Ontogeny and Evolution of the Social Child

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Danny was roaming the Fond Vert area of the village with two of his closest friends on a rainy Saturday morning. They had eaten their fill of mangoes, after pelting a heavily laden tree with stones for nearly an hour, taking turns testing their skill at knocking down breakfast. Now Danny was up the cashew tree in Mr. Pascal's yard, tossing the yellow and red fruits to the smaller children below who had gathered to benefit from this kindness. Suddenly the sharp voice of his stepfather rang out from the nearby footpath. The bird-like chatter and laughter of the children immediately stopped. Danny's hand froze mid-way to its next prize, and his head turned to face the direction of the yell with a mixed expression of surprise and fright. Ordered down from the tree, Danny headed quickly home, head bowed in apparent numb submission.¹ Danny's cortisol (a stress hormone) level, measured from his saliva collected several times a day, rose from 2.2 to 3.8 µg/dl in little more than an hour. That afternoon, his secretory immunoglobulin-A levels dropped from 5.70 to 3.83 mg/dl. Three days later he had common cold symptoms: runny nose, headache, and fever. His two companions did not suffer the same fate, instead resuming their morning play, exhibiting a normal circadian decline in cortisol, and remaining healthy over the next two weeks.

This case example contributes to a common pattern. Children in this rural Dominican community are more than twice as likely to become ill during the week following a stressful event than children who have not recently experienced any significant stressors (Flinn & England, 2003). People everywhere appear sensitive to their social environments, often with negative consequences for their health (Cohen, Doyle, Turner, Alper & Skoner, 2003; Maier, Watkins, & Fleschner, 1994; Marmot & Wilkinson, 1999). Mortality rates for children in orphanages and hospitals in early 20th century America, lacking the evolutionarily-normal

¹ From MVF field notes, July 1994.

intimacy of the family, were appalling (e.g., Chapin, 1922, p. 214). It is not lack of food or hygienic care, nor just the occurrence of traumatic events that affect child health, but the lack of social support, including parental warmth and other factors that influence emotional states (Belsky, 1997; Davidson, Jackson, & Kalin, 2001; Field, Diego, Hernandez-Reif, Schanberg, & Kuhn, 2003). Why should this be so? Why do social interactions, and a child's perceptions of them, affect physiology and morbidity? And, more generally, why is the social environment of such paramount importance in a child's world?

In Danny's village, located on the east coast of the island of Dominica where one of us (MVF) has lived and studied over the past sixteen years, most of a child's mental efforts seem focused on negotiating social relationships with parents, siblings, grandparents, cousins and other kin, friends, teachers, bus drivers, neighbors, shop owners, and so forth. Foraging for mangos and guavas, hunting birds with catapults (i.e., 'sling-shots'), or even fishing in the sea from rock cliffs, are relatively simple cognitive enterprises, complicated by conflicts with property owners, and decisions about which companions to garner and share calories with. After a few weeks of playing together, the foraging behaviors of our nine-year-old son were nearly indistinguishable from those of Danny and his other village peers. Even a novice readily acquires what initially appear to be remarkable skills. The mind of the child seems more taxed by solving social puzzles than with utilitarian concerns of collecting food.

In this chapter we examine potential evolutionary linkages between these two most distinctive human characteristics: childhood and the social mind. We begin with a review of current theories of human life history and the family. We then evaluate the different models for the evolution of human childhood, emphasizing evidence from the fossil record. We argue that conspecific social competition was the primary selective pressure shaping the uniquely human

combination of physically altricial but mentally and linguistically precocial infancy, extended childhood, and extended adolescence, enabled by extensive bi-parental and kin care.

Evolution of childhood

"Most of us see a picture of innocence and helplessness: a clean slate. But, in fact, what we see in the crib is the greatest mind that has ever existed, the most powerful learning machine in the universe."

(Gopnik, Meltzoff, & Kuhl, 1999, p. 1)

The human child is a most extraordinary organism, possessed of 'the greatest mind' and yet 'innocent and helpless' – in effect, a larva equipped with an enormous brain. This is contrary to the general pattern among mammals: precocial species have neonatal brain sizes twice those of comparable altricial species (Martin & MacLarnon, 1990). Even relative to other primates the human infant is unusually altricial, and highly dependent upon parents and other relatives for protection, transport, resources (e.g., food), and information (Lamb, Bornstein, & Teti, 2002). Humans, moreover, have an extended juvenile period, unlike most other altricial young who use their protected environments to grow and mature rapidly (e.g., Ricklefs, 1983). Parental and other kin investment continues for an unusually long time, often well into adulthood and perhaps even after the death of the parents.

The selective pressures responsible for this unique suite of life history characteristics appear central to understanding human evolution (Alexander, 1987, 1990a, 1990b, 2003; Bjorklund & Pellegrini, 2002; Hill & Hurtado1996a, 1996b; Jolly, 1966, 1999; Kaplan, Hill, Lancaster, & Hurtado, 2000; Low, 2001). The delay of reproduction until almost twenty years of age, nearly double that of our hominoid relatives the chimpanzees and gorillas, involves

prolonged exposure to extrinsic causes of mortality and longer generation intervals. What advantages of an extended childhood could have outweighed the heavy costs of reduced fecundity and late reproduction (Williams, 1966; Stearns, 1992) for our hominin² ancestors?

The physical growth of the child, although unusual in its temporal pattern (Bogin, 1999; Leigh, 2001), does not appear to involve especially significant challenges. The relatively slow rate of overall body growth during childhood, followed by a rapid growth spurt during puberty, may economize parental resources supporting dependent offspring. A small child requires fewer resources than a large one. Hence delayed physical growth during childhood may have facilitated shortened birth intervals, providing a demographic advantage (Bogin & Silva, 2003).

Brain growth, however, has a different trend than overall body growth. The baby human has a large brain with high energetic and developmental costs that use more than half (!) of its total metabolism (Holliday, 1986; Leonard & Robertson, 1994; Passmore & Durnin, 1955).

Although neurogenesis is mostly completed by middle childhood, reproduction is postponed for more than a decade. What aspects of the phenotype require so much additional development?

And why burden the growing child, and its caregivers, with a brain that requires so much energy for so long?

One possibility is that these anomalous patterns of brain and physical growth during human childhood are not adaptations *per se*, but instead are inadvertent outcomes of basic growth processes such as neoteny and heterochrony (Schultz, 1969; Gould, 1977; see also Lovejoy, 1981). Perhaps selection for an extended lifetime or increased body size involved mechanisms that could not adaptively fine-tune life history stages or growth of different parts of the phenotype. The extended juvenile period, for example, may be interpreted as an incidental

² "Hominin" refers to taxa more closely related to humans than to chimpanzees.

outcome of selection for a longer lifespan in general. From this perspective, human childhood and the big brain were viewed in the context of major developmental processes that constrain adaptive solutions.

The recent integration of molecular genetics with evolutionary developmental biology, however, has provided a more nuanced view of the constraints on ontogeny. Detailed knowledge of developmental mechanisms at the genetic and cellular levels (e.g., Gerhart & Kirshner, 1998) has important implications for understanding the evolution of human life histories (Finch & Sapolsky, 1999; Konner, 1991; Lovejoy, McCollum, Reno, & Rosenman, 2003). The broad scaling trends among life history events suggested by Schultz (1969) and Gould (1977), in which all phases of the lifespan remain proportional when lifespan is altered, do not accord with recent comparative analyses that indicate these more specific mechanisms result in diverse and species-specific ontogenies (Leigh, 2001; West-Eberhard, 2003). Human childhood is not likely to be an inadvertent consequence of selection for an extended lifetime or some other life history constraint (Alexander, 1987). We need a functional evolutionary explanation for this 'most powerful learning machine in the universe.'

The foraging "practice" model

Human childhood has traditionally been viewed as a period of edification: "immatures are enabled to live a protected existence whilst they learn skills necessary for adult life" (Bowlby, 1969, p. 63). The primary question has been: What information is so important and difficult to acquire that many years are needed for its mastery? Most juvenile primates spend considerable effort playing and practicing with their physical environment and developing fighting skills (e.g., Symons, 1978; Pellegrini & Archer, this volume). Compared with other primates, our motor skills do not appear especially challenging; a terrestrial environment seems

more easily mastered than an arboreal one. Children may need time to acquire knowledge for tool use and complex foraging including hunting (Darwin, 1871; Hill & Kaplan, 1999; see also Byrne, 2002a, 2002b). An extraordinarily long developmental apprenticeship is seen as useful for acquiring learned solutions to ecological problems unique to our niche (Bock, 2002). Investment in 'embodied capital,' via an extended childhood, has been suggested to have a fitness payoff from increased adult foraging ability (Kaplan et al., 2000).

Studies of the effects of childhood experience on subsequent adult foraging efficiency, however, do not provide clear support for the "practice" model. Ethnographic accounts of childhood have long suggested a lack of urgency or focus on training of foraging skills relative to other activities in many human societies (e.g. Chagnon, 1977; Levine, Miller, & West, 1988; Whiting & Edwards, 1988; Hirschfeld, 2002). Specific tests of the effects of childhood foraging practice on adult performance indicate little benefit from training; relatively inexperienced individuals appear to perform equal to their more experienced peers (Blurton Jones & Marlowe, 2002). Children, moreover, are capable of some types of complex foraging at an early age, suggesting that a long apprenticeship is not necessary (Bliege Bird & Bird, 2002). Previous observations of adult foraging advantage may be more appropriately interpreted as a consequence of physical size and maturity rather than from finely honed acquired skills (Bird & Bliege Bird, 2002; Blurton Jones, & Marlowe, 2002). In addition to failing to support the 'childhood as foraging practice' model, these studies cast further doubt on the hypothesis that physical growth is delayed to conserve parental resources, because if size is a primary determinant of foraging efficiency, then precocial early growth would seem adaptive.

Childhood as an extended "practice" period is also difficult to reconcile with the recent argument that the human brain is at least partly the evolutionary result of a Fisherian sexual

selection process (Miller, 1999). From this perspective, mental abilities are viewed as a human equivalent to the Peacock's tail, an ornament whose primary function is to attract mates. The development of most sexually selected ornaments and weapons (e.g., antlers, bright coloration), however, are temporally associated with sexual maturity (Andersson, 1994). For example, among many species of birds, the parts of the brain involved with the production of song are influenced by androgens released in response to the breeding season (see review in Kelley & Brenowitz, 2002). The precocial ontogeny of brain and mind during infancy and childhood seems ill suited to an ornamental courtship function during early adulthood. Why develop and maintain such a costly display so many years before (and after!) its use to attract mates? This temporal disjunction seems contrary to a Zahavian "handicap" function as well, in which apparently nonfunctional traits are maintained to illustrate sufficient genetic quality to overcome the handicap.

The ecological dominance—social complexity model

A different approach to the problem of the evolution of human childhood involves consideration of the brain as a "social tool" (Alexander, 1971, 1989; Bjorklund & Rosenberg, this volume; Brothers, 1990; Byrne & Whiten, 1988; Dunbar, 1998; Humphrey, 1976, 1983). This hypothesis suggests that many human cognitive and psychological adaptations function primarily to contend with social relationships, with ecological constraints (e.g., hunting or extractive foraging) being a more secondary source of recent evolutionary change. It appears that some human cognitive competencies, such as theory of mind and language, are most readily understood in terms of social selection pressures, although cognitive competencies for interacting with the physical (e.g., navigating) and biological world are evident as well (Geary & Huffman, 2002). The primary mental chess game shaping the distinctive changes in the

neocortex (Adolphs, 2003; Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001), however, was with other intelligent hominin competitors and cooperators, not with fruits, tools, prey, or snow. Human social relationships are complex and variable. Predicting future moves of a social competitor-cooperator, and appropriate countermoves, amplified by networks of multiple relationships, shifting coalitions, and deception, make social success a difficult undertaking (Alexander, 1987, 1990a; Daly & Wilson, 1988ab; Henrich et al., 2001; Stanford, 2001; de Waal, 1982, 2002).

Indeed, the potential variety of human social puzzles is apparently infinite; no two social situations are precisely identical, nor are any two individuals ever in exactly the same social environment. Moreover, social relationships can change rapidly, requiring quick modification of strategy. Variability in these dynamics creates conditions that should favor the evolution of brain and cognitive systems above and beyond more traditional modular systems (Fodor, 1983; Tooby & Cosmides, 1995). These systems have been cast in terms of general intelligence, domain-general abilities, or executive functions that are capable of integrating and co-opting information processed by more restricted, domain-specific mechanisms (e.g., Adolphs, 2003; Geary, in press; Hirschfeld & Gelman, 1994; cf. Chiappe & MacDonald, under review; La Cerra & Bingham, 2002; Quartz & Sejnowski, 1999) and using mental simulations, or "scenario-building" (Alexander, 1989) to construct and rehearse potential responses to changing social conditions. These complex cognitive processes would be more capable of contending with, and producing, novelties of cultural change and individual-specific differences (Bjorklund & Rosenberg, this volume; Flinn, 1997; Tomasello, 1999).

Childhood, therefore, evolved as a mechanism whereby individuals can develop these necessary social skills (Joffe, 1997). Learning, practice, and experience are imperative for social

success. The sophistication and cognitive problem-solving of this type are considerable, and perhaps significantly greater than those involved with foraging skills. An extended human childhood can be directly attributed to the selection for development and necessity of a social brain that requires a lengthy ontogeny to master complex dynamic tasks such as moral reasoning (Alexander, 1987).

While it is widely recognized that human childhood is a learning period, there is discussion about what necessary skills are the driving force behind increased time for learning to take place. The "social tool" hypothesis to explain human intelligence was initially considered to suffer from similar limitations as the physical environment hypotheses. Comparative analyses indicated that group size and proxy measures for brain size (e.g., cranial capacity, neocortex ratios) were associated in a wide range of taxa, including primates (e.g., Kudo & Dunbar, 2001; Pawlowski, Lowen & Dunbar, 1998; van Schaik & Deaner, 2003). A major problem, however, remained unresolved: given that hominin group size was unlikely to have been larger than that of their close relatives (the other hominoids), what was qualitatively different about the hominin social environment? Of course, the most appropriate comparisons would include other species of *Homo* as well as australopithecines (Povinelli & Bering, 2002), but unfortunately these species are now extinct. Why did hominins in particular form more socially complex groups, hence creating an environment in which more sophisticated forms of social cognition (e.g., theory of mind) and general intelligence would have been favored by natural selection? Why were coalitions more important, and more cognitively taxing, for our hominin ancestors than they were for any other species in the history of life? Why did hominins evolve special cognitive abilities such as "understanding other persons as intentional agents" (Tomasello, 1999, p. 526)? Richard Alexander (1989, 1990a) suggests the following solution:

"... humans had in some unique fashion become so ecologically dominant that they in effect became their own principle hostile force of nature, explicitly in regard to evolutionary changes in the human psyche and social behavior... the real challenge in the human environment throughout history that affected the evolution of the intellect was not climate, weather, food shortages, or parasites – not even predators. Rather, it was the necessity of dealing continually with our fellow humans in social circumstances that became ever more complex and unpredictable as the human line evolved. Social cleverness, especially through success in competition achieved by cooperation, becomes paramount ... nothing would select more potently for increased social intelligence ... than a within-species co-evolutionary arms race in which success depended on effectiveness in social competition" (1990a, pp. 4-7).

Alexander's scenario posits that hominins increasingly became an "ecologically dominant" species. Evidence that humans evolved into ecologically dominant predators and foragers comes from patterns of human migration and demography, as well as our variable and flexible subsistence strategies. Darwin and Wallace's (1858, p. 54) conceptualization of natural selection as a "struggle for existence" becomes in addition a *struggle with other human beings for control* of the resources that support life and allow one to reproduce. In this situation, the stage is set for a form of runaway selection, whereby the more cognitively, socially, and behaviorally sophisticated individuals are able to out maneuver and manipulate other individuals in order to gain control of resources in the local ecology, and to gain control of the behavior of other people. To the extent that access to these resources covaries with survival and

reproductive outcomes – and it does in many contexts (Betzig, 1986; Chagnon, 1988; Flinn, 1986; Hed, 1987; Irons, 1979; Malthus, 1798; United Nations, 1985) – the associated sociocognitive competencies, and supporting brain systems, would be favored by natural selection.

In other words, to the extent that ecological dominance was achieved, humans became "their own principal hostile force of nature" (Alexander, 1989, p. 469) via inter- and intra-group competition and cooperation. Increasing linguistic and sociocognitive capacities were favored because such skills allowed individuals to better anticipate and influence social interactions with other increasingly intelligent humans. This "runaway" directional selection produced greater and greater modular (e.g., language, theory of mind) and more general cognitive competencies, because success was based on relative (rather than absolute) levels of ability. Unlike static ecological challenges, the hominin social environment became an autocatalytic process, ratcheting up the selective advantage associated with the ability to anticipate the social strategies of other hominins and to mentally simulate and evaluate potential counter strategies (Alexander, 1989). Modular competencies allowed hominins to quickly and efficiently process social information that was static, or invariant, across generations and contexts (e.g., the ability to read basic human facial expressions), whereas the more variable and thus less predictable features of one-on-one and coalitional social relationships favored the ability to mentally construct and manipulate a range of potential social scenarios. These more general competencies are known as working memory, attentional control, and executive functions (e.g., Baddeley, 1986; Engle, 2002; for review see Allmann, 1999; Geary, in press). Practice during childhood for the development of social skills using these components is paramount (Bjorklund

& Pellegrini, 2002) and likely to be facilitated by a protective and informative family environment.

Evolution of the human family as a nest for the child's social mind

The human family is extraordinary and unique in many respects (Alexander, 1989, 2003; Geary & Flinn, 2001; Lancaster & Lancaster, 1983). Humans are the only species to live in multi-male groups with complex coalitions and extensive paternal care. Humans have concealed ovulation, altricial infants, lengthy child development, female orgasm, and menopause. These traits may be causally linked and provide important clues towards reconstructing the evolution of our (human) unusual life history.

The altricial infant is indicative of a protective environment provided by intense parenting and alloparenting in the context of kin groups (Chisholm 1999). The human baby does not need to be physically precocial. Rather than investing in the development of locomotion, defense, and food acquisition systems that function early in ontogeny, the infant can work instead towards building a more effective adult phenotype. The brain continues rapid growth, and the corresponding cognitive competencies largely direct attention toward the social environment. Plastic neural systems adapt to the nuances of the local community, such as its language (Alexander, 1990b; Bjorklund & Pellegrini, 2002; Bloom, 2000; Geary & Bjorklund, 2000; Geary & Huffman, 2002; Small, 1998, 2001). In contrast to the slow development of ecological skills of movement, fighting, and feeding, the human infant rapidly acquires skill with the complex communication system of human language (Pinker, 1999). The extraordinary information-transfer abilities enabled by linguistic competency provide a conduit to the knowledge available in other human minds. This emergent capability for intensive and extensive communication potentiates the social dynamics characteristic of human groups

(Dunbar, 1997) and provides a new mechanism for social learning and culture. The recursive pattern recognition and abstract symbolic representation central to linguistic competencies enable the open-ended, creative, and flexible information-processing characteristic of humans -- especially of children.

An extended childhood appears useful for acquiring the knowledge and practice to hone social skills and to build coalitional relationships necessary for successful negotiation of the increasingly intense social competition of adolescence and adulthood, although ecologically related play and activities (e.g., exploration of the physical environment) occur as well. The unusual scheduling of human reproductive maturity, including an "adrenarche" and a delay in direct mate competition among males (Herdt & McClintock, 2000; McClintock & Herdt, 1996) appears to extend the period of practicing social roles and extends social ontogeny.

The advantages of intensive parenting, including paternal protection and other care, require a most unusual pattern of mating relationships: moderately exclusive pair bonding in multiple-male groups. No other primate (or mammal) that lives in large, cooperative multiple-reproductive-male groups has extensive male parental care, although some protection by males is evident in baboons (Buchan, Alberts, Silk, & Altmann, 2003). The only other primates that have paternal care (e.g., indris, marmosets, tamarins, titi monkeys, night monkeys, and to a lesser extent, gibbons and gorillas) do not live in large groups. Competition for females in multiple-male groups usually results in low confidence of paternity (e.g., chimpanzees). Males forming exclusive 'pair-bonds' in multiple-male groups would provide cues of non-paternity to other males, and hence place their offspring in great danger of infanticide (Hrdy, 1999). Paternal care is most likely to be favored by natural selection in conditions where males can identify their offspring with sufficient probability to offset the costs of investment, although reciprocity

with mates is also likely to be involved (Smuts, 1985; Smuts & Smuts, 1993). Humans exhibit a unique "nested family" social structure, involving complex reciprocity among males and females to restrict direct competition for mates among group members. It is difficult to imagine how this system could be maintained in the absence of another unusual human trait: concealed ovulation (Alexander & Noonan, 1979). Human groups tend to be male philopatric (males tending to remain in their natal groups), resulting in extensive male kin alliances, useful for competing against other groups of male kin (Chagnon, 1988; Wrangham & Peterson, 1996; LeBlanc, 2003). Females also have complex alliances, but usually are not involved directly in the overt physical aggression characteristic of inter-group relations (Campbell, 2002; Geary & Flinn, 2002). Menopause reduces mortality risks for older women and allows them to concentrate effort on dependent children and other relatives (e.g., grandchildren) with high reproductive value (Alexander, 1974; Hawkes, 2003). Parents and other kin may be especially important for the child's mental development of social maps because they can be relied upon as landmarks who provide relatively honest information. We suggest that the evolutionary significance of the human family in regard to child development is more as a nest from which social skills may be acquired than as an economic unit centered on the sexual division of labor.

The fossil record

The fossil record is the single source of information we have for documenting the order and timing of acquisition of key human characteristics. For example, the discovery of the Taung skull (*Australopithecus africanus*, Dart, 1925) disproved the notion that upright, bipedal locomotion in hominin evolution was accompanied by significant brain expansion. We now have substantial data documenting that hominins were bipedal for at least two (Leakey, Feibel, MacDougall, & Walker, 1995; White, Suwa, & Asfaw, 1994), and perhaps as long as four

(Brunet et al., 2002; Haile-Selassie, 2001; Senut et al., 2001; Senut, 2002), million years prior to the emergence of the genus *Homo* and the accompanying significant increases in brain size.

Paleontologic data, therefore, provide a critical test of hypotheses about how and why humans evolved. We can use these data to explore associations among the evolution of childhood and other attributes such as intelligence, social dynamics, and ecology, testing the hypothesis that childhood evolved as a mechanism for developing social competency (Alexander et al., 1979; Clutton-Brock, 1977; Dunbar, 1998; Foley, 1999; Plavcan, Van Schaik, & Kappeler, 1995), although definitive conclusions are difficult (Plavcan, 2000). This hypothesis is based on the argument that human intelligence evolved as a response to social competition in an ecologically dominant species (ecological dominance-social competition, or EDSC model), described in detail elsewhere (Flinn, Geary, & Ward, in press). Specifically, we predict that evidence for prolongation of childhood should co-occur with increased intelligence and social complexity and accompany or postdate significant changes in ecological dominance (see Bjorklund & Rosenberg, this volume).

The fossil record indicates that during the past four million years there has been a three-fold increase in brain volume (Figure 1a), a significant reduction in the magnitude of the sex difference in physical size (Figure 1b), a disappearance of related species of hominins, and a near-doubling of the length of the developmental period (Figure 1c). As displayed in Figure 1c, in most mammals infancy is followed by the juvenile stage, in which the young animal is not sexually mature but is independent of its parents. According to this model (see Bogin, 1999), childhood, a period following infancy in which the children are mobile but unable to fend for themselves (e.g., they require adults to gathering and prepare food for them), characterizes only humans and their *Homo* predecessors. Similarly in this model, adolescence, with its rapid

growth spurt and period of post-menarche infertility, is a late-evolving phenomenon, being found only in *Homo sapiens*-and *Homo erectus*. All of these changes postdate the first occurrence of stone tool use and increased meat in the diet. The first stone tools date to 2.5 million years ago (mya) (Asfaw et al., 1999; Semaw et al., 1997), and tool use is widespread among chimpanzees. Hunting is common among chimpanzees (Mitani & Watts, 2001; Stanford, 2001), and evidence of meat-eating precedes significant brain expansion in the hominin paleontological record (Asfaw et al., 1999).

[Figure 1 a-c goes about here]

Human childhood is the result of having secondarily altricial infants born early in their ontogenies coupled with extended juvenile periods, an adolescent growth spurt, and delayed timing of maturation relative to apes (Bogin, 1991, 1997, 1999). Each of these changes has anatomical correlates and is visible in the fossil record. Moreover, these shifts do not appear to have co-occurred, suggesting that the timing of each transition in life history may have been under independent selective pressures, rather than reflecting a single selective pressure for childhood itself as a stage *per se*. In other words, altriciality likely evolved for somewhat separate reasons from an adolescent growth spurt, and thus has appeared at different times in human evolutionary history.

The first hominin to have had relatively altricial infants was probably *Homo erectus*, roughly 1.8 mya. Female pelvic dimensions are constrained by locomotor and thermoregulatory requirements, so birth canal size in *H. erectus* was not substantially larger than in australopithecines (Begun & Walker, 1993). Adult brain sizes, however, were nearly doubled

(650-900 cc in early *Homo erectus* compared with 380-610 cc in *Australopithecus*; reviewed in Lee & Wolpoff, 2003). This means that in order to have appropriate neonatal proportions relative to the size of the mother's pelvic inlet, infants must have been born at a relatively small size and been relatively altricial early (Martin, 1989; Portman, 1941), likely with rapid fetal rates of postnatal brain growth (Martin, 1983). Early *Homo* individuals thus do not appear to have attained adult brain size simply by prolonging growth, given their relatively rapid rates of development (Deacon, 1997; Dean et al., 2001; Leigh, 2003; Smith, 1993). Having more altricial infants would have required more intensive parenting by the mother (see Rosenberg, 1992) and, given the decrease in sexual dimorphism occurring at this time (which may signal pair-bonding), perhaps also by the father and/or alloparents.

Despite these ontogenetic shifts associated with the timing of birth, delayed maturation does not appear to have occurred until later in hominin evolution. Development of the dentition as a whole appears correlated with life history variables such as age at sexual maturity in primates and other mammals (e.g. Smith, 1989), and so can be used to infer the timing of important life history stages. Dental crown formation times are correlated with brain size, and therefore to life histories (e.g. Beynon, Dean, & Reid, 1991; Beynon & Dean, 1987; Bromage, 1991; but see Macho & Wood, 1995; Macho, 2001). Early *Homo erectus* appears to have had relatively rapid development, similar in rate to *Australopithecus* and great apes, whereas that of modern humans is much slower (Dean et al., 2001).

Coincident with its rapid rate of development, early *H. erectus* (1.6 mya) is interpreted as having lacked a human-like adolescent growth spurt, based on the fact that the single known juvenile skeleton, KNM-WT 15000, had accelerated dental relative to postcranial skeletal development, typical of the pattern seen in humans prior to the growth spurt (Smith, 1993).

There are no comprehensive data on rates of child development for hominins between 1.6 mya and 60 thousand years ago (kya), but the single Neandertal specimen examined by Dean and colleagues (2001) was modern in its dental developmental trajectory, indicating a human-like extended childhood had occurred by this time. The apparently large brain relative to dental development observed for some Neandertal individuals (e.g. Dean, Stringer, & Bromage, 1986) may simply reflect the relatively larger adult brain in many Neandertal individuals as compared with modern humans (see Lee & Wolpoff, 2003, for summary data). A modern human pattern of dental development was present by 800 kya (Bermudez de Castro, 1999), perhaps suggesting delayed maturation (Smith, 1994, 2000), but this may not imply a similar rate to modern humans (Dean et al., 2001). If it does, it might be reasonable to hypothesize that the human adolescent growth spurt was already in place by this time as well.

Longevity appears to have increased gradually from *Australopithecus* to humans with a higher proportion of individuals living to old age, although definitive evidence is lacking. If ecological dominance reduced mortality from extrinsic causes, this would allow for selection for delayed reproduction and extended life histories (Williams, 1957). Taking all the data together, it appears that the evolution of altriciality may have begun with brain expansion, but that delayed maturation and an adolescent growth spurt may have evolved later in human evolution, perhaps as brain-size increase continued throughout the Pleistocene.

If these developmental shifts that resulted in a prolonged childhood were the result of selection for social learning, we would predict they should occur in the context of increasing social complexity. One key change in hominin social structure is the increasing stability of male-female pair bonds and associated male coalitionary behavior. The best indicator of these behaviors in the fossil record is sexual dimorphism. Reduced body mass dimorphism is

associated with both monogamy (Plavcan, 2000, 2001) and male coalitionary behavior (Pawlowski et al., 1998; Playcan et al., 1995) in extant primates. Although the large canine-size dimorphism that characterizes all living and fossil great apes had greatly diminished in Australopithecus (Ward, Leakey, & Walker, 2001; Ward, Walker, & Leakey, 1999), the reduced body mass dimorphism typical of modern humans did not occur until sometime during the evolution of *Homo erectus* (McHenry, 1992a, 1992b, 1994a; cf. Reno, Meindl, McCollum, & Lovejoy, 2003). The body mass increase accompanying the origin of *H. erectus* suggests that female body size increased from the australopithecine condition more than did male body size. Body mass dimorphism in early *H. erectus* is difficult to estimate accurately, but disparities in size and robusticity among even early *H. erectus* crania are less than in australopithecine species, signaling a reduction in body size sexual dimorphism. By the early mid-Pleistocene body mass dimorphism was similar to that found in modern humans (McHenry, 1994a; Ruff, Trinkaus, & Holliday, 1997). The changes in social behavior accompanying the shift in mating and parenting strategies are likely to have presented novel cognitive challenges involving complex reciprocity among coalition members (Steele 1996). Unlike gorillas, with one-male breeding groups, and chimps, with promiscuous mating and little male parental behavior, the evolving hominins were faced with the difficulties of managing increasingly exclusive pair bonds in the midst of increasingly large coalitions of potential mate competitors.

One approach to interpreting hominin social behavior evolution would be to assume that the behavioral characteristics of the ancestor common to the australopithecine species and humans were similar to those observed in modern chimpanzees (*Pan troglodytes*) or bonobos (*Pan paniscus*) (de Waal & Lanting, 1997; Kano, 1992; Wrangham, 1999; Wrangham & Peterson, 1996; Zihlman, 1978). This is a reasonable assumption in some respects. Brain size

relative to body size in chimpanzees, bonobos, australopithecines, and presumably the common ancestor was very similar (McHenry, 1994a, 1994b). However, sexual dimorphism in body weight is about 20% for chimpanzees and bonobos (Goodall, 1986; Kano, 1992). Although bonobo males are not known to show consistent coalitional aggression, male-on-male physical aggression is common and presumably a feature of the ancestor common to chimpanzees and bonobos (Wrangham, 1999). In any case, the degree of body mass dimorphism in chimpanzees and bonobos is considerably lower than that estimated for A. anamensis (Ward et al., 1999, 2001) and A. afarensis (McHenry, 1992b; but see Reno et al., 2003), in which males were much larger than females. The contrast suggests that the reproductive strategies of australopithecines may have differed in some respects from that of male chimpanzees or bonobos, and thus the social patterns found with chimpanzees and bonobos might not fully capture the social dynamics in australopithecines, or the selective pressures that favored larger females in the transition to *Homo*. Australopithecus body mass dimorphism suggests that these early hominins were polygynous, as significant mass dimorphism is not associated with monogamy in any extant primate (Plavcan, 2001). Thus, data from the hominin fossil record suggest that not only were developmental shifts resulting in the evolution of human childhood somewhat decoupled in human evolution, they co-occurred with indicators of increasing social complexity, such as brain-size expansion and decreased sexual dimorphism. Moreover, they do not appear to be correlated with significant shifts in dietary or ecological variables (reviewed in Flinn et al., in press).

Concluding remarks: Culture and ontogeny of the social mind

Human childhood functions to create successful adults. In particular, it is a time that allows a child to master the mental processing skills necessary to negotiate the complex social

and cultural interactions necessary for success as an adult. Humans are unique in the extraordinary levels of novelty that are generated by the processing of abstract mental representations. Human culture is cumulative; human cognition produces new ideas built upon the old. To a degree that far surpasses that of any other species, human mental processes must contend with a constantly changing information-environment of their own creation. Cultural information may be especially dynamic because it is a fundamental aspect of human social coalitions. Apparently arbitrary changes in cultural traits such as clothing styles, music, art, food, dialects, etc. may reflect information 'arms races' among and within coalitions. The remarkable developmental plasticity and cross-domain integration of some cognitive mechanisms may be products of selection for special sensitivity to variable social context (e.g. Boyer, 2001; Carruthers, 2000; Adolphs, 2003). Human "culture" is not just a pool or source of information; it is an arena and theater of social manipulation and competition via cooperation. Culture is contested because it is a contest. Success at social manipulation and cooperation requires a lifetime of learning, starting at birth.

Data from comparative studies and the fossil record support the hypothesis that it is social competition that selects for intelligence in an ecologically dominant species. Dietary and ecological variables, and associated learning, do not appear to require years of learning to master and are not well correlated with changes in life history stages or indicators of cognitive sophistication in the paleontological record. The prolonged childhood of humans results from at least two separate factors; it is not the result of a single evolutionary process. It begins with the relatively early birth of altricial infants necessitated by enlargement of the brain coupled with constraints on maternal pelvic size imposed by locomotion and thermoregulatory requirements. This initial life history shift occurred early with the evolution of early *Homo erectus* and initial

brain size expansion. Slower maturation rates and prolongation of a juvenile role via an adolescent growth spurt appear to have accompanied the origin of earliest *Homo sapiens* later in the Pleistocene. The fossil record is too sparse to detect whether this change occurred gradually with brain expansion (Lee & Wolpoff, 2003), but we would predict that it did. Delayed maturation, therefore, may also have accompanied greater longevity (Caspari & Lee, 2004). With the origin of *Homo*, there is evidence of increased reliance on meat in the diet, but as brain size continued to expand no clear dietary changes were evident. Diverse ecologies were encountered by the various hominin populations, indicating increased ecological dominance and flexibility. Still, the apparent lack of need for years of practice for some types of foraging casts serious doubt on ecological factors being the driving force behind intelligence (Burton Jones & Marlowe, 2002; Bliege Bird & Bird, 2002).

Returning to the anecdotal example at the beginning of this chapter, consider the relations among stress, health, and culture. People in difficult social environments tend to be less healthy in comparison with their more fortunate peers (e.g. Flinn, 1999; Dressler & Bindon, 2000; Wilkinson, 2001; Cohen et al., 2003). Social support has reproductive consequences (e.g., Silk, Alberts, & Altmann, 2003). The obvious explanation of a better physical environment — improved housing, work conditions, nutrition, healthcare, and reduced exposure to pathogens and poisons — is insufficient (Marmot et al., 1991; Ellis, 1994). The specific mechanisms underlying the association between socio-economic conditions and health are uncertain. Psychosocial stress and associated immunosuppression are possible intermediaries (Adler et al., 1994; Kiecolt-Glaser, Malarkey, Cacioppo, & Glaser, 1994). If the brain evolved as a social tool, then the expenditure of somatic resources to resolve psychosocial problems makes sense. Relationships are of paramount importance. Children elevate their stress hormone

(cortisol) levels much more frequently and extensively in response to psycho-social stimuli than to challenges associated with foraging (Flinn, Quinlan, Turner, Decker, & England, 1996). The adaptive effects of the major stress hormones on neural reorganization (Huether, 1996, 1998) are consistent with the observation that children are especially sensitive to their social worlds (Flinn, 1999). "Environmental stimuli (in children mainly psychosocial challenges and demands) exert profound effects in neuronal activity through repeated or long-lasting changes in the release of transmitters and hormones which contribute, as trophic, organizing signals, to the stabilization [Norepinephrine] or destabilization [Cortisol] of neuronal networks in the developing brain" (Huether, 1998, p.297).

Social competence is extraordinarily difficult because the target is constantly changing and similarly equipped with theory of mind and other cognitive abilities. The sensitivity of the stress-response system to the social environment enables adaptive neural reorganization to this most salient and dynamic puzzle. Childhood is necessary and useful for acquiring the information and practice to build and refine the mental algorithms critical for negotiating the social coalitions that are key to success in our species.

References

- Adler, N. E., Boyce, T., Chesney, M. A., Cohen, S., Folkman, S., Kahn, R. L., & Syme, S. L. (1994). Socioeconomic status and health. *American Psychologist* 49, 15-24.
- Adolphs, R. (2003). Cognitive neuroscience of human social behavior. *Nature Reviews, Neuroscience*, *4*, 165-178.
- Alexander, R. D. (1971). The search for an evolutionary philosophy of man. *Proceedings of the Royal Society of Victoria*, 84, 99-120.
- Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics*, 5, 325-383.
- Alexander, R. D. (1987). *The biology of moral systems*. Hawthorne: Aldine de Gruyter.
- Alexander, R. D. (1989). Evolution of the human psyche. In P. Mellars & C. Stringer (Eds.), *The human revolution: Behavioural and biological perspectives on the origins of modern humans* (pp. 455-513). Princeton: Princeton University Press.
- Alexander, R. D. (1990a). *How did humans evolve? Reflections on the uniquely unique species*.

 Museum of Zoology (Special Publication No. 1). Ann Arbor: The University of Michigan.
- Alexander, R. D. (1990b). Epigenetic rules and Darwinian algorithms: The adaptive study of learning and development. *Ethology and Sociobiology, 11,* 1-63.
- Alexander, R. D. (2003). Evolutionary selection and the nature of humanity. In V. Hosle & C.H. Illies (Eds.), *Darwinism and philosophy*. University of Notre Dame Press.
- Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M., & Sherman, P. W. (1979).

 Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. In N.A. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social*

- *behavior: An anthropological perspective* (pp. 402-435). North Scituate: Duxbury Press.
- Alexander, R. D., & Noonan, K. M. (1979). Concealment of ovulation, parental care, and human social evolution. In N. A. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective* (pp. 436-453). North Scituate: Duxbury Press.
- Allman, J. M. (1999). Evolving Brains. New York: Scientific American Library.
- Allman, J. M., Hakeem, A., Erwin, J. M., Nimchinsky, E., & Hof, P. (2001). The anterior cingulate cortex: The evolution of an interface between emotion and cognition. *Annals of the New York Academy of Sciences*, 935, 107-117.
- Andersson, M. (1994). Sexual selection. Princeton, NJ: Princeton University Press.
- Asfaw B., White T. D., Lovejoy C.O., Latimer B., Simpson S., & Suwa G. (1999).

 **Australopithecus garhi: A new species of early hominid from Ethiopia. Science, 284, 629-635.
- Baddeley, A. D. (1986). Working memory. Oxford: Oxford University Press.
- Begun, D. R., & Walker, A. (1993). The endocast. In A. Walker & R. Leakey (Eds.), *The Nariokotome* Homo erectus *skeleton* (pp. 326-358). Cambridge: Harvard University Press.
- Belsky, J. (1997). Attachment, mating, and parenting: An evolutionary interpretation. *Human Nature*, *8*, 361-381.
- Bermudez de Castro, J. M., Rosas, A., Carbonee, E., Nicolás, M. E., Rodríguez, J., & Arsuaga, J.-L. (1999). A modern human pattern of dental development in Lower Pleistocene

- hominids from Atapuerca-TD6 (Spain). *Proceedings of the National Academy of Sciences*, 96, 4210-4213.
- Betzig, L. L. (1986). *Despotism and differential reproduction: A Darwinian view of history*.

 New York: Aldine Publishing Company.
- Beylin, A. V., & Shors, T. J. (2003). Glucocorticoids are necessary for enhancing the acquisition of associative memories after acute stressful experience. *Hormones and Behavior*, 43, 1124-131.
- Beynon, A. D., & Dean, M. C. (1987). Crown formation time of a fossil hominid premolar tooth. *Archives of Oral Biology*, 32, 773-790.
- Beynon, A. D., Dean, M. C., & Reid, D. J. (1991). Histological study on the chronology of the developing dentition in gorilla and orangutan. *American Journal of Physical Anthropology*, 86, 189-203.
- Bird, D. W., & Bliege Bird, R. (2002). Children on the reef: Slow learning or strategic foraging? *Human Nature 13*, 269-297.
- Bjorklund, D. F., & Pellegrini A. D. (2002). *The origins of human nature: Evolutionary developmental psychology*. Washington, DC: American Psychological Association press.
- Bliege Bird, R., & Bird, D. W. (2002). Constraints of knowing or constraints of growing? *Human Nature*, 13, 239-267.
- Bloom, P. (2000). How children learn the meaning of words. Cambridge: MIT Press.
- Blurton Jones, N. & Marlowe, F. (2002). Selection for delayed maturity: does it take 20 years to learn to hunt and gather? *Human Nature 13*, 199-238.

- Blurton Jones, N., Hawkes, K., & O'Connell, J. F. (1999). Some current ideas about the evolution of human life history. In P.C. Lee (Ed.), *Comparative primate socioecology* (pp. 140-166). Cambridge: Cambridge University Press.
- Blurton Jones, N., Hawkes, K., & O'Connell, J. F. (2002). Antiquity of post-reproductive life:

 Are there modern impacts on hunter-gatherer postreproductive life spans? *American Journal of Human Biology, 14,* 184-205.
- Bock, J. (2002). Learning, life history, and productivity: Children's lives in the Okavango delta, Botswana. *Human Nature*, *13*, 161-197.
- Bogin, B. (1991). The evolution of human childhood. *BioScience*, 40, 16-25.
- Bogin, B. (1997). Evolutionary hypotheses for human childhood. *Yearbook of Physical Anthropology*, 40, 63-89.
- Bogin, B. (1999). *Patterns of human growth* (2nd edition). Cambridge: Cambridge University Press.
- Bogin, B. & Silva, M. I. V. (2003). Anthropometric variation and health: A biocultural model of human growth. *Journal of Children's Health*, *1*(2): pp. 149-173.
- Bowlby, J. (1969). Attachment and loss: Volume 1. Attachment. London: Hogarth.
- Boyer, P. (2001). *Religion explained: The evolutionary origins of religious thought.* New York, NY: Basic Books, Inc.
- Bromage, T. G. (1991). Enamel incremental periodicity in the pig-tailed macaque: a polychrome fluorescent labeling study of dental hard tissue. *American Journal of Physical Anthropology, 86,* 205-214.
- Brothers, L. (1990). The social brain: A project for integrating primate behavior and neurophysiology in a new domain. *Concepts in Neuroscience*, *1*, 27-51.

- Brunet, M., Guy, F., Pilbeam, D., Mackaye, H. T., Likius, A., Ahounta, D., et al. (2002) A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*, *418*, 14-151.
- Buchan, J. C., Alberts, S. C., Silk, J.B. & Altmann, J. (2003). True paternal care in a multimale primate society. *Nature*, 425, 179-181.
- Byrne, R. W. & Whiten, A. (Eds.) (1988) *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford: Oxford University Press.
- Byrne, R.W. (2002a). The primate origins of human intelligence. In: R. J. Sternberg & J. C. Kaufman (Eds.). *The evolution of intelligence* (pp. 79-95). Mahwah, NJ: Lawrence Erlbaum Associates.
- Byrne, R. W. (2002b). Social and technical forms of primate intelligence. In F. B. M. de Waal, (Ed.), Tree of origin: What primate behavior can tell us about human social evolution. (pp. 145-172). Cambridge, MA: Harvard University Press.
- Campbell, A. (2002). *A mind of her own: The evolutionary psychology of women.* London: Oxford University Press.
- Campbell, A., & Muncer, S. (Eds.) (1998). *The social child*. Hove, East Sussex: Psychology Press.
- Carruthers, P. (2000). The evolution of consciousness. In P. Carruthers & A. Chamberlain (Eds.), *Evolution and the human mind* (pp. 254-275). Cambridge: Cambridge University press.
- Caspari, R. & Lee, S-H. (2004). Longevity and the evolution of modernity. *American Journal of Physical Anthropology Supplement*, 41, 73-74.
- Chagnon, N. A. (1977). *Yanomamö, the fierce people* (2nd edition). New York: Holt, Rinehart and Winston.

- Chagnon, N. A. (1988). Life histories, blood revenge, and warfare in a tribal population. *Science*, *239*, 985-992.
- Chapin, H.D., . (1922). Heredity and child culture. New York: E.P. Dutton & Co.
- Chiappe, D., & MacDonald, K. (2004). The evolution of domain-general mechanisms in intelligence and learning. Manuscript under review.
- Chisholm, J. S. (1999). *Death, hope and sex.* Cambridge: Cambridge University Press.
- Clutton-Brock, T. H. (1977). Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature*, *269*, 797-800.
- Cohen, S., Doyle, W. J., Turner, R. B., Alper, C. M., & Skoner, D. P. (2003). Emotional style and susceptibility to the common cold. *Psychosomatic Medicine* 65, 652-657.
- Daly, M., & Wilson, M. (1988a). Homicide. Hawthorne: Aldine de Gruyter.
- Daly, M., & Wilson, M. (1988b). Evolutionary social psychology and family homicide. *Science*, *242*, 519-524.
- Dart, R. A. (1925). *Australopithecus africanus*: The man-ape of South Africa. *Nature, 115*, 195-199.
- Darwin, C. (1871). The descent of man, and selection in relation to sex. London: John Murray.
- Darwin, C. (1877). Biographical sketch of an infant. *Mind*, 2, 285-294.
- Darwin, C., & Wallace, A. (1858). On the tendency of species to form varieties, and on the perpetuation of varieties and species by natural means of selection. *Journal of the Linnean Society of London, Zoology, 3*, 45-62.
- Davidson, R. J., Jackson, D. C., & Kalin, N. H. (2001). Emotion, plasticity, context, and regulation. *Psychological Bulletin*, *126*, 890-906.

- Deacon, T. W. (1997). What makes the human brain different? *Annual Review of Anthropology*, 26, 337-357.
- Dean, M. C., Stringer, C. B., & Bromage, T. G. (1986). Age at death of the neanderthal child from Devil's Tower, Gibraltar, and the implications for studies of general growth and development in neanderthals. *American Journal of Physical Anthropology*, 70, 301-310.
- Dean, M. C., Leakey, M. G., Reid, D., Schrenk, F., Schwartz, G. T., Stringer, C., & Walker, A. (2001). Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature*, *414*, 628-631.
- Dressler, W. W. & Bindon, J. R. (2000). The health consequences of cultural dissonance:

 Cultural dimensions of lifestyle, social support, and arterial blood pressure in an African American community. *American Anthropologist*, 102, 244-260.
- Dunbar, R. I.M. (1997). *Gossip, grooming, and evolution of language*. Cambridge: Harvard University Press.
- Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology*, 6, 178-190.
- Ellis, L. (1994). Social status and health in humans: the nature of the relationship and its probable causes. In L. Ellis (Ed.), *Social stratification and socioeconomic inequality* (vol. 2, pp. 123-144). Westport, CT: Praeger.
- Engle, R. W. (2002). Working memory capacity as executive attention. *Current Directions in Psychological Science*, 11, 19-23.
- Field, T., Diego, M., Hernandez-Reif, M., Schanberg, S., & Kuhn, C. (2003). Depressed mothers who are "good interaction" partners versus those who are withdrawn or intrusive. *Infant Behavior & Development*, 26, 238-252.

- Finlay, B. L., Darlington, R. B., & Nicastro, N. (2001). Developmental structure in brain evolution. *Behavioral & Brain Sciences*, *24*, 263-308.
- Flinn, M. V. (1986). Correlates of reproductive success in a Caribbean village. *Human Ecology* 14, 225-243.
- Flinn, M. V. (1997). Culture and the evolution of social learning. *Evolution and Human Behavior*, 18, 23-67.
- Flinn, M. V. (1999). Family environment, stress, and health during childhood. In C. Panter-Brick & C. Worthman (Eds.), *Hormones, health, and behavior* (pp. 105-138).

 Cambridge: Cambridge University Press.
- Flinn, M. V., & England, B. G. (2003). Childhood stress: endocrine and immune responses to psychosocial events. In J.M. Wilce (Ed.), *Social & cultural lives of immune systems*, (pp. 107-147). London: Routledge press.
- Flinn, M. V., Geary, D. C., & Ward, C. V. (in press). Ecological dominance, social competition, and coalitionary arms races: Why humans evolved extraordinary intelligence.

 Evolution and Human Behavior, 25,
- Flinn M. V., Quinlan, R., Turner, M. T., Decker, S. D., & England, B. G. (1996). Male-female differences in effects of parental absence on glucocorticoid stress response. *Human Nature*, 7, 125-162.
- Fodor, J. A. (1983). *The modularity of mind: An essay on faculty psychology*. Cambridge: MIT Press.
- Foley, R. A. (1999). Hominid behavioral evolution: Missing links in comparative primate socioecology. In P. C. Lee (Ed.), *Comparative primate socioecology* (pp. 363-386). Cambridge: Cambridge University Press.

- Geary, D. C. (in press). *The origin of mind: On the evolution of brain, cognition, and general intelligence.* Washington, DC: American Psychological Association.
- Geary, D. C., & Bjorklund, D. F. (2000). Evolutionary developmental psychology. *Child Development*, 71, 57-65.
- Geary, D. C., & Flinn, M. V. (2001). Evolution of human parental behavior and the human family. *Parenting: Science and Practice*, *1*, 5-61.
- Geary, D. C., & Flinn, M. V. (2002). Sex differences in behavioral and hormonal response to social threat. *Psychological Review*, *109*, 745-750.
- Geary, D. C., & Huffman, K. J. (2002). Brain and cognitive evolution: Forms of modularity and functions of mind. *Psychological Bulletin*, *128*, 667-698.
- Gerhart, J., & Kirschner, M. (1998). *Cells, embryos, and evolution*. Oxford: Blackwell Science.
- Goodall, J. (1986). The chimpanzees of Gombe. Cambridge: Harvard University Press.
- Gopnik, A., Meltzoff, A. N., & Kuhl, P. K. (1999). *The scientist in the crib: Minds, brains, and how children learn*. New York: William Morrow & Co.
- Gould, S. J. (1977). Ontogeny and phylogeny. Cambridge: Harvard University Press.
- Haile-Selassie, Y. (2001). Late Miocene hominids from the Middle Awash, Ethiopia. *Nature*, *412*, 187-191.
- Hawkes, K. (2003). Grandmothers and the evolution of human longevity. *American Journal of Human Biology*, 15, 380-400.
- Hed, H. M. E. (1987). Trends in opportunity for natural selection in the Swedish population during the period 1650-1980. *Human Biology*, *59*, 785-797.

- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., & McElreath, R. (2001).

 Cooperation, reciprocity and punishment in fifteen small-scale societies. *American Economic Review*, 91, 73-78.
- Herdt, G., & McClintock, M. K. (2000). The magical age of 10. *Archives of Sexual Behavior*, 29, 587-606.
- Hill, K. & Hurtado, A. M. (1996a). *Ache life history: The ecology and demography of a foraging people.* New York: Aldine de Gruyter.
- Hill, K. & Hurtado, A. M. (1996b). The evolution of premature reproductive senescence and menopause in human females: An evaluation of the grandmother hypothesis. In L.Betzig (Ed.), *Human Nature: A Critical Reader*. New York: Oxford University Press.
- Hill, K., & Kaplan, H. (1999). Life history traits in humans: Theory and empirical studies. Annual Review of Anthropology, 28, 397-430.
- Hirschfeld, L. (2002). Why don't anthropologists like children? *American Anthropologist*, 104, 611-627.
- Hirschfeld, L. A. & Gelman, S. A. (1994). *Mapping the mind: Domain specificity in cognition and culture*. Cambridge: Cambridge University Press.
- Holliday, M. A. (1986). Body composition and energy needs during growth. In F. Falkner & J. M. Tanner (Eds.), *Human Growth: A Comprehensive Treatise, Volume 2* (pp. 101-117). 2nd ed. New York: Plenum Press.
- Hrdy, S. B. (1999). *Mother nature: A history of mothers, infants, and natural selection*. New York: Pantheon.

- Huether, G. (1996). The central adaptation syndrome: Psychosocial stress as a trigger for adaptive modifications of brain structure and brain function. *Progress in Neurobiology*, 48, 568-612
- Huether, G. (1998). Stress and the adaptive self organization of neuronal connectivity during early childhood. *International Journal of Developmental Neuroscience*, 16, 297-306.
- Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 303-317). New York: Cambridge University Press.
- Humphrey, N. K. (1983). Consciousness regained. Oxford: Oxford University Press.
- Irons, W. (1979). Cultural and biological success. In N. A. Chagnon & W. Irons (Eds.), *Natural selection and social behavior* (pp. 257-272). North Scituate, MA: Duxbury Press.
- Joffe, T. H. (1997). Social pressures have selected for an extended juvenile period in primates. *Journal of Human Evolution*, *32*, 593-605.
- Jolly, A. (1966). Lemur social behavior and primate intelligence. Science, 153, 501-506.
- Jolly, A. (1999). *Lucy's legacy: Sex and intelligence in human evolution*. Cambridge: Harvard University Press.
- Kano, T. (1992). *The last ape: Pygmy chimpanzee behavior and ecology*. Stanford: Stanford University Press.
- Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology*, *9*, 156-185.
- Kelly, D. B. & Brenowitz, E. (2002). Hormonal influences on courtship behaviors. In J. B.
 Becker, S. M. Breedlove, D. Crews, & M. M. McCarthy (Eds.), *Behavioral Endocrinology*, 2nd edition (pp. 289-330). Cambridge: MIT Bradford Press.

- Kiecolt-Glaser, J. K., Malarkey, W. B., Cacioppo, J. T. & Glaser, R. (1994). Stressful personal relationships: immune and endocrine function. In R. Glaser & J. K. Kiecolt-Glaser (Eds.), *Handbook of human stress and immunity* (pp. 301-319). New York: Academic Press.
- Konner, M. (1991). Universals of behavioral development in relation to brain myelination. In K.
 R. Gibson & A. C. Petersen (Eds.), *Brain maturation and cognitive development:* comparative and cross-cultural perspectives (pp. 181-223). New York: Aldine de Gruyter.
- Kudo, H. & Dunbar, R. I. M. (2001). Neocortex size and social network size in primates. *Animal Behaviour*, 62, 711-722.
- La Cerra, P. & Bingham, R. (1998). The adaptive nature of the human neurocognitive architecture: an alternative model. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 11290-4.
- Lamb, M. E., Bornstein, M. H., & Teti, D. M. (2002). *Development in infancy* (4th Edition). Mahwah, NJ: Lawrence Erlbaum Associates.
- Lancaster, J. B., & Lancaster, C. S. (1983). Parental investment: The hominid adaptation. In D. Ortner (Ed.), *How humans adapt: a biocultural odyssey* (pp. 33-65). Washington, DC: Smithsonian press.
- Lancaster, J. B., & Lancaster, C. S. (1987). The watershed: Change in parental-investment and family-formation strategies in the course of human evolution. In J. B. Lancaster, J. Altmann, A. S. Rossi, & L.R. Sherrod (Eds.), *Parenting across the life span: Biosocial dimensions* (pp. 187-205). New York: Aldine de Gruyter.

- Leakey, M. G., Feibel, C. S., MacDougall, I., & Walker, A. (1995). New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature*, *376*, 565-571.
- Leblanc, S. A. (2003). *Constant battles: The myth of the peaceful, noble savage.* New York: St. Martin's press.
- Lee, S. H., & Wolpoff, M. H. (2003). The pattern of evolution in Pleistocene human brain size. *Paleobiology*, 29, 186-196.
- Leigh, S.R. (2001). The evolution of human growth, Evolutionary Anthropology, 10, 223-236.
- Leonard, W. R., & Robertson, M. L. (1994). Evolutionary perspectives on human nutrition: the influence of brain and body size on diet and metabolism. *American Journal of Human Biology, 4,* 77-88.
- Levine, R. A., Miller, P. M., & West, M. M. (Eds.) (1988). Parental behavior in diverse societies. New Directions for Child Development 40. San Francisco: Jossey-Bass.
- Lovejoy, C. O. (1981). The origin of man. Science, 211, 341-350.
- Lovejoy, C. O., McCollum, M.. A., Reno, P.L, & Rosenman, B.A. (2003). Developmental biology and human evolution. *Annual Reviews of Anthropology*, *32*, 85-109.
- Low, B. S. (2000). Why sex matters. Princeton: Princeton University Press.
- Mace, R. (2000). Evolutionary ecology of human life history. *Animal Behaviour*, 59, 1-10.
- Macho, G. A. (2001). Primate molar crown formation times and life history evolution revisited. *American Journal of Primatology*, 55, 189-201.
- Macho, G. A. & Wood, B. A. (1995). The role of time and timing in hominid dental evolution. *Evolutionary Anthropology, 4,* 1-17.
- Maier, S. F., Watkins, L. R., & Fleschner, M. (1994). Psychoneuroimmunology: The interface between behavior, brain, and immunity. *American Psychologist*, 49, 1004-1007.

- Malthus, T. R. (1798). An essay on the principle of population as it affects the future improvement of society with remarks on the speculations of Mr. Godwin, M. Condorcet, and other writers. London: Printed for J. Johnson, in St. Paul's church-yard.
- Marmot, M. G., Smith G. D., Stansfield, S., Patel, C., North, F., Head, J., White, I., Brunner, E., & Feeney, A. (1991). Health inequalities among British civil servants: The Whitehall II study. *Lancet*, *337*, 1387-1393.
- Marmot, M. & Wilkinson, R. G. (Eds.) (1999). *Social determinants of health*. Oxford: Oxford University Press.
- Martin, R. D. (1983). Primate origins and evolution. Princeton: Princeton University Press.
- Martin, R. D., & MacLarnon, A. (1990). Reproductive patterns in primates and other mammals:

 The dichotomy between altricial and precocial offspring. In C.J. DeRousseau (Ed.),

 Primate life history and evolution (pp. 47-79). New York: Wiley-Liss.
- McClintock, M. K., & Herdt, G. (1996). Rethinking puberty: The development of sexual attraction. *Current Directions in Psychological Science*, *5*(6), 178-183.
- McHenry, H. M. (1992a). Body size and proportions in early hominids. *American Journal of Physical Anthropology*, 87, 407-431.
- McHenry, H. M. (1992b). How big were early hominids? *Evolutionary Anthropology*, 1, 15-20.
- McHenry, H. M. (1994). Behavioral ecological implications of early hominid body size. *Journal of Human Evolution, 27,* 77-87.
- Miller, G. F. (2000). *The mating mind: How sexual choice shaped the evolution of human nature*. New York: Doubleday.
- Miller, E. K., & Cohen, J. D. (2001). An integration of theory of prefrontal cortex function. *Annual Review of Neuroscience*, 24, 167-202.

- Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, *59*, 885-893.
- Mitani, J. C., & Watts, D. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour*, 61, 915-924.
- Mithen, S.J. (1996). *The prehistory of the mind: The cognitive origins of art, religion, and science*. London: Thames and Hudson.
- Miyake, A., & Shah, P. (Eds.) (1999). *Models of working memory: Mechanisms of active maintenance and executive control.* Cambridge, United Kingdom: Cambridge University Press.
- Pawlowski, B., Lowen, C.B., & Dunbar, R.I.M. (1998). Neocortex size, social skills and mating success in primates. *Behaviour*, *135*, 357-368.
- Pinker, S. (1994). *The language instinct*. New York: William Morrow.
- Pinker, S. (1997). How the mind works. New York: W. W. Norton & Co.
- Plavcan, J. M. (2000). Inferring social behavior from sexual dimorphism in the fossil record. *Journal of Human Evolution*, 39, 327-344.
- Plavcan J. M. (2001). Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology*, 44, 25-53.
- Plavcan, J. M., van Schaik, C. P., & Kappeler, P. M. (1995). Competition, coalitions and canine size in primates. *Journal of Human Evolution*, 28, 245-276.
- Portman, A. (1941). Die Tragzeiten der Primaten und die Dauer der Schwangerschaft beim Menschen: Ein Problem der vergleichenden Biologie. *Revue Suisse de Zoologie, 48,* 511-518.

- Povinelli, D. J., & Bering, J. M. (2002). The mentality of apes revisited. *Current Directions in Psychological Science*, 11, 115-119.
- Quartz, S. & Sejnowski, T. (1999). Constraining constructivism: Cortical and sub-cortical constraints on learning in development. *Behavioral & Brain Sciences*, 23, 785-792.
- Reno, P. L., Meindl, R. S., McCollum M. A., Lovejoy, C.O. (2003). Sexual dimorphism in Austrolopithecus afarensis was similar to that of humans. Proceedings of the National Academy of Sciences, 100, 9404-9409.
- Ricklefs, R. E. (1983). Avian postnatal development. In D.S. Farner, J.R. King, & K.C. Parkes (Eds.), *Avian Biology* 7 (pp. 1-83). New York: Academic Press.
- Ruff, C. B., Trinkaus, E., & Holliday, T. W. (1997). Body mass and encephalization in Pleistocene *Homo. Nature*, *387*, 173-176.
- Schultz, A. H. (1969). *The life of primates*. New York: Universe Press.
- Semaw, S., Renne, P., Harris, J. W. K., Feibel, C. S., Bernor, R. L., Fesseha, N., & Mowbray, K. (1997). 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature*, *382*, 333-336.
- Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., & Coppens, Y. (2001). First hominid from the Miocene (Lukeino Formation, Kenya). *C R Acad Sci Paris*, 332, 137-144.
- Senut, B. (2002). From apes to humans: Locomotion as a key feature for phylogeny. *Zeitschrift* fur Morphologie und Anthropologie 83, 351-60.
- Silk, J. S., Alberts, S.C. & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, *302*, 1231-1234.
- Small, M. F. (1998). Our babies, ourselves. New York: Random House.
- Small, M. F. (2001). *Kids*. New York: Doubleday.

- Smith, B. H. (1989). Dental development as a measure of life history in primates. *Evolution*, *43*, 683-688.
- Smith, B. H. (1993). The physiological age of KNM-WT15000. In A. Walker & R.E. Leakey (Eds.), *The Nariokotome* Homo erectus *skeleton* (pp, 195-220). Cambridge: Harvard University Press.
- Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*, *283*, 1657-1661.
- Smuts, B. (1985). Sex and friendship in baboons. New York: Aldine de Gruyter.
- Smuts, B. B. & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications.

 *Advances in the Study of Behavior 22, 1-63.
- Stanford C. B. (2001). The ape's gift: meat-eating, meat-sharing, and human evolution. In F. B.

 M. de Waal (Ed.), *Tree of origin: What primate behavior can tell us about human*social evolution (pp. 95-119). Cambridge: Harvard University Press.
- Stearns, S. C. (1992). The evolution of life histories. Oxford: Oxford University press.
- Steele, J. (1996). On the evolution of temperament and dominance style in hominid groups. In J.

 Steele & S. Shennan (Eds.), The archeology of human ancestry: power, sex, and

 tradition. New York: Routledge
- Symons, D. (1978). *Play and aggression: A study of rhesus monkeys*. New York: Columbia University Press.
- Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge: Harvard University Press.

- Tooby, J., & Cosmides, L. (1995). Mapping the evolved functional organization of mind and brain. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1185-1197).Cambridge: Bradford Books/MIT Press.
- Trevathan, W. R. (1990). The evolution of helplessness in the human infant and its significance for pre- and peri-natal psychology. *Pre- & Peri-Natal Psychology Journal 4(4)*, 267-280.
- United Nations (1985). Socio-economic differentials in child mortality in developing countries.

 New York: Author.
- Van Schaik, C., & Deaner, R. (2003). Life history and cognitive evolution in primates. In F. B.
 M. de Waal & P. Tyack (Eds.), *Animal social complexity: intelligence, culture and individualized societies* (pp. 5-25). Cambridge: Harvard University Press.
- de Waal, F. B. M. (1982). Chimpanzee politics. New York: Harper & Row.
- de Waal, F. B. M. (2001). The ape and the sushi master. New York: Basic Books.
- de Waal, F. B. M. & Lanting, F. (1997). *Bonobo: The forgotten ape*. Berkeley: University of California Press.
- de Waal, F. B. M. & Tyack, P. L. (Eds.) (2003). *Animal social complexity*. Cambridge: Harvard University Press.
- Ward, C. V., Walker, A., & Leakey, M. G. (1999). The new hominid species *Australopithecus* anamensis. *Evolutionary Anthropology*, 7, 197-205.
- Ward, C., Leakey, M. G., & Walker, A. (2001). Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *Journal of Human Evolution*, 41, 255-368.
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford: Oxford University Press.

- White, T. D., Suwa, G., & Asfaw, B. (1994). *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature*, *371*, 306-312.
- Whiting, B. B., & Edwards, C. P. (1988). *Children of different worlds*. Cambridge: Harvard University press.
- Williams, G. C. (1957). Plieotropy, natural selection, and the evolution of senescence. *Evolution*, 11, 398-411.
- Williams, G.C. (1966). *Adaptation and natural selection*. Princeton: Princeton University Press.
- Worthman, C. M. (1999). The epidemiology of human development. In C. Panter-Brick & C. Worthman (Eds.), *Hormones, health, and behavior* (pp. 47-104). Cambridge: Cambridge University Press.
- Wrangham, R. W. (1999). Evolution of coalitionary killing. *Yearbook of Physical Anthropology*, 42, 1-30.
- Wrangham, R., & Peterson, D. (1996). *Demonic males*. New York: Houghton Mifflin Company.
- Zihlman, A., Cronin, J., Cramer, D., & Sarich, V. M. (1978). Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees and gorillas. *Nature*, *275*, 744-746.

Figure 1 a - c: Hominid life history, cranial capacity, and sexual dimorphism.

Figure 1 (a): Cranial capacity (based on Lee and & Wolpoff, 2003; vertical lines represent normal ranges).

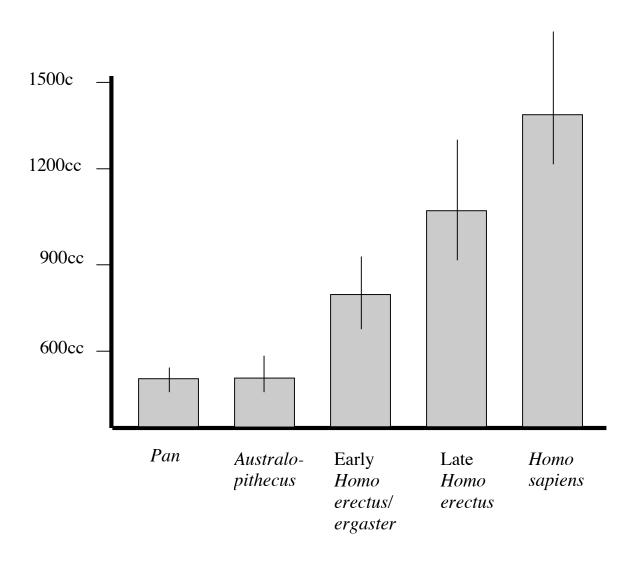


Figure 1 (b): Body mass sexual dimorphism. Question marks reflect speculative inferences from small sample sizes.

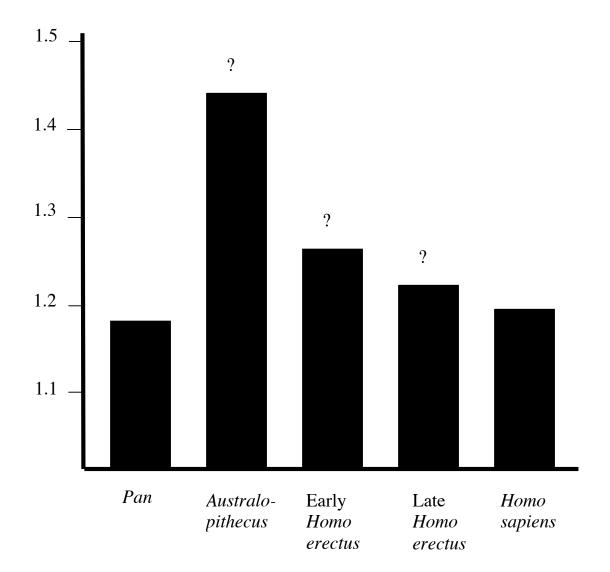


Figure 1 (c): Hominid life history stages (based on Bogin, 1999, Figure 4.9; Leigh, 2001). Adult lifespan is compressed in illustration. Question marks indicate speculation based on limited data.

