

*Original Research Article***Childhood, Adolescence, and Longevity: A Multilevel Model of the Evolution of Reserve Capacity in Human Life History**

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ABSTRACT The grandmother hypothesis (GH) of Hawkes et al. ([1998]: Proc Natl Acad Sci USA 95: 1336–1339) finds that selection for lower adult mortality and greater longevity allow for the evolution of prolonged growth in human beings. In contrast, other researchers propose that the evolution of the human childhood and adolescent stages of life history prolonged the growth period and allowed for greater biological resilience and longevity compared with apes. In this article, the GH model is reanalyzed using new values for some of its key variables. The original GH set the age at human feeding independence at 2.8 years of age (weaning) and used demographic data from living foragers to estimate average adult lifespan after first birth at 32.9 years. The reanalysis of the GH uses age 7.0 years (end of the childhood stage) as the minimum for human feeding independence and uses data from healthier populations, rather than foragers, to derive an estimate of 48.9 years for average adult life span. Doing so finds that selection operated to first shorten the infancy stage (wean early compared with apes), then prolong the growth period, and finally result in greater longevity. The reanalysis provides a test of the reserve capacity hypothesis as part of a multilevel model of human life history evolution. *Am. J. Hum. Biol.* 21:567–577, 2009. © 2009 Wiley-Liss, Inc.

Students of Life History Theory study the evolutionary derived strategies used by species to allocate, "... energy toward growth, maintenance, reproduction, raising offspring to independence, and avoiding death. For mammals, these are the strategies of when to be born, when to be weaned, how many and what type of prereproductive stages of development to pass through, when to reproduce, and when to die" (Bogin, 1999a, p 154). Life history traits have coevolved, often in a manner that results in a complex pattern of trade-offs between investments in somatic growth of the individual, reproduction, and mortality reduction (Stearns, 1992). Living things on earth have greatly different life history strategies, and understanding what shapes these histories is one of the most active areas of research in whole-organism biology. "Human life history ... and much of human culture, is based around the rearing of infants and children necessitated by our unique pattern of growth" (Crews, 2003, p 86). Among the unique or at least unusual features of the human pattern of growth, when compared with the other apes, are neonates with about twice the body mass, more rapid brain growth during infancy, early weaning, a 4-year period of post-weaning childhood feeding dependency with slow growth, and an adolescent life history stage with a skeletal growth spurt (Bogin, 1988, 1999a,b, 2006a,b; Gurven and Walker, 2006; Leigh, 1996, 2004; Walker et al., 2006b).

This article is based on research presented at the workshop "Trade-offs in female life histories: raising new questions in an integrative framework" held at the University of Bristol in July, 2008. The purpose of this article is to raise new questions about the causal relationship between slow and prolonged human growth prior to adulthood and human longevity. Specifically, the goals of this article are two-fold: (1) to reanalyze the mathematical model of the grandmother hypothesis (GH) as presented by Hawkes et al. (1998) using new value estimates for variables in the model; and (2) test the reserve capacity (RC) hypothesis, that the development of increased biocultural resilience during the years of human growth and development pro-

motes greater survival to adulthood, adult survival, longevity, and reproductive success (RS) when compared with any other primate species (Crews, 2003; Larke and Crews, 2006).

The definition of RC as it relates to life history is given by Crews (2003) and Larke and Crews (2006) as those somatic resources that exceed the minimum required for sustaining life and allowing reproduction. Individuals with greater RC have a redundancy and higher quality of cells, tissues, and organ system function and are better able to avoid predation, mount immune defense, recover from trauma, and withstand periods of hunger. These individuals will, on average, have greater RS and in classic Darwinian selection the, "... demand for increased RC to achieve greater RS drives the system" (Larke and Crews, 2006, p 122).

Crews (2003) provides examples of RC building in human beings. One is the proliferation of nephrons in early life in the kidney that allows survival even after removal of one kidney, as well as for good health for several decades after age 40 years, when nephrons decline by 10% each decade. Another example is the production of millions of primary oocytes during human female embryonic/fetal development. Less than 25% of these primary oocytes survive to reproductive maturity at about age 18 years, but even this diminished reserve is more than sufficient for RS. In contrast to the nephrons of the kidney, the store of oocytes is so depleted by age 50 years that the hormonal changes leading to menopause are inevitable and universally experienced in women. These two examples and many others (brain and nervous system, dental

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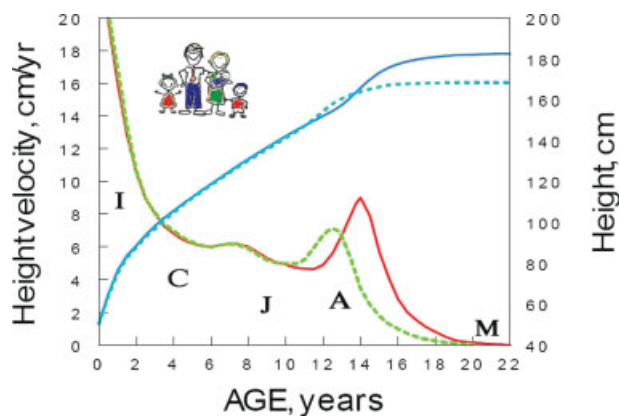


Fig. 1. Distance and velocity curves of growth for healthy, well-nourished human beings. Boys, solid line; girls, dashed line. These are modal curves based on height data for the Western Europe and North America populations. The stages of postnatal growth are abbreviated as follows: I, infancy; C, childhood; J, juvenile; A, adolescence; M, mature adult (Modified from Bogin, 1999a) [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com].

system, immune system, etc.) show that RC building in early life is common to different organs or systems, but that RC decline in these systems can proceed at different rates in later life. A question is, how does the strength of selection vary from early to later life? A model of human life history that includes RC dynamics may help to answer these questions. Such a model is presented and tested in this article.

Brief overview of human life history and fertility

Prior to presenting the RC model some of the key features of human life history evolution are reviewed. Social mammals, such as most primate species, have three postnatal life history stages: infancy, juvenile, and adult (Pereira and Fairbanks, 1993, 2002). Human life history is characterized by the addition of childhood, adolescence, and grandmotherhood (postmenopausal stage) as biologically, behaviorally, and mathematically definable stages of the life cycle (Bogin, 1988, 1999a,b; Bogin and Smith, 1996; Hawkes et al., 1998). The pattern of human life history from birth to adulthood is shown in Figure 1. 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. The human postnatal growth stages of infancy (I), childhood (C), juvenile (J), and adolescence (A) are indicated. The changes in growth velocity are related to trade-offs between energy investment in the body versus other demands of life in a social group. Gurven and Walker (2006) provide a highly useful mathematical quantification of these energy demands and trade-offs. Detailed definitions of these life history stages are given in the publications by Bogin cited earlier. Briefly, in terms of feeding behavior for traditional human subsistence societies, infancy lasts from birth to age 30–36 months and is characterized by feeding via lactation, with complimentary foods added by the end of the first year (Sellen, 2006, 2007). The transition to childhood is characterized by the termination of maternal lactation and the completion of deciduous tooth eruption. The limi-

tations of a deciduous dentition and small digestive system require that children eat easy to chew and nutrient-dense foods. Older members of the social group acquire, prepare, and provision these foods to children. This style of cooperative care frees the child's mother from lactation and much care and feeding of the child. The mother may then accumulate new RC, such as fat stores and bone mass lost during pregnancy and lactation, and in time, devote her resources to a new pregnancy and lactation of a new infant. The childhood stage ends at about age 6.9 years.

The juvenile stage spans age 7.0 years to onset of the adolescent growth spurt (approximately age 10 for girls and age 12 for boys in healthy, well-nourished populations). Juvenile mammals are sexually immature, but physically and mentally capable of providing for much of their own care (Pereira and Fairbanks, 1993, 2002). Human juveniles have the physical capabilities to eat the adult-type diet, as the first permanent molars and the central incisors have erupted by age 7 years. Human juveniles may produce some of their own food intake but still require provisioning to achieve energy balance. This is the case in many traditional societies, such as the Ache, Hiwi, !Kung, and Maya (Kaplan et al., 2000; Kramer, 2002), as well as in historical and contemporary urban-industrial societies (Bogin, 1999a, 2001). In many human societies, juveniles perform important work including food production and the care of children ("babysitting" sensu Weisner, 1987).

Adolescence includes the years of postpubertal growth (approximately ages 10–18 years for girls and ages 12–21 years for boys, including the adolescent growth spurt). Human skeletal growth velocity in body length stands in contrast to all other mammals, even the African Apes. The childhood stage of relatively moderate and stable growth velocity and the adolescent growth spurt in virtually all skeletal dimensions are not found in other mammals, even the apes (Bogin, 1999a,b). Modal growth curves for body length (growth of the summed length of crown-to-rump, thigh, and leg) for the chimpanzee (*Pan troglodytes*) are shown in Figure 2 as a contrast with the velocity growth curves of humans shown in Figure 1.

Human female reproductive maturity takes place during the later part of the adolescent stage. Healthy, well-nourished girls achieve physiologically defined fecundity (i.e., 80% of menstrual cycles release an ova) at a median age of 18 years. The world-wide median age of first birth is age 19 years (Bogin, 2001). Boys may produce fertile spermatozoa by 13.5 years, but are not likely to become fathers until after age 20 years (Bogin, 1999a). Even though sexually mature and capable of producing sufficient quantities of food to exceed their own energy requirements, teenage boys and girls remain immature in terms of sociocultural knowledge and experience (Bogin, 1993; Kaplan et al., 2000; Schlegel and Barry, 1991). Human adolescents in all societies, both boys and girls, engage in many types of economic, social, sexual, and ideological apprenticeships that lead to greater adult reproductive and sociocultural success (the Discussion section of this paper provides more detail). Adolescence ends with the eruption of the third molar (if present) and the termination of growth of the skeleton.

The childhood and adolescence stages of human life history evolved due to the selective advantages for increased reproductive fitness (Bogin, 1988, 1997, 1999a,b, 2006a,b). In essence, this reproductive fitness hypothesis predicts that childhood and adolescence: (1) enhance the fertility of

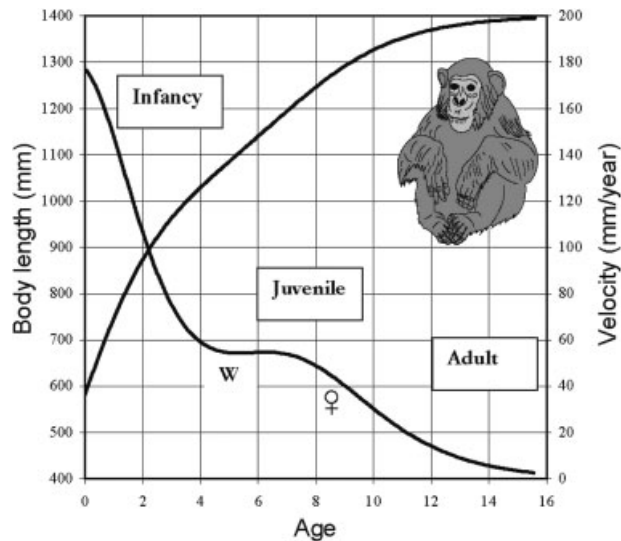


Fig. 2. A model of distance and velocity curves for chimpanzee growth in body length (growth of the summed length of crown to rump, thigh, and leg). This is based on the longitudinal study of captive chimpanzee growth conducted by Hamada and Udono (2002). In the wild, weaning (W) usually takes place between 48 and 60 months of age (Pusey, 1983). (Reproduced with permission from Bogin, 2006a, In: *The Evolution of Human Life History*, Hawkes K, Paine RP, editors, p 197–230, © School of American Research).

mothers, (2) improve the survival of mothers, and (3) lower the mortality of offspring prior to adulthood. The embodied capital hypothesis of Kaplan et al. (2000, 2003) encompasses some of these same principles. The major difference is that the embodied capital hypothesis emphasizes that survival and RS are a function of delays in growth leading to increases in body size and learning (Gurven et al., 2006; Kaplan et al., 2003). In contrast, Bogin's reproductive fitness hypothesis emphasizes that early weaning and the transfer of responsibility to other social group members for the feeding and care of children frees the mother to reproduce more quickly than any ape, without increasing the risks for morbidity and mortality of the children (Bogin 1997, 1999a, 2006a,b). The benefits for increased brain growth and learning are important, but secondary, outcomes of the selection for increased fertility of the mothers.

The first point of Bogin's reproductive fitness hypothesis, enhanced maternal fertility, is dependent on several factors. One factor is the age-specific fertility rate (ASFR). Figure 3 illustrates the ASFR for a captive group of chimpanzees (Littleton, 2005), the combined ASFR for six wild-living or free-living chimpanzee groups (Emery Thompson et al., 2007), and four human societies (Ellison and O'Rourke, 2000). ASFR, on the y-axis, indicates the number of births per female of a given age, per year, per 1,000 females in the population. The captive chimpanzees reside at an Australian zoo where they have been allowed natural breeding (no contraception) for the past 50 years. Excellent records by zoo staff ensure the quality of the fertility data. Controlled diets and health care allow for greater building of RC and greater fertility of these captive females when compared with wild-living females. Estimated ASFR for wild-living chimpanzees average about 25–30% lower than rates for the captive chimpanzees until age 30–

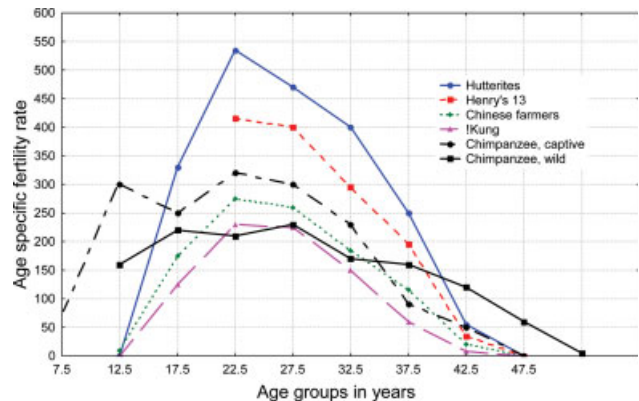


Fig. 3. ASFRs for captive chimpanzees and for married women in natural fertility populations. The captive chimpanzee data are from Littleton (2005). The wild chimpanzee data are the combined values for six populations analyzed by Emery Thompson et al. (2007). The human data are redrawn from Ellison and O'Rourke (2000). Despite lower ASFR for the Chinese farmers and the !Kung, these human groups have shorter birth intervals and higher offspring survival than chimpanzees. In total, all of these human groups have greater lifetime offspring production and survival to adulthood than any chimpanzee population (Emery Thompson et al., 2007; Kaplan et al., 2000). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com]

35 years. After age 35 years the ASFRs for the wild-living are greater, but still low and declining.

The human groups illustrated in Figure 3 are so-called natural fertility populations. These are defined as societies without conscious family size limitations due to contraception or induced abortion, but in practice all human societies employ some forms of "family planning" (Benedict, 1972; Bogin, 2001, p 59–62). Only married women are represented in this figure, because in natural fertility populations it is more likely that married women will reproduce than unmarried women. The Hutterites are a religious order in North America who prize high fertility of women. Adherents marry after age 15 years and there is a cultural proscription against any form of birth control. The curve labeled "Henry's 13" represents 13 natural fertility small societies studied by the French demographer Louis Henry (1961), who first noted the relatively constant shape of the ASFR in different human populations. The "Chinese farmers" represent a group of rural villagers and the "!Kung" are a society of hunters and gatherers living in the Kalahari desert of Botswana in southern Africa. Although the rural Chinese farmers and the !Kung are considered to be "natural fertility," note that their levels of fertility are lower at all ages than the other two groups. In fact, !Kung women are known to use herbal medicines and other means to prevent or terminate pregnancies (Howell, 1979) and also suffer from fertility-limiting sexually transmitted disease (Wood, 1994).

At one or more ages, all of the human groups have greater ASFR than the wild-living chimpanzees. Humans reproduce approximately 1.9 times faster than wild chimpanzees because of shorter birth intervals (Walker et al., 2008). The interval between successful births averages only 3.4 years for women in the Ache, Hadza, Hiwi, and !Kung forager societies (Kaplan et al., 2000). Women living in agricultural societies, such as the Hutterites and Henry's 13, may reduce the birth interval to 2 years, or

less. Chimpanzee females average 5.9 years between successful births (defined as survival to at least age 4 years for the infant) at the six African research sites reviewed by Emery Thompson et al. (2007). The greater ASFR of the captive versus wild-chimpanzees prior to age 35 years is also due to shorter birth intervals; the captive chimpanzees average 4.1 years between successful births. The greater ASFR of wild-living chimpanzees after age 35 years is likely due to the fact that only a few high-ranking, and very reproductively successful, females survive past that age (Emery Thompson et al., 2007).

The advantage in ASFR of some human populations over chimpanzees is due to the evolution of human childhood allowing earlier weaning—point one of Bogin's reproductive fitness hypothesis. The second point is that the new human life history stages enhance the survival of mothers. The mean age at first birth is 19 years for human women in foraging societies. These women can expect to live an additional 54 years and be fertile for about 20 of those years (Kaplan et al., 2000). In contrast, wild chimpanzee females have a mean age at first birth of 14.3 years, and can expect only 30 more years of life after first birth (Emery Thompson et al., 2007; Kaplan et al., 2000). The difference in life expectancy is due to higher female chimpanzee mortality at every age after first birth and this reduces total chimpanzee fertility when compared with humans (Goodall, 1983; Nishida et al., 1990; Teleki et al., 1976). The Discussion section of this article provides more detail about this part of the reproductive fitness hypothesis in relation to building RC, human cooperative breeding, health, and longevity.

The third part of Bogin's reproductive fitness hypothesis is the survival of the young to adulthood, when the young begin their own reproduction. The average total fertility rate for captive and wild chimpanzee populations is 6.7 offspring per female (Littleton, 2005). Typically, only two of these offspring, or about 30%, live to adulthood (age 15 years, Pusey, 2001). In contrast, between 50% and 60% of live-born human offspring survive to adulthood in contemporary foragers, such as the Dobe !Kung, Hazda, and Ache (Blurton Jones et al., 1992; Hill and Hurtado, 1996; Howell, 1979). In agricultural and industrial societies the rate of human survival is greater, reaching more than 99% in the wealthy nations today (Gage, 1998, www.census.gov). Human survival to reproductive age is the best of any animal species and chimpanzee survival is the second best of all primate species (Bogin, 1999a). Elephants and whales appear to have greater survival to adulthood than non-human primates (Wachter and Finch, 1997).

Reasons for such extraordinary human survival include growth of a large complex brain and what those brains can do, such as mapping social ecology, language, and symbolic reasoning (Deaner et al., 2003; Locke and Bogin, 2006), and cultural behavior, such as marriage and kinship. But, it is the premise of this article that big brains, language, and kinship are secondary outcomes of the evolution of childhood and adolescence. The primary selective value for these new life history stages is the building of RC leading to reproductive and survival advantages for adult women and men.

Reserve capacity model

Physiological systems of the mammalian body must grow, develop, mature, and perform at some minimal level for postnatal life of the individual to be possible. These

systems (nervous, pulmonary, cardiovascular, kidney, etc.) usually, "...overshoot their physiologically necessary capacity (NC)..." during the preadult and early adult years (Crews, 2003, p.76, italics original). By overshooting the NC an individual has RC that may be channeled into trade-offs between greater growth, immune function, mating behavior, and/or reproduction and parental investment. This relationship may be expressed as:

$$\text{Reserve capacity (RC)} = \text{Total achieved capacity (TAC)} - \text{Necessary capacity (NC)} \quad (1)$$

Crews (2003) propose that human RC is greater than that found in other primate species, and many other mammalian species, due to either an increase in TAC, a decrease in NC, or both. Crews provides possible explanations for the increase in human RC, including: (1) the fact that human newborns are about twice as massive as ape newborns, meaning there is greater resource investment via a more efficient placenta during prenatal development; (2) human newborns have the greatest body fat, an energy reserve, of all primates and rapidly gain body fat to age 6 months postpartum (see also Kuzawa, 1998); (3) human brain size is larger than any ape at birth and brain growth continues along a relatively fast, fetal-like trajectory for at least 1 year after birth (see also Leigh, 2004; Martin, 1983); (4) humans grow more slowly and prolong the prepubertal stages of life when compared with other ape species (see also Gurven and Walker, 2006; Walker et al., 2006a,b); (5) humans insert the new life history stages of childhood and adolescence between infancy and adulthood (see also Bogin, 1999a).

Expressed in terms of the life history stages of RC building, the Crews model may be expressed conceptually as follows for non-human primates:

$$RC_t = \text{gestation} \pm \text{infancy} \pm \text{juvenile} - \text{adult} \quad (2)$$

For the human species the formula is:

$$RC_t = \text{gestation} \pm \text{infancy} \pm \text{childhood} \pm \text{juvenile} \pm \text{adolescence} \pm \text{early adult} - \text{later adult} \quad (3)$$

where RC_t is reserve capacity at age = t , and the life history stage of gestation, infancy, etc. are developmental periods when RC may be gained or lost. Equations (2) and (3) assume that maternal investment and RC accumulation during gestation is positive only. Dire situations in which embryonic or fetal reserves are depleted prior to birth are likely to preclude survival. Life stages after birth may have positive or negative investment into RC building, but the investments cannot be less than NC at any stage. For humans, RC building may continue into early adulthood, ending by age 25–35 years when senescent declines are noted in many body systems (Crews, 2003). Women in traditional societies, and female primates in general, are likely to experience declines in RC with their first pregnancy. The demands of reproduction mean that RC is lost via pregnancies, lactations, and other maternal investments in offspring (Altmann and Alpert, 2003; DaVanzo et al., 2008; King, 2003). Because of the loss of RC with pregnancy and birth, the age at first reproduction for women is equivalent to the age at onset of aging (Hayflick, 2007).

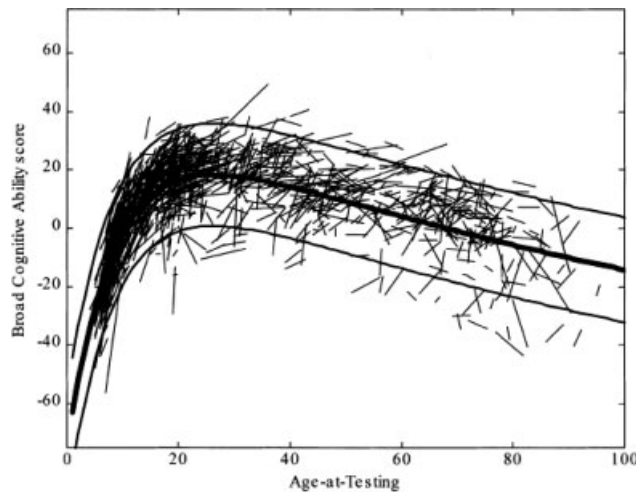


Fig. 4. Age changes in broad cognitive ability (BCA). The smoothed curves estimate the mean and 95% confidence boundaries around the scores for latent variance components in BCA, which peaks at age 26.2 years. Also shown are the individual line plots of the longitudinal data to illustrate the goodness of fit of the fitted smoothed curves. (Reproduced with permission from McArdle et al., *Dev Psychol*, 2002, 38, 115–142, © American Psychological Association).

Longitudinal change in the growth and decline of intellectual abilities over the life span is an important human example of building both NC and RC. McArdle et al. (2002) analyze a sample of about 1,193 individuals, each of whom was tested on two occasions with the Woodcock–Johnson Psycho-Educational Battery, Revised (WJ-R), “... a wide-range comprehensive set of individually administered tests of intellectual ability, scholastic aptitude, and achievement” (p 119). The participants were aged 2–95 years old at the time of testing. Longitudinal structural equation modeling was used to estimate age changes in test scores. The findings for broad cognitive ability (BCA, the average of seven composite scores of intellectual functioning) are shown in Figure 4. The age trends estimate that cognitive capacity reaches its zenith at age 26 years and then declines. Equally important to note is the variance among individuals as estimated by the 95% confidence interval. This interval shows an approximate 40 point range by age 20 years. Those individuals at the higher boundary, that is those with greater RC building before age 20 years, may still have positive BCA scores up to age 100 years. Those with average BCA development will deplete positive RC for BCA by age 60 years. This is a striking range of difference and has important implications for cognitive performance, human capital formation, adult economic and social abilities, parental and grandparental investment in offspring, and healthy aging (see also Allen et al. 2005).

The human species has more life stages than any other mammal and more time for growth and development than any primate. If environments are favorable, with excesses of physical, biological, social, and emotional resources above those needed to maintain NC, then human beings have the potential for greater RC at the start of adulthood, and reproduction, than any other primate. Adverse environments will cause a reduction of RC, usually expressed in reduced body size, work capacity, cognitive functioning, RS, and longevity (Bogin et al., 2007).

The package of human species-specific characteristics and RC building potential, “... represent a massive alteration in the life history of large-bodied primates” (Crews, 2003, p 85). Crews and other researchers (e.g., Austad, 2006; Crimmins and Finch, 2006; Gurven et al., 2008; McDade, 2005) hypothesize that this human package of characteristics leads to greater RC in early and later life, “and the unusually long postreproductive survival of women” (Crews, 2003).

MATERIALS AND METHODS

Hypotheses

There are several forms of the GH, and the mother hypothesis, in the literature (Alvarez, 2000; Hawkes et al., 1998; Hawkes, 2006; Madrigal and Meléndez-Obando, 2008; Peccei, 2001; Shanley et al., 2007). Here the focus is on the GH of Hawkes et al. (1998). The GH model of Hawkes et al. (1998) is a highly creative, insightful, and stimulating approach to the mathematical specifications of life history for the great apes and human beings.

A key element of this version of the GH is the proposed invariant symmetrical relationship between the instantaneous adult mortality rate (M) and, “... the period of independent growth, from weaning to maturity,” abbreviated as α (Hawkes et al., 1998). Hawkes et al. calculate the values of α and M for the great apes and humans and show that these values vary widely, are inversely related, and, “Their product (αM) is approximately invariant” (ibid), ranging from 0.44 to 0.46. The symmetrical invariance leads to other predictions for life history variables, including fertility rates.

Theoretical support for the reciprocal relationship between adult mortality and age at first birth is provided by the invariant symmetry models of Charnov (1993, 2001). Hawkes et al. apply these models to the great apes and humans. Their conclusion is that reductions in adult mortality lead to slower aging and longer life spans compared with other primates. Hawkes (2006, p 122) proposes that extension of human female longevity past menopause (cessation of reproduction) evolved, “... when females who were slightly more vigorous as their fertility declined could have a novel effect on their own fitness. Without infants of their own, the older females could help their daughters feed weanlings ... [and] their vigor was represented in more descendants.” In this view, postreproductive longevity was naturally selected and a longer preadult period of growth and development, including the human childhood and adolescence stages, was a consequence.

The RC hypothesis, in contrast, posits that it was the evolution of the childhood life history stage that is the primary impetus for the increase in women’s fertility, survival, and longevity. The RC hypothesis predicts life history trade-offs using a multilevel evolutionary model (Wilson and Wilson, 2007 review these models in the context of sociobiology). The first level is that of the parent–offspring, in that early weaning leads to increased RS of the mother, but at the risk of starvation, reduced RC, or death for the child. This leads to second level of trade-off, social group versus child. A new pregnancy for the mother requires that her current child receive food provisioning and care that is provided by other social group members. In human societies, these people may be genetic or social kin. Their investments come at some cost to themselves in

TABLE 1. Average values for selected life history variables

Species	Average adult lifespan ^a	Age at maturity ^b	Age at weaning/independence	α^c	αM	Ratio of weaning/independence weight to adult weight	Daughters per year, b	αb
Original values								
Orangutan	17.9	14.3	6.0	8.3	0.46	0.28	0.063	0.52
Gorilla	13.9	9.3	3.0	6.3	0.45	0.21	0.126	0.79
Chimpanzee	17.9	13.0	4.8	8.2	0.46	0.27	0.087	0.70
Humans	32.9	17.3	2.8	14.5	0.44	0.21	0.142	2.05
New values								
Humans, weaning	48.9	18.3	2.8	15.5	0.32	0.23	0.155	2.40
Humans, juvenile	48.9	18.3	7.0	11.3	0.23	0.39	0.155	1.75
Humans, energy balance	48.9	18.3	12.0	6.3	0.13	0.73	0.155	0.98

^aOriginal values" from Hawkes et al. (1998), "new values" from the present analysis (see text for explanation).

^bEstimated as $1/M$ for all values.

^cAge at first birth minus gestation (Bogin, 2001).

^dPeriod of independent growth. See text for details.

terms of energy and time that might be invested elsewhere. A third trade-off is at the within-child level, in that additional years of growth, development, and maturation allow for greater adult body size, capital formation, and RC, but at the expense of delayed reproductive maturation. This third level of trade-off is exacerbated with the evolution of the adolescent stage of hominin life history. Current fossil evidence indicates that childhood evolved before adolescence (Thompson et al., 2003, see the Discussion section for more detail). The third level leads to the fourth level of trade-off, that between reproduction in early-life versus greater lifespan.

In essence, the RC hypothesis predicts that postmenopausal longevity of women did not evolve by direct selection for vigorous grandmothers, but rather by improved growth and development prior to maturity that creates greater RC and a more resilient biocultural hominin. This type of biocultural hominin lives to a greater age and is capable of greater total reproductive effort (Bogin, 2001; Crews, 2003). Once life expectancy passed the age of 45–50 years (the cessation of fertility for *Homo sapiens* women), "... a postreproductive life stage of significant duration and menopause became commonplace" (Bogin and Smith, 1996, p 714).

The data

The GH of Hawkes et al. (1998) is revisited to test the RC hypothesis for human life history and longevity. The basic variables of the mathematical formulae—average adult lifespan, age at reproductive maturity (i.e. first birth), age at feeding independence, length of independent period of growth, production of daughters per year, and the products of these variables—apply equally well to human life history from any perspective. Accordingly, the GH mathematical formulae are retained in the new analysis presented here. None of the variables is redefined or changed in meaning. The variable "age at weaning" of the original GH is expanded to "age at weaning/independence" to accurately reflect what that variable means in the published uses of the model (e.g. Charnov, 1991, 1993, 2001; Charnov and Berigan, 1993; Charnov et al., 2007). For virtually all nonhuman mammals weaning and feed-

ing independence are synonymous, but this is not the case for human beings.

The GH is silent about the impact of the evolution of human childhood (and adolescence). The GH treats the human "juvenile" stage of life, defined as the period from weaning to first birth, as equal to that of the great apes. In the following analysis, the mathematical models and formulae for the GH are reevaluated in light of the RC Hypothesis, specifically taking into account the childhood stage of human life history.

RESULTS

The parameter values of the GH provided by Hawkes et al. (1998) are shown in Table 1, and are labeled "original values."

The "original values" for humans are based on data for foragers; the Ache and the Dobe !Kung. The "new values" in Table 1 used to test the RC hypothesis are based on healthy, well-nourished human population data for physical growth, reproductive maturation, and demography (i.e., fertility and mortality). The important changes in the "new values" are for the variables "average adult lifespan," "age at maturity," estimates of "age at weaning/independence," "ratio of weaning/independence weight to adult weight," and "daughters per year." Average adult lifespan (the length of life from reproductive maturity, that is first birth, until death) is estimated using the same formula employed by Hawkes et al. (1998), which is that devised by Charnov (1991, 1993, 2001; Charnov and Berigan, 1993) as the reciprocal of the instantaneous adult mortality rate ($1/M$). Rather than the average for the oldest age at death for Ache and !Kung, the estimate used here is based on the age at death of Jeanne Louis Calment, the woman with the longest confirmed human lifespan, at 122.45 years. This procedure follows more closely the methodology of Charnov, which uses the absolute oldest age at death on record for a species. Charnov's method includes captive individuals, in the case of nonhuman primates, and domesticated species. Criticism that the age at death of Ms. Calment is artificial or "just an outlier" would have to be applied to the majority of applications of Charnov's model to all mammal species.

The new estimate of human average adult lifespan of 48.9 years accords better with actuarial data for healthy human populations than does the forager value. Women at age 20 years in Japan have a life expectancy of 65.79 more years, Australian women have an expectancy of 64.1 more years of life, and Portuguese women have an expectancy of 62.81 more years life (data from publicly available life tables for 2004–2007). Criticism that these contemporary societies have artificially prolonged lifespan must be tempered by the fact that in the year 1900, 20-year-old women in the United States had a life expectancy of 43.5 more years (Haines, 1998), even with relatively high female adult mortality from complications of childbirth and infectious disease. The new value for average adult lifespan shown in Table 1 of 48.9 years falls well within the range of these actuarial data.

The variable “age at maturity” is increased by 1 year based on a world-wide survey of age at first birth for human women, which is 19 years (Bogin, 2001). The variable “age at weaning/independence” was called “age at weaning” in the original article. It is relabeled here because the mean human age at weaning, at 2.8 years, is not equivalent to feeding independence. Human children (ages ~2.8–6.9 years) are dependent on older individuals for food and will die if not provisioned (Bogin, 1999a; Hawkes, 2006; Kaplan et al., 2000). Moreover, age at weaning is a very imprecise measure of parental investment in humans, as such investments come from many sources besides the mother and carry-on well after weaning (Quinlan et al., 2003). Accordingly, age 7.0 years, the transition to the juvenile stage, may better serve as the age for feeding independence. A third alternative shown in Table 1 is age 12 years for “independence.” This is based on the age at energy balance, in terms of energy inputs from older people versus energy production by the 12-year-old. After this age the adolescent has net positive returns on food production, meaning more food energy produced than consumed. Ethnographic and ecological research shows this occurs only after age 10 years for girls in rural Bangladesh (Robinson et al., 2008) and more often only after age 12 years for girls in other traditional societies (Kaplan et al., 2000; Kramer, 2002).

The variable “ratio of weaning/independence weight to adult weight,” is adjusted according to the three ages for independence using the 50th percentile of the World Health Organization standards and references (de Onis et al., 2007; <http://www.who.int/childgrowth/en/>;¹ for body weight of girls and women: 2.8 years = 13.3 kg, 7.0 years = 22.4 kg, 12 years = 41.7 kg, 20- to 30-year-old women = 56.9 kg. These body weights represent better the median values of the human species than do the forager values.

¹The World Health Organization Growth Standards are designed to show how growth in length and weight *should be* for all healthy boys and girls between birth and age 60 months. The standards are based on “... approximately 8500 children from widely different ethnic backgrounds and cultural settings (Brazil, Ghana, India, Norway, Oman, and the USA),” who were fed by, “... exclusive or predominant breastfeeding for at least 4 months, introduction of complementary foods by the age of 6 months, and continued partial breastfeeding up to at least 12 months), no maternal smoking before and after delivery, single term birth, and absence of significant morbidity.” The WHO standards, “... provide a single international standard that represents the best description of physiological growth for all children from birth to five years of age and to establish the breastfed infant as the normative model for growth and development (all quoted material from the WHO growth standards web site). The WHO growth references are designed to show how growth *is* for 5 to 19 years olds, based on nationally representative data from the United States.)

Finally, the variable “daughters per year” is based upon data for the Hutterites for the period 1940–1950 (Eaton and Mayer, 1953; Morgan, 1983; Wood, 1994). The Hutterites of this period attained the highest known fertility of any human population. Following the methodology of Charnov et al. in their application of invariant symmetry models, the known maximum value for species fertility is used here.

The parameter estimates for the “new values” do not change some of the findings of Hawkes et al. For any value of α , humans have a greater product of $\alpha \times b$ (number of years of mother’s body growth after feeding independence \times production of female offspring per year). Using age 7.0 years as the best approximation of age at independence (the onset of the juvenile stage) the value of αb is 2.2 times that of any of the apes.

Other parameters of the GH model do change values. The value of αM is no longer a symmetrical invariant relationship. The human value of αM is lower than that for the apes for any value of independent growth. This shows that human adult mortality is lower than expected for the amount of independent growth. A ratio, such as αM , does not indicate causality; nevertheless one interpretation is that increases in the length of time for human growth and development, due to the addition of childhood and adolescence, lead to lower adult mortality. The new value for the “ratio of human weaning/independence weight to adult weight” remains near to the ape values, i.e., weaning at about 25% of adult female body mass using a mean weaning age of 2.8 years. But, this ratio increases with later ages at independence, and the ratio is no longer symmetrically invariant. If age 7 years is used for feeding independence, then human offspring must achieve nearly 40% of adult body mass. If age 12 years is used, the transition to positive energy production, then humans must reach nearly 75% of adult body mass for feeding independence.

DISCUSSION

The new parameter estimates reported here indicate that some important human life history trade-offs are variant and not symmetrical. These novel aspects of human life history include:

1. *Human lifespan* ($1/M$) is about three times longer than that of the apes.
2. The period of human independent growth (α), measured from the end of the childhood stage to adulthood, is 1.5 times longer than for apes. However, the human independent growth period is of similar length to that of apes when measured from the age of net energy balance (i.e., early adolescence) to adulthood.
3. The product of αM (period of independent growth \times instantaneous mortality rate) for humans is 50% of the ape value for independence at age 7 years and 28% of the ape value for independence at age 12 years.
4. Humans have greater fertility, as expressed by daughters per year (b), and the product of αb (period of independent growth \times production of daughters per year) averages 2.6 times greater for humans than for apes.

Some of these findings are a confirmation of well-known aspects of human growth and demography—long prereproductive growth and development, long life span, and high fertility relative to most mammals. One novel aspect

of the analysis is the lower values of αM for humans when compared with great apes, which indicates that the length of the preadult period is atypically long for humans. This focuses attention on the selective pressures that extended the preadult period, especially the period of feeding dependency, as well as adult longevity. The greater value of the ratio αb for humans when compared with great apes shows the fitness advantage of the atypically long human preadult period. These new findings seem more consistent with the RC hypothesis than with the GH as proposed by Hawkes et al.

These new findings depend, of course, on the validity of the parameter value estimates presented here. The "original values" of Hawkes et al. (1998) were derived from living foragers. The "new values" used here for the growth and demographic data are derived from human groups that are healthier and better-nourished than living foragers. This seems well justified in terms of the invariant symmetry life history model used by Hawkes et al. When applied to extant nonhuman mammals, the invariant symmetry model often employs data from captive and domesticated species that are usually provided with veterinary care, and are better nourished, than their wild counterparts (e.g., Charnov et al., 2007). The source of data for the "new values" also seems justified from the paleontological, archaeological, and contemporary ethnographic-biological forager record. Human forager groups show evidence of nutritional deprivation in terms of low height- and weight-for-age and low body fat stores (De Souza, 2006; Jenike, 2001). Contemporary foragers have relatively high infant mortality, which lowers expectation of life at birth (De Souza, 2006; Pennington, 2001). High levels of infant mortality are also widely used as a measure of adversity in overall health (Bogin et al., 2007). On the basis of a review of forager nutritional ecology (8–12 societies per variable studied), Jenike (2001, p 229.) concludes that the living foragers, "... suffer functional, reproductive, growth, and health deficits relative to those with greater dietary sufficiency." In another review of contemporary forager health, Froment (2001) finds that, "Coping with hazards and a heavy burden of diseases, hunter-gatherers do not live—and have never lived—in the Garden of Eden; they are not affluent, but poor, with limited needs and limited satisfaction, and little access to any facility" (p 259).

From these perspectives, the living foragers are not representative of optimal, favorable, or even normative human biological conditions. Rather, the living foragers are remnants of the past. They have suffered from exploitation by more powerful pastoral and agriculture-based societies in the historical past, by Colonial-era powers in the recent past, and by the nation-states in which the foragers now reside (Bodley, 1999; Trigger, 1999). The extent of the adversity experienced by the living foragers may be measured in centimeters of stature and kilograms of body mass. A sample of 20 small-scale societies including the living foragers (but excluding African Pygmies) are 9.8% shorter and have 8.8% less body mass than a world-wide sample of living humans from traditional agricultural and industrial societies (Ruff, 1994). These differences in body size are biologically significant in terms of health (Bogin et al., 2007) and statistically significant (statistical analyses available from the author). The skeletal biology of our ancestors from *Homo erectus* to modern *H. sapiens* shows that these Paleolithic and early Neolithic adults were, on

average, 10% taller and 30% heavier, due to greater muscular and skeletal mass, than diverse samples of living adult humans (Mathers and Henneberg, 1995; Rosenberg et al., 2006; Ruff et al., 1993). These difference make the adult Paleolithic and Neolithic people that much larger than living foragers.

The skeletal remains of the preadult early modern human Sungir specimens from central European Russia, dated from 19,200–27,200 BP (Kuzmin et al., 2004), indicate statures greater than those of well nourished, healthy living juveniles and adolescents. Sungir 2 was about 13-years-old and Sungir 3 about 10-years-old at the time of death, but their estimated statures are closer to those of the median 18- and 15-year-old on the WHO growth references (Mednikova, 2007). The skeletal biology and the archaeology of food remains from the preagricultural period also indicate better health profiles for Neolithic people than for living foragers (Eaton and Eaton, 1999; Formicola and Giannecchini, 1999).

Recent research shows that many living foragers and traditional horticulturalists and pastoralists live within adverse nutritional and infectious disease ecologies, often exacerbated by social instability and warfare (Gray et al., 2008; Gurven et al., 2008; McDade et al., 2008). These insults place many foragers and people living in traditional societies under a high allostatic load, which decreases the possibilities to build RC during the years of growth and development. The allostatic load also decreases any RC available to adults at a relatively fast rate. This may increase infant and child mortality, impair adult health and reproduction, and increase adult mortality. The physiological basis for these associations are well enough understood to show the causal links between health, nutritional status, fertility, and mortality in relation to the neuroendocrinology of the hypothalamic-pituitary-gonadal and adrenal axes (Ellison and Jasienska, 2007; Ellison, 2001; Jasienska et al., 2006).

The RC hypothesis, in combination with the evolution of human childhood and adolescence, seem best able to explain the novel biological and mathematical features of human growth and demography. Childhood reduces the infancy lactation period and allows human mothers the potential to produce two offspring in time it takes a great ape female to produce and rear one offspring to independence. To do so, the mother must have the energy reserves following the first pregnancy and lactation to quickly enter into a new pregnancy (Ellison, 2001). The evolution of childhood, therefore, comes with several levels of life history trade-offs. One level is that other members of the human social group must provide appropriate foods and protection to dependent children and their mothers. The GH proposes that in hominin evolutionary history these inputs originally came from postmenopausal women. There is some paleodemographic evidence that longevity of this sort appears only with modern humans of the Early Upper Paleolithic (Caspari and Lee, 2004, 2006). In contrast, there is evidence for a childhood life history stage at about 2.2 million BP and both the childhood and adolescence stages by 780,000 BP (Thompson et al., 2003). If this fossil evidence is true, then "valuable grandmothers" could not be the source of provisioning for children. The RC hypothesis and the ethnographic record indicate a larger social base of such support. Participants include siblings of the mother and the child, other genetic and social kin, and men and women of all ages (Kramer, 2007;

Weisner and Gallimore, 1977; Weisner, 1987). This pattern of support to both mothers and their newly weaned children is nearly universal in contemporary and historical human societies (Bentley and Mace, 2009; Hrdy, 1999). Human food provisioning and care to children and their mothers goes beyond the cooperative breeding of other mammals. The human case makes use of biological relationships and also marriage, systems of economic exchange, political power structure, and gender-role construction—in other words, it is culturally patterned.

Human food provisioning and care are also extended to juveniles, adolescents, adults, and the elderly. Such care is derived from the biological basis for human attachment, compassion, and love (Chisholm, 1999; Hrdy, 1999). The investments of energy and care from prenatal to early adult life stages build a greater level of RC than found in any other primate. There is nothing quite like this elsewhere in the social world of mammals. It has been called “the hominid adaptation” (Lancaster and Lancaster, 1983). Perhaps the best label for the human condition is bio-cultural cooperative breeding or, more succinctly, biocultural reproduction (Bogin, in press).

Human adult RC depends on the 4-year period of childhood and on adolescence, which adds another 6–8 years to the preadult phase of the human life cycle. The new values for the ratio of αM (the period of independent growth \times the adult instantaneous mortality rate) for humans are especially important in this context, as these values show lower human adult mortality with a longer period of growth. The interpretation of the αM ratio here is that greater longevity is possible only when sufficient biological and social RC is established early in life. The historical data for the Hutterites of North American that are used here (Eaton and Mayer, 1953; Howells and Bleibtreau, 1970; Morgan, 1983; Wood, 1994), for example, show the benefits of RC in terms of fertility, survival, and longevity. Another example is pre-Industrial Finland, where, “... the poorest women had the lowest age-specific survival throughout their lives, they started reproduction later, delivered fewer offspring during their lifetime, ceased reproduction younger, had poorer offspring survival to adulthood and, hence, had lower fitness compared to the wealthier women” (Pettay et al., 2007, p e606).

Adolescence may have evolved by interplay between natural and sexual selection (Bogin, 1993, 1999a, in press). Adolescents may contribute significant amounts of food and labor to their families and this enhances reproduction by the parents and survival of their offspring (natural selection). The sex-specific features of adolescent girls and boys enhances opportunities for an apprenticeship-type of learning and practice of the wide variety of economic, social, political, and sexual skills. This learning enhances biological and, especially social RC. Apprenticeships and learning are consequences (not causes) of the natural selection for adolescence, but acquiring skill proficiency enhances “attractiveness” (sexual selection) and successful adult reproduction (natural selection). The Embodied Capital Hypothesis of Kaplan and coworkers (Gurven et al., 2006; Hill and Kaplan, 1999; Kaplan and Robson, 2002; Kaplan et al., 2000) further develops the biological selection aspects for the evolution of adolescence.

These apprenticeships and learning are made possible by the physical features of adolescents. In the case of girls, the development of adult-like fat patterning, including

breasts and menarche, occur years before fertility. Adolescent girls appear to be more mature than they are, at least in terms of reproduction. Their appearance triggers a variety of rites of passage to initiate the girls into womanhood (Bogin, 1999a; Schlegal and Barry, 1991). The physical, economic, and social resources that the community invests in these girls during the rites of passage increase the RC of the girls and their reproductive value. This, in turn, increases their likelihood of marriage, motherhood, and survival of their offspring.

Another selective advantage of the slow human pattern of growth is that it allows for more precise “tracking” of ecological conditions via additional opportunities for developmental plasticity in body size, body shape, behavior, and cognition (Bogin, 1999a; Gurven and Walker, 2006). The fitness of a given phenotype varies across the range of variation of an environment. When phenotypes are fixed early in development environmental change and high mortality are positively correlated, such as in mammals that mature sexually soon after weaning (e.g., rodents). The human childhood stage adds 4 years of relatively slow physical growth and allows for behavioral experience that further enhances developmental plasticity. Adolescence adds several more years and furthers the fine-tuning between the individual and the biocultural environment. The net result is the potential for building considerable RC.

CONCLUSION

The RC hypothesis, in combination with a multilevel selection model, provides a complex, but comprehensive, perspective on some aspects of the evolution of human life history. Multilevel evolutionary hypotheses are not “circular reasoning.” The hypothesis presented here begins with a fundamental Darwinian-type selection for decreased birth intervals via the evolution of early weaning and childhood. Additional levels of interrelated selection processes follow from this primary level. Multilevel selection is part of a maturing view of biological evolution in terms of a nested set of selective processes (Wilson and Wilson, 2007).

The building of RC during human childhood and adolescence, combined with biocultural reproduction, explain in large part why a greater percentage of human young survive to adulthood than the young of any other primate species. The new life history stages also help to account for the greater RS and greater longevity of human adults over other primates. It is not lower adult mortality that prolongs the period of human growth and development. Rather, it is the building of a better, healthier body and the developing of greater biological, behavioral, and cultural resilience prior to sexual maturity that leads to greater adult health, fitness, and longevity. A significant period of postreproductive life for women, and for men, is derived from the selection for RC building during a longer prereproductive life span. “Valuable grandmothers” are a consequence of the limitations of mammalian biology in terms of the senescent decline of the reproductive system after age 40 years (Leidy, 1994; Pavelka and Fedigan, 1999; Pecchio, 2001) combined with human biocultural strategies to take greatest advantage of this situation (Bogin and Smith, 1996).

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