence*

Introduction

Gerontologists and anthropologists often resort to ethnographic analogy when attempting to reconstruct the life ways and life history (LH) stages of modern humankind's hominid and human forbearers[1–8]. Over the past 6 or more million years (MY) of hominid and 300 or more thousand years (KY) of human evolution, multiple environmental and sociocultural pressures contributed to alterations in human life histories. The complexity of this process suggests that contemporary human and ape populations may not provide direct models of LH, growth and development, reproductive, or sociobehavioral/demographic patterns for either early or late hominid or early human ancestors. Any biocultural interactions that sculpted human life history in the past likely were unique to those phases of hominid and human evolutionary and sociocultural development and are unlikely to be recapitulated in modern settings. Ages of attainment of biological life history phases (e.g.: juvenile, adult) likely varied and changed often during humankind's biophysical evolution, with life history phases apparently more compressed in time during earlier phases.

During earlier periods (circa 4–6 MY ago), hominid LH likely was more similar to those observed among extant non-human apes and those reconstructed for fossil apes and hominids[9–13]. Slowing of early life developmental processes later in evolutionary time (circa 300–500 KY ago) must have resonated through all later life history phases. This process, of extending early developmental phases and thereby life span, is easily mimicked in modern laboratories using rodent, insect, and worm populations. When breed for longevity, these animal models also show slower attainment of developmental LH milestones (e.g.: reproductive capacity, growth cessation) than do their wild-type cousins. As extensions and insertions of pre-mature developmental stages increased the minimum necessary life span (MNLS, the life span needed to complete process of life, e.g.: growth, development, maturation, mating, reproduction, and fledging of offspring[14], among humans, extended survival potential post-maturation followed. That is extension of early life phases preceded late-life survival rather than the converse (i.e. late-life survival occurring before slowing and extension of development). Extended post-mature/late-life adult survival followed the advent of altricial (the opposite of precocial) and slow-maturing offspring, not the reverse as implied elsewhere[1,2,7,15]. Alterations in pre-reproductive human LH phases preceded post-reproductive and late-life survival because resetting of the MNLS allowed human organisms investing in long-term maintenance of their somas to provide greater care for their dependent young and thereby contribute more alleles to future generations.

This paper reviews current and evolutionary patterns of human growth, development, and maturation, along with hypothesized patterns for the evolution of human LH stages in earlier hominids and comparisons of these to extant and fossil pongids and humans. We then examine demographic trends, life expectancies, maximum life spans (MLS), and the MNLS to complete the required tasks of life among pongid, hominid, and human groups. This review sets the stage for examining LH patterns and particularly late-life survival among extant and fossil hominids. It also allows us to examine how well current transitional populations (i.e. sociocultural systems that still retain many aspects of their traditional life ways, but have been influenced by the worldwide monetary- and media-dominated culture) may reflect demographic and survival realities during hominid evolution or provide accurate models for the

evolution of human senescence and LH. Last, we explore how biocultural adaptations and cultural processes help to structure human LH and interact to produce lags in cultural perceptions of aging. These same cultural processes also likely influence current views of LH and senescence among earlier hominids and humans.

Growth and development in hominids

Over the evolutionary history of hominids (4–7 MY, Australopithecus species, 5–4 MY Homo erectus species) and humans (100–500 KY, Homo sapiens species), multiple environmental and cultural pressures influenced variation in biophysical traits such as skeletal shape, dentition, muscularity, height, limb lengths, and encephalization. During this same period, new patterns of growth, development, maturation, reproductive physiology, and reproductive investment emerged in concert with these somatic changes[9,10,13,16–19]. Multiple biocultural interactions also sculpted the human genome to produce increasingly physically altricial, but neurologically precocial newborns[9,17,18,20–22]. Alterations in fetal developmental processes that allowed slower growth and a longer period of life (both absolutely and relatively) from birth to maturation also accommodated rapid neurological development *in utero* and the first years of post-natal life, while delaying multiple aspects of prenatal growth to the postnatal period of life compared to other apes and earlier hominids. This process extended the length of time needed (temporal investment) to attain specific LH milestones (e.g.: menarche, adult body size and function, age of maximum reproductive potential (MRP)) to around twice those observed for extant chimpanzees and the time until completion of reproductive effort/parental investment to over 3 decades[13,17,19–23]. Among humans, gestation length (about

260–280 days) does not differ greatly from that of other large-bodied primates (e.g.: chimps 240–260, gorillas 260–280 days), although all are significantly longer than those among smaller-bodied primates (e.g.: baboons, 175–180 days)[23]. Although humans and other apes appear to have retained a common gestational length (a plesiomorphic trait), human fetuses show very different patterns of growth and allocation of energy to somatic structures particularly in the last trimester.

Due to intrinsic (allometric) relationships among gestational size, post-natal growth rates, age of attainment of mature adulthood, commencement of reproductive effort, and length of parental care needed to fledge human offspring, extension of early growth and development increases the MNLS[14,15]. Whether earlier life phases were expanded, extended, or new ones were inserted as described by Bogin[16] and by Bogin and Smith[9,10], pre-reproductive phases of human life are absolutely and relatively longer than observed among other large-bodied apes (i.e.: chimp, gorilla, orangutan) with similar gestation lengths. Lengthening of biophysically determined LH stages seems to have been most concentrated in the immediate post-natal or infant and child stages and the pre-reproductive or juvenile and adolescent stages[9,10,19]. Increased temporal investment (i.e.: amount of time devoted to a LH stage) in growth, development, and maturation during pre-reproductive life necessitates extensions of all later phases of life and allometrically extends the species MNLS. This process characterizes most mammals, particularly primates[24,25]. Among extant large-bodied primates, only humans show differential investment of fetal resources into neurological structures to the detriment of other somatic tissues during the last trimester in utero[17,19,21]. Allocation of limited fetal resources to the

developing neurological system late in gestation (third trimester) contributes greatly to the production of secondarily altricial human newborns (other apes are physically precocial at birth, whereas humans are physically altricial, suggesting that the human/ape ancestor was precocial and humans developed altricial newborns after their phylogenetic split from other apes[18,22], for further details). Allocating fetal energies to neurological structures at the expense of somatic structures produces less physically developed fetuses, requires greater physical growth post-natally, increases the need for parental care and investment during life, and extends the MNLS. Selective investment in neurological development by human offspring continues throughout the first 5 years of life, as growth rates of neurological structures outpace those of general somatic growth[10,16,19,20,23].

Compared to other large-bodied primates and mammals, humans spend a greater proportion of their total life spans as immature pre-reproductives[16,17,19,21,24,25]. Both extending previously existing infant, juvenile and adult phases of life history and inserting new pre-reproductive phases likely contributed to the extension of hominid and human developmental phases[9,10,16,26]. However, these processes may have developed at different periods during hominid and human evolution. Other apes progress directly from infancy through juvenile to adult stages[9,10]. Only humans show 3 stages, childhood, juvenile, and adolescent, rather than just one between infancy and adulthood, and allot each stage specific developmental tasks[9,10,16,21,27,28]. During infancy (0–1 years) and childhood (ages 1–5 years) development of the brain and related neurological tissues is most rapid, reaching 85% of adult weight and size before the end of 5 years and being complete by age 7. The juvenile phase (ages 6–11) is marked by the lowest rates of general somatic growth seen before the end of maturation. This reduction in overall growth preceding adolescence (ages 12–18) and the pubertal growth spurt also represents a low point in energy inputs needed to maintain and grow the soma[9,16]. During this period, the dentition matures, while physical, physiological, and cognitive abilities take on more adult forms[16]. This brief lull in growth rates is followed by the pubertal growth spurt and adolescence, during which the soma proceeds to full adult height and the reproductive organs mature.

Many mammals show a pubertal stage in their life histories[12,16]. However, adolescence in humans is unique because of the rapid and prolonged acceleration in skeletal growth (pubertal growth spurt) and the maturation of the endocrine system that accompanies this final stage of growth[9,10,16]. Either extension or insertion of developmental LH stages has the same result; both require additional time spent in development and allometrically increase the MNLS for the species to be evolutionarily competitive[20]. With longer periods of growth, longer periods of reproductive and parental investment in dependent offspring are required. Consecutive single births over the reproductive span require an adequate number of adult years in which to find a mate(s), reproduce, gestate, rear, and fledge multiple offspring. Multiple endocrine pathways influence the processes of growth and reproductive maturation[29]. Thus, alterations across multiple loci and protein systems may lead to extended growth and development and consequently alter the survival potential of organisms. Patterns of growth and development are likely to respond rapidly to even minor alterations in aspects of endocrine regulation[29]. Alterations in hormone receptors, intercellular transmitters, or circulating levels of hormones may potentiate rapid alterations in LH variables[29]. Those that im-

prove defenses against external and internal hazards, improve systemic communication, provide for better somatic integration and stability, or allow greater organ capacity leading to improved performance and physiological function may increase life span potential while also altering patterns of growth and development.

One way for organisms to successfully compete evolutionary is by providing themselves with redundant organs and overlapping physiological systems that allow them to better maintain their somas and survive to and beyond the species MNLS. One of the surest ways to assure reproductive success and relatively high fitness is by providing sufficient physiological integration, redundancy, and defense such that the soma's reserve capacity exceeds that needed in the current environment. When the environment becomes less stressful (such as with the introduction of culturally-based adaptive systems) this excess biophysical capacity remains available for somatic maintenance and reproductive investment. This suggests that human longevity today may reflect the advantages culture provided for retaining somatic re- serve capacity and maintaining the soma. A similar model applies to the culturally developed environments humans have created for their favored domestic animals (e.g.: dogs, cats, rodents) that survive as much as 10 times longer than do their wild counterparts.

Precisely when during human evolution altricial pre-natal development and slowed post-natal growth relative to other hominoids and hominids came to characterize the lineage is not completely clear. Even Neanderthals and their contemporaries appear to have had variable patterns of dental eruption and long bone growth, with the former apparently growing and developing more rapidly[11,13,18,22]. Growth patterns of Neanderthals and sa-

piens also differ from those of modern extant chimps and gorillas, while multiple different patterns characterize extant large- and mid-sized primates[12,7,21,23]. Given the rapidity with which altered endocrine regulation may affect growth patterns, recent alterations may explain differences between Neanderthals and sa- piens in rates of growth and timing of tooth eruptions, and why earlier hominids differed from modern apes. The fully human pattern of growth and development may not have been part of the adaptive suite of the joint ancestor of evolutionary modern humans and Neanderthals of about 300 KYBP. It may have arisen later, perhaps as late as 100–300 KYBP just before modern sapiens migrated around the world, or even later, within the past 30 KY or so. Earlier hominid forms were more dentally advanced and apparently matured at earlier ages. Earlier dental/physical development often coincides with more rapid somatic development, early attainment of reproductive maturity, high rates of reproduction, shorter-term parental investment in offspring, and shorter life spans among contemporary mammals[25].

During hominid/human evolution, the length and pattern of development, maturation, reproduction, and adult survival all appear to have been altered from the ancestral (plesiomorphic) condition. All evolutionary changes are specific to the prevailing environment, ecological and social setting. Alterations in human life history traits appear to have developed when prevailing mortality hazards, cultural competencies, and physical environments were quite different from those among contemporary human or large-bodied primate populations[24,25] and Charnov[15] review relationships between LH parameters and mortality hazards). In general, compared to other large-bodied mammals, among extant large-bodied primates LH generally is characterized

by late reproduction, large investments in a few offspring, birthing of single infants sequentially over a reproductive span of 10–30 years, and life spans of 30 years and more (synaphomorphic traits with humans). Among later hominids (i.e.: *Homo erectus*) and humans (i.e.: *Homo sapiens*), physical and physiological manifestations of senescence (old age) must have been altered many times as individuals with genetic predispositions to long life occurred with greater frequency, out-competed those predisposed to shorter lives, and through cultural mechanisms created an environment with lower mortality hazards. Unfortunately, the environmental/ecological settings and cultural mechanisms that influenced human life history during this period no longer exist. In the contemporary world, human life history unfolds in settings of socioeconomic rather than environmental extremes, with multiple and variable life styles from sedentary with abundant calories to those of poverty, malnutrition, and constant labor. None of these reflect the ancestral condition or patterns of LH and survival that prevailed even 30 KYBP, let alone during earlier periods in hominid evolution.

Relationships between life history and life span

Human LH differs significantly from extant and fossil apes, and fossil hominids, Erectines, Neanderthals, and early modern humans. This is particularly so for patterns of prenatal and postnatal growth, development, and maturation, and age-related reproductive and parental investment. Available fossil elements suggest more rapid maturation among earlier hominid forms including Neanderthals. If true, they likely differed in their pattern, degree, and timing of reproductive effort (including age of first reproduction) and parental investment as well. Further, based upon observed allo-

metric relationships among rates of maturation, body size, reproductive patterns, and life span in living mammals, these earlier hominids also would have senesced more rapidly than modern humans, with few surviving their 4th decade of life[15,30–32]. Given earlier reproduction and short life spans, survivors to their mid- to late-30s likely would already be grandparents, and few individuals would have survived to 40+ (similar to extant large-body primates).

Among primates, particularly humankind but also most non-human primates, both life span extension and extended periods of infant and juvenile growth have been stable evolutionary strategies. Primates exhibit a suite or matrix of LH characteristics that set them apart from most similar-sized mammals. This matrix includes a high proportion of life spent as a pre-reproductive, slow somatic development, female reproduction through the 3rd and 4th decades of life (among species that live so long), single births, few offspring over the reproductive cycle, long-term and efficient parental care, and frequent survival into the 4th decade of life. Together these LH traits allow non-human and human primates in generally to show positive deviations from life expectancy and maximum life span estimates based upon regressions of body size, encephalization, and lifetime energy expenditures among mammals[30].

Humans have elaborated these features the most. Their slowed physical development and rapid neurological development in utero and during early life produced secondarily altricial newborns (Smith suggests that since most large-bodied apes bare physically precocial infants (plesiomorphic condition), the altricial newborns of humans (an autapomorphic trait) must have been derived from the basic large-bodied ape trait)[18] and extended offspring dependency. These alterations produced the new develop-

mental stages, childhood and adolescence, between infancy and adulthood and necessitated a pubertal growth spurt to attain adult height during adolescence (all autapomorphies). This late attainment of reproductive maturity and commencement of reproductive effort prepared humans for a long period of reproductive effort (fertility of women up to 35+ years, of men 60+ years). Interrelationships among hormones, growth rates, patterns of parental care, and the development of cultural competencies that ameliorated mortality hazards provided the bases for these alterations. Neither cessation of reproduction in mid-life among women (menopause) nor late-life survival between both sexes is necessary adaptive aspects of this primate adaptive matrix (Note: Late-life may be said to start even later today. For example, it may begin at age 75 when half of that living will is dead. It may have commenced even earlier, perhaps as early as age 40 among the first fully modern humans). Late-life survival is the byproduct of humankind's unique adaptive strategies that included culturally maintained environments and altricial offspring (autapomorphies).

During the evolution of the hominids, multiple environmental and biocultural pressures combined to produce the current matrix of human LH traits that is shared with no other known mammal or primate[9,10,12,16,19–21,27,28]. Components of this matrix neither arose in unison nor did they all evolve at the same pace. Today, these related trends allow height to increase through the early 20s; life spans to average over 70 years, approaching 85 years in select settings; maximum achieved life span to exceed 122 years: and 90% of persons born to survive to their 50th birthday in more cosmopolitan settings. Precocial at birth, non-human large-bodied apes grow more rapidly, attain adult size earlier in life, reproduce at earlier ages, die at average ages when many human females continue to reproduce, and seldom survive beyond age 50, the age at which menopause is observed among most women in contemporary populations. Still, compared to other mammals, non-human primates show aspects of the primate matrix, few offspring, slow growth, late reproduction, and high parental investment, in common with humans.

Lengthening of the pre-mature developmental period of growth increases both the age at maturity and the age at which reproduction may commence. Extension of organismal growth is a feasible evolutionary strategy only when organisms are assured of low mortality hazards not only during development, but also during mature ages to allow sufficient time to complete reproductive tasks such as parental investment[14,15,25]. One simple way to slow development in a complex organism is incremental accelerations and retardations in the pace and/or timing of endocrine regulation of DNA activity, protein synthesis, and cellular responses to hormones[29]. Altered hormonal regulation of growth phases [similar to but less severe than seen during intrauterine growth retardation, starvation, and numerous genetic diseases affecting growth[33]] may easily alter both the pace and length of growth, maturation, and reproductive effort.

Life history reconstructions for hominids

Numerous estimates of average and maximum life spans of our hominid and early human ancestors along with reconstructions of their life histories have been published[5,8,13,18,19,22,30,32,34]. Often these are based upon estimates of mortality and survival patterns observed among contemporary, historic, and prehistoric populations for which large living or skeletal samples are available. Estimates from contemporary populations are in turn

used to reconstruct demographic and life history estimates for earlier hominid populations. However, developmental, reproductive, and survival patterns among humans of 100–300 K years ago with a different level of sociocultural development, less developed tool kit (technology), and unknown cultural behaviors, beliefs, and expectations are not likely to be reflected in any contemporary human populations. Comparisons of fossil materials to modern humans and apes, suggest that Neanderthals and erectines matured earlier than do boys and girls today[9–11,13,16]. Earlier maturation suggests they also began reproducing at earlier ages. If they were reproducing, as early as extant apes (ages 7 or 8), hominid females of a million or even 100,000 YBP easily could have been grandmothers in their early 20s. Those of more recent times such as archaic *sapiens* and *neanderthalensis* may have matured more slowly than earlier forms, but still much faster than modern humans. Today, large-bodied non-human female apes reproduce as early as 7 years, show their highest fertility in their late teens, and reproduce continually until about age 30–35, after which they gradually cease reproduction as their ovaries fail to produce fertilizable ova[16,17,19,21,30,34]. Such a reproductive pattern may represent to some degree the plesiomorphic condition among early hominids.

Based upon estimated average and maximum life spans for fossil and extant primates and hominids[30–32,35,36], over most of hominid evolution few individuals likely survived long enough to experience the loss of fecundity characteristic of all contemporary mid- to large-bodied mammals who live beyond about 30–35 years[37,38]. Even during the 19th century, high female mortality prevented many women from attaining menopause. For example, even as late as 1891 in India only 40% of women survived to age 30, 30% to age 40, and 20% to age 50[39]. Demographic data, available for many populations worldwide, suggest that over the past 6–7 MY of hominid and 100–300 KY of »modern human« evolution, mortality hazards at all ages have declined. Apparently sometime around or after the advent of fully modern humans, mortality hazards had declined so greatly that growth, development, and attainment of maturity could be extended to encompass 2 decades of life, compared to the shorter spans that apparently characterized earlier fossil hominids and the less than 10 years that characterize modern large-bodied apes[9–11,13,16]. Extension of infant/child development and dependence necessitates that parental investment be available during this period of dependency. In a species that takes almost 2 decades to reproduce, commonly bares only one offspring per pregnancy, experiences multiple pregnancies over its reproductive span, and must invest in rearing multiple offspring over an extended period, the MNLS to provide sufficient opportunity for reproductive success must be extended through at least the 3rd decade of life. As longer survival became necessary to rear more dependent offspring, women who could survive longer would have a reproductive advantage. Based upon the fossil record, all of these changes appear to have occurred relatively recently[9,10,13], but before the advent of either horticultural/agricultural or herding life styles. Even so, our ancestors' lives were short and precarious compared to today's 122+ year maximum life span and 85-year life expectancies. Still, even with average life spans around 25 years, women of these early human populations would have substantial opportunities to invest in their grandchildren and men opportunities to sire offspring after their prime physical years, arbitrarily set at 35 years[20,40].

Projecting current demographic distributions of the few remaining chimpanzee and human foraging populations onto

hominid and early human ancestors likely will yield misleading patterns of survivorship and expectation of life. Reduction of human mortality hazards during developmental and reproductive phases was a gradual process tied to many and variable evolutionary and biocultural processes. Included among these were increases in encephalization that allowed improved control of the environment, and the invention and elaboration of material culture, language, and sociocultural structures promoting the welfare of infants, juveniles and adults alike. Late-life survival as seen today seldom (if ever) occurred among any human population before the advent of settled agriculture. Such extended late-life survival also does not even exist among extant apes; even in captivity their MLS is well under 60 years. In wild settings, large-bodied apes may survive to 35 years, but only 35–38% survive into their mid-20s, and their average age at death is a mere 25 years[9,23]. In captivity, survival to the mid-40s is more common, but living past 50 years is not. Nor are the few remaining remnant populations of chimps and other apes valid models against which to test proposed models for the evolution of human LH traits, as has been proposed elsewhere[7]. Living ape populations are as far removed from the common ancestor of humans and apes as are humans and they likely have evolved their own suite of LH traits since the hominid-pongid split. Late-life survival of any population can only be objectively estimated based upon demographic profiles of the specific population. Based upon estimates from fossil materials, few Neanderthals and/or early humans survived to age 35; among earlier hominids even fewer did so[30–32,36].

Giant tortoises (200 years), elephants (77 years), sturgeons (100 years), whales (80 years), birds (80 years), and humans (122 years) are numbered among the long-lived species. Each species shows at least one LH trait found only among K-selected species, but is not shared with short-lived species. Tortoises, sharks, and sturgeons all show increasing probabilities of reproductive success with increasing age, elephants and whales show long gestation times, large infants, slow development and extended parental care, while birds avoid predators by flying and have very low rates of reproductive success. Humans show dependent offspring, slow maturation, and unique biocultural influences on reproduction and survival. Elaboration of culture as a major adaptation, slow development both *in utero* and post-natally, encephalization, and prolonged reproductive effort for decades beyond first reproduction produced unique pressures on hominid and human LH and somatic development. These unique pressures produced a LH requiring a MNLS of about 40 years. As stated earlier, life need be only sufficiently long to insure reproductive success, since continued survival alone does not provide a return on somatic investment[14]. For humans, material culture, language, and socioculturally elaborated life ways, including long-term care of family members and late-life reproduction by men were included in the matrix that helped extend the MNLS. These attributes of human reproductive effort made survival beyond the age when most female mammals show fertility declines a time of continued male fertility, and reproductive effort, through parental and grandparental investment, for both sexes[20,40].

Cultural influences on human life span

By providing environments in which long-lived phenotypes could flourish and express their life span and reproductive advantages, culture provided earlier hominids and humans, and continues to provide modern humans, multiple fitness advantages. Cultural innovations that reduced humankind's extrinsic and intrin-

sic mortality hazards allowed longer-lived genotypes opportunities to express their innate propensities for longer life and thereby increase their total relative fitness (total fitness = reproductive success + inclusive fitness). Either continued reproduction by long-lived men or investment in kin by long-lived women and men helps increase the representation of longevity-enhancing alleles in the gene pool. Shorter-lived genotypes, less capable of surviving over the longer periods needed to fledge altricial offspring, become less represented in later generations.

Cultural competencies possessed by *Homo sapiens* and *Homo erectus* beyond those of earlier forms likely were instrumental in allowing human post-natal dependence to stretch across 2 decades and more of life and directly contributed to the prolongation of somatic survival. *H. erectus* may already have differed from other large-bodied primates by maintaining a home base and by using tools on a regular basis, thereby elaborating culturally patterned behavior. During their evolutionary history, abilities to communicate vocally, use fire, and build and maintain shelters also came to characterize this lineage. By the time of late *H. erectus* and early *H. sapiens*, biocultural evolution had already molded much of the biology that today underlies human senescence and life span in contemporary settings. However, their cultural repertoire continued to be elaborated upon as new forms developed and modern humans emerged. *Homo sapiens* of all forms (e.g.: Neanderthals and sapiens) must have shared, for the most part, the same biology and culture, but perhaps not all the same biocultural pressures of development. Patterns of post-natal growth and development may have differed widely across some closely related subgroups. This supports the idea that LH traits and phases, including timing and patterns of tooth eruption, gestational and post-natal growth rates, period of infancy/childhood, and age of attainment of maturity, may readily differ between closely related sub-species and species. Furthermore, differences in LH patterns may develop between closely related lineages within a relatively short period of evolutionary time[29]. Among humans and their relatives, rates of change in LH traits and the timing of phases have been and continue to be influenced by cultural elaborations. Understanding biocultural influences on the evolution and pacing of human life history is a necessary step to understanding patterns of senescence, mortality, and life span in modern humans. Part of this modeling will depend upon better understanding of how material culture and sociocultural beliefs buffered evolving hominids and humans sufficiently from the vagaries and risks of the physical environment to allow opportunities for slow maturation, long-term parental investment, and late-life survival, and the influences these had upon birth and death rates and distributions of populations across age and sex categories.

Demographic and cultural influences on life history stages

Western European definitions of old age developed when life span averaged only 25 years, survival to age 50 was still an exceptional achievement, and few ever lived to their 65th birthday[41]. Today, life expectancy at birth in many cosmopolitan settings averages over 75 years, with Japanese women approaching 85 years. Living to age 65 is no longer remarkable; over 80% of persons now born in many contemporary settings may expect to survive so long. Similarly, forced retirement at age 65 is an anachronism of the 1930s, enshrined forever in the 1935 US Social Security Act. At that time, life expectancy was only about 60 years and less than 30% of United States citizens could expect to survive to collect benefits. Only

during the 20th century has life expectancy exceeded 50 years for large segments of the human population. Thus, it is not likely that earlier in hominid/human evolution any large proportion, let alone a majority, of individuals survived to achieve their 50th birthday[31,32,41,42]. Models of senescence positing life expectancies of over 40 years among pre-modern and early modern humans[3–7] are premised on mortality hazards similar to those observed among contemporary transitional populations having existed in past populations. However, even in settings such as the US and Europe, average life expectancies over 50 years were never observed prior to the late-19th century. It was the mid-20th century before such life expectancies came to characterize most populations, for example India where infectious diseases still compete as leading causes of death today.

In all populations with recorded histories, some members appear to have lived beyond 65 years. Still, over most of human history, survival to age 50 was not common nor was it common among prehistoric skeletal samples[43–46]. Among many contemporary transitional populations survival to age 50 is more common today[8], than it was among the most cosmopolitan of sociocultural settings during the 18th and early 19th centuries[41,42,47]. Most contemporary transitional populations are influenced sufficiently by non-traditional life ways that their survival and mortality patterns do not reflect those experienced even by their grandparents, let alone their ancient or prehistoric forbearers. Given that their survival and reproductive patterns have been influenced by the worldwide monetary- and media-dominated culture, existing transitional groups provide poor models on which to base demographic estimations during earlier phases of human evolution. Mortality hazards and demographic distributions likely have changed many times during hominid/human evolution in response to both biocultural and environmental pressures and these changes likely have been much more rapid in recent millennia than in any previous era.

Cultural lags, adaptations, and biocultural evolution

Given continually changing mortality hazards, population structures, life histories, and survival, when human societies have constructed age classes they likely have been based upon current demographic profiles, individual functional abilities, and leadership qualities, with little attention to actual chronological age. Often these criteria may have been similar to those used for age class constructions and definitions in contemporary transitional populations that use age classes. The major difference is that in earlier settings one likely became an elder at a significantly younger chronological age, as was illustrated by data from American Samoa[48,49].

The island territory of American Samoa provides one example of changing definitions of old age based upon demographic and ethnographic data. There, cultural definitions of old age (matua) changed gradually over the 20th century, lagging significantly behind changes in population age distributions and survival of those aged 40+ years between 1920 and 1990[49]. This period also coincided with a period of rapid, but fluctuating, modernization in the South Pacific islands, including 2 world wars, transfer of oversight of the territory of American Samoa from the United States Navy to the Department of the Interior, and monetization and commoditization of the American Samoan economy. Contemporary Samoan elders were viewed as having invested a lifetime of effort into the traditional Samoan sociocultural system and unwilling to forgo the late life rewards associated with elderhood, status and pres-

tige through titles held within their families and villages. However, it was not just elders who appeared to be retaining traditional definitions of matua. Younger cohorts also did. They seemed to retain their desire for attaining traditional titles and prerogatives, while also seeking monetary and commodity rewards within the wage and market economy[49]. Definitions and meanings of matua within the Samoan sociocultural system appeared to be retained close to their traditional forms; however, during interactions with the market economy these same Samoans participated in a system wherein quantification of age and labor were the norm. These data suggest that multiple, countervailing, and fluid age class systems may exist within a single cultural group, as they do elsewhere[50] (Johnson-Hanks suggests that »age« status of a girl is based not upon »…having achieved a set of life history transitions, but rather the role that she inhabits in a given social interaction.« p. 870). Age classes used within a culture reflect the actors' construction of social reality, and, consequently, how members perceive themselves and others. Similarly, currently prevailing concepts of age, aging, age classes, senescence, longevity, and life span among gerontologists, anthropologists, and others influence how modern researchers interpret LH among the ancestors of modern humans and more traditional-living populations.

Many scenarios developed to explain the evolution of senescence and life span in humankind reflect demographic, reproductive, and social behaviors observed among humans in modern and historical settings. Archaeologists and others long ago illustrated the pitfalls of such ethnographic analogy and reported that social behaviors are not dependent upon material culture[51,52]. Groups sharing material culture do not necessarily share social, religious, or mating behaviors. Historical

contingency, environment, subsistence strategy, and cultural competencies determine prevailing patterns of reproduction, maturation, senescence, morbidity, mortality, and life span. Small sample sizes, lack of representativeness of available fossil materials, and well-documented variances in rates of growth and senescence across known fossil and extant taxa provide only limited data for reconstructing population dynamics or patterns of growth, development, maturation, reproduction, mortality, and senescence among early hominid or *Homo* species[13,18,22]. Even these are seldom reviewed when models of old age, aging, senescence, and life span are developed. Those using survival patterns among modern gathering/hunting/scavenging or subsistence horticultural/agricultural groups to model the life histories of our ancestors are applying a model of lineal evolution to human survival and senescence. Today such populations represent only remnants of their past culture and often are displaced to marginal ecological areas. In addition, they are in close contact with outside societies and have access to modern technologies, lamps, metal utensils, and firearms to name a few. Some models of human LH seem to imply that late-life survival occurred before alterations in human growth and development occurred[1,2,7]. This implies that one late-occurring aspect of this human evolutionary mosaic, longevity, was the driving force in the development of human LH and senescence. More likely various components of human LH developed and shifted at different points in human evolution in response to altering mortality hazards at all ages when new cultural competencies were acquired. Human LH evolution most likely proceeded along a complex and non-lineal evolutionary course, as did human evolution itself.

As the sex and age structure of a population changes, society often redefines

perceptually, behaviorally, and historically constructed age categories to concur with new realities. However, alterations in socioculturally constructed age categories and expectations oftentimes must have lagged behind new patterns of development, maturation, reproduction, retention of physical capacity through adulthood, mortality, and survival. Current sociocultural constructions of age classes generally are predicted upon previously existing patterns of reproductive effort, morbidity, and survival. Often previously validated and subjective cultural impressions of who is aged, elderly, or matua may be retained until new realities are integrated into cultural expectations and obligations[48].

Although societies show wide variation, some may articulate few or none, and others may have fluid or situational categories, in general socioculturally constructed age categories structure the lives of many contemporary peoples and their interactions with others. These sociocultural classes also may structure how we interpret age and age structure among our historical, prehistorical, and evolutionary ancestors and relatives. Early in hominid and human evolution, alterations in life history and extension of the time spent in various life stages likely changed gradually as members of these lineages responded to multiple and variable environmental and sociocultural conditions affecting fitness differentials. As the evolving human lineage diverged from other hominids it is likely that patterns of gestational and postnatal development, reproductive effort, and parental investment diverged also, as appears to have happened between modern humans and Neanderthals. This also reflected differences in other aspects of their LH. Such differences and alterations in survival likely produced a broad range of survivorship patterns across human populations along with multiple definitions of age classes and age-related competencies.

Infant, juvenile, and reproductive adult correspond to what are thought to be biologically determined life history stages in most mammals. Among non-human apes, infants mature directly into juveniles and juveniles into adults without the intervening periods described among modern humans as childhood and adolescence[9,10,16,18,19,22]. In modern humans, life history is divided into 5 basic phases: infants, children, juveniles, adolescents, and reproductive adults, while women over 50 are termed post-reproductive[9,10,16], constituting a 6th age class. In some traditional settings, girls are »married« at menarche, or earlier, and the transition from juvenile to adult often is marked by a rite of passage; boys also may undergo rituals marking their ascent into adulthood. Some religious groups still retain such rituals and continue to use them to establish when children pass into adulthood. Many traditional social-age categories were established when life expectancy was shorter and elders less common. Today in cosmopolitan settings additional social life history stages are being established. These include neonatal, toddler, reproductive adult, mature adult, young-old, old-old, the oldest-old, septuagenarians, octogenarians, nonagenarians, and centenarians. Because the frequencies and proportions of elders have increased dramatically, current cohorts reflect emerging age classes, observed as improved survival produces a major new demographic trend, high proportions of human elders. The slow pace of human growth and development with its multiple accelerations and decelerations, and the large proportion of life devoted to maturation have all contributed to the amount of life remaining after the age of cessation of female reproductive potential (autapomorphic traits), among both men and women. This has created new opportunities for

late- life investment in total fitness by post-reproductive women and men, who may survive past 50 and 60 years while still retaining some reproductive potential.

Discussion and Conclusions

Never before in human history have the majority of individuals born survived through their 4th decade of life. Models of senescence positing life expectancies over 40 years among pre-modern and early modern humans are based on the premise that mortality hazards similar to those observed among contemporary transitional populations existed in the past. However, such extended life expectancies were never reported for any population prior to the late 19th and 20th centuries, they have only come to characterize most populations during the 20th century. Those hypothesizing such long life expectancies in prehistory and earlier are applying a model of »unilineal evolution« to human LH, life span, and senescence. Fossil, archaeological, and historical records do not support that such extended life spans ever occurred in prehistory.

Almost any wild organism may be brought into the laboratory and in a short span breed for either shorter or longer life. This suggests that multiple species have within their genomes variation in survival capacity similar to that of humans. However, no other species has developed sociocultural adaptations to the extent humans have. Through culture, humankind long ago created for itself an ecological niche similar to those provided for today's laboratory animals. This culturally-created niche has allowed humans to express their survival potential and survive sufficiently long to birth altricial offspring well into their 5th decade

of life, sire them into their 9th decade, and invest in offspring and kin across more than 10 decades of life. This long-term survival likely places additional biocultural pressures upon human biology that continue to alter allele frequencies toward greater representation of senescence-retarding alleles. It also reduces the relative fitness of individuals possessing senescence-enhancing alleles such that these types already are poorly represented in current generations. Today, more people survive to age 50 than ever before because both environmentally-mediated and culturally-mediated pressures on biological traits have molded our developmental, and thereby our reproductive and senescent biology. That is, extended late-life survival followed alterations in development, not the opposite. During this evolutionary history biocultural and physiological pressures, along with demographic processes that allowed elderhood to occur and life expectancies and life span to increase, have also been altered such that no contemporary population represents past populations. These processes have shaped human evolution since biocultural interactions, such as today influence human senescence, were first set in motion. Contemporary human populations do not provide direct models or analogies for these earlier evolutionary phases. Those who suggest that survival potentials among fossil members of our lineage were similar to those among any contemporary non-industrial transitional population have failed to incorporate historical demographic profiles of populations, reconstructions of demographic profiles for fossil hominids, and comparative life histories among large-bodied primates and other mammals into their models of human life history reconstruction.

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D. E. Crews

*Department of Anthropology, The Ohio State University, 244 Lord Hall,
124 W. 17th Avenue, Columbus, Ohio 43210, USA*

REKONSTRUIRAJUĆI POVIJEST HOMINIDA I ČOVJEKA

S A Ž E T A K

Aspekti životnog ciklusa kao što su procesi i vrijeme razvoja, dob sazrijevanja i duljina života konzistentno su povezani jedni s drugima u čitavom životinjskom svijetu. Vrste koje se razvijaju brzo obično rano sazrijevaju i rano se razmnožavaju, imaju puno potomaka i kraće žive (r-selekcija), a one koje se razvijaju polako imaju produženo vrijeme rasta prije spolne zrelosti, kasnije sazrijevaju, razmnožavaju se kasnije i manje često, imaju manji broj potomaka (u jednom reprodukcijskom ciklusu često samo jednog), i imaju duži životni vijek (K-selekcija). Općenito, primati su u najvećoj mjeri vrste izabrane K-selekcijom. Ljude karakterizira niz jasno izraženih osobitosti životnog ciklusa. Među njima su tjelesna nezrelost novorođenčadi, spor tjelesni razvoj (i prenatalni i postnatalni), kasna reproduktivna zrelost i kasno rađanje prvog potomka, produljeno preživljavanje nakon dosizanja zrelosti. Danas je predmetom mnogobrojnih pretpostavki i rasprava, točno kada, zašto i kojim tipovima evolucijskih interakcija se ovaj niz razvio. Biokulturne prilagodbe čovjeka pomogle su u strukturiranju evolucije životnog ciklusa čovjeka na jedinstven način koji nije viđen u drugim životinjskim vrstama. Među svim vrstama osobine životnog ciklusa mogu brzo odgovoriti na promjene u selektivnim pritiscima putem hormonalnih procesa. Selektivni pritisci na životni ciklus vjerojatno su znatno varirali među hominidima i ljudima, tijekom njihovog evolucijskog razvoja. Ovo sugerira da današnji obrasci rasta, razvoja sazrijevanja, reprodukcije i post-reprodukcijskog preživljavanja čovjeka mogu biti novijeg porijekla, prije negoli dalekosežne adaptacije. Tako obrasci životnog ciklusa koji se mogu vidjeti u današnjim populacijama ljudi i čimpanza mogu pružiti tek mali uvid u one koji su postojali ranije tijekom evolucije hominida/čovjeka.