# 2 Evolution of the Human Family: Cooperative Males, Long Social Childhoods, Smart Mothers, and Extended Kin Networks

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## THE HUMAN FAMILY: KEY EVOLUTIONARY PUZZLES

Humans are characterized by a distinctive set of traits, including: (1) large brains, (2) long periods of juvenile dependence, (3) extensive bi-parental care including large transfers of information, (4) multigenerational bilateral kin networks, (5) habitual bipedal locomotion, (6) use of the upper limbs for handling tools, including throwing projectile weapons, (7) concealed, or "cryptic," ovulation, (8) menopause, (9) culture including language, and (10) lethal competition among kin-based coalitions. A few other species exhibit several of these traits; only humans, however, are characterized by the entire combination (Alexander, 2005). The evolution and co-evolution of this suite of traits present several evolutionary questions or puzzles that are central to understanding the human family. Here we first briefly describe these puzzles then suggest a resolution based on the importance of social competition during human evolution. Afterward we turn to the developmental issue of how the family social environment may affect the timing of reproductive maturation and how this timing is essential to an understanding of the family.

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## Paternal Care in Multi-Male Groups

Mammals that live in groups with multiple males—such as chimpanzees (*Pan troglodytes*)—usually have little or no paternal care, because the non-exclusivity of mating relationships obscures paternity (Clutton-Brock, 1991). In contrast, it is common for human fathers to provide protection, information, food, and social status for their children. Paternal care in humans appears to be facilitated by relatively stable pair bonds, which not only involves co-operation between mates that often endures over the lifespan, but which requires an unusual type of cooperation among co-residing males—respect for each other's mating relationships.

The relatively exclusive mating relationships that are characteristic of humans generate natural factions within the group. Mating relationships also can create alliances in human groups, linking two families or clans together. By way of comparison, in chimpanzee communities it is difficult for even the most dominant male to monopolize an estrous female; most of the males in a community mate with most of the females (Goodall, 1986). Chimpanzee males in effect "share" a common interest in the community's females and their offspring. Human groups, in contrast, are composed of family units, each with distinct reproductive interests. Men do not typically share mating access to all the group's women; consequently, there are usually reliable cues identifying which children are their genetic offspring and which are those of other men (for exceptions, see Beckerman & Valentine, 2002). Because humans live in multi-male groups yet maintain fairly stable mating relationships, the potential for fission along family lines is high. Still, human groups overcome this inherent conflict between family units to form large, stable coalitions.

This unusual tolerance among co-residential men stands in contrast to the norm of polygamous mate competition in non-human primates. Selection pressures favoring such tolerance are uncertain but likely involve the importance of both male parental investment (Geary & Bjorklund, 2000) and male coalitions for intra-specific conflict (Bernhard, Fischbacher, & Fehr, 2006; Geary & Flinn, 2001; Wrangham, 1999). We term this evolutionary puzzle "cooperative males."

## An Extended Period of Juvenile Dependence and Child Development

The human baby is unusually altricial (helpless). Infants must be carried, fed, and protected for a long period in comparison with other primates. Human childhood and adolescence are also lengthy (Bogin, 1999; Leigh, 2004; Smith, 1994).

This extension of the juvenile period that delays reproduction for much longer than for other hominoids appears costly in evolutionary terms. Parental and other kin investment continues for an unusually long time, often well into adulthood and sometimes even after parents die (Coe, 2003).

The selective pressures responsible for this unique suite of life-history characteristics appear central to understanding human evolution (Alexander, 1990a, 1990b; Bjorklund & Pellegrini, 2002; Kaplan, Hill, Lancaster, & Hurtado, 2000; Rosenberg, 2004). The delay of reproduction until at least 15 years of age involves prolonged exposure to extrinsic causes of mortality and longer generational intervals. What advantages of an extended childhood could have outweighed the heavy costs of reduced fecundity and late reproduction (Stearns, 1992; Williams, 1966) for our hominin ancestors? We term this evolutionary puzzle "long social childhoods."

## Intelligence, Information, and Female Social Power

The human brain is an astonishing organ. Its cortex comprises 30 billion neurons of 200 different types, each of which are interlinked by about 1,000 synapses, resulting in a million billion connections working at rates of up to 10 billion interactions per second (Edelman, 2006). Quantifying the transduction of these biophysical actions into specific cognitive activities—for example, thoughts and emotions—is difficult, but it is likely that humans have more information-processing capacity than does any other species (Roth & Dicke, 2005).

The human brain evolved rapidly: hominin cranial capacity tripled (from an average of about 450cc to 1,350 cc) in less than 2 million years (Lee & Wolpoff, 2003), or roughly 100,000 neurons and supportive cells per generation. Structural changes such as increased convolutions, thickly myelinated cortical neurons, lateral asymmetries, von Economo neurons, expansion of the neo-cortex, and enhanced integration of the cerebellum also appear significant (Allman, 1999; Amodio & Frith, 2006). In comparison with most other parts of the human genome, selection on genes involved with brain development was especially intense (Gilbert, Dobyns, & Lahn, 2005).

The human brain has high metabolic costs: about 50% of an infant's and 20% of an adult's energetic resources are used to support this neurological activity (Aiello & Wheeler, 1995). The obstetric difficulties associated with birthing a large-headed infant generate additional problems (Rosenberg & Trevathan, 2002). The selective advantages of increased intelligence must have been correspondingly high to overcome these costs.

The human brain is, in short, a big evolutionary paradox. It is developmentally and metabolically expensive; evolved rapidly; enables uniquely human cognitive abilities such as language, empathy, foresight, consciousness, and theory of mind; and generates unusual levels of novelty. The advantages of a larger brain may include enhanced information-processing capacities to contend with ecological pressures that involve sexually dimorphic activities such as hunting and complex foraging (Kaplan & Robson, 2002). There is little evidence, however, of sufficient domain-specific enlargement of those parts of the brain associated with selective pressures from the physical environment (Adolphs, 2003; Geary & Huffman, 2002). Indeed, human cognition has little to distinguish itself in the way of specialized ecological talents. A large brain may have been sexually selected because it was an attractive trait for mate choice (Gavrilets & Vose, 2006; Miller, 2000). However, there is little sexual dimorphism in encephalization quotient or intelligence psychometrics (Jensen, 1998).

One area in which humans are truly extraordinary is sociality. Humans are able to mentally represent the feelings and thoughts of others. Humans have unusually well-developed mechanisms for theory of mind (Amodio & Frith, 2006; Leslie, Friedmann, & German, 2004) and associated specific pathologies in this domain (Baron-Cohen, 1995; Gilbert, 2001). We have exceptional linguistic abilities for transferring information from one brain to another (Pinker, 1994), enabling complex social learning. Social and linguistic competencies are roughly equivalent in both men and women, although human mothers appear to have especially important roles in the development of their children's socio-cognitive development (Deater-Deckard, Atzaba-Poria, & Pike, 2004; Simons, Paternite, & Shore, 2001). In apparent contrast with chimpanzees and gorillas, women have substantial social influence or power, based not only on modeling a behavior, but on the use of information transmitted via language (see Hess & Hagen, 2006). We term this evolutionary puzzle of large brains, female social power, and the associated development of social competency "smart mothers."

We use the term "smart" here to describe mental capabilities and the resulting behavioral repertoire required for complex social life. Human interactions, influenced initially largely by male physical strength, were increasingly coming to be based on social information and skill. Intense inter-group competition created pressure for within-group social cohesion (Flinn, Geary, & Ward, 2005), which required not only strength but complex social strategies.

Among contemporary "tribal" populations, increased inter-group aggression is associated with decreased levels of bi-parental care (Ember & Ember, 2002; Whiting & Whiting, 1975). Bi-parental care implies, to some extent, skills for promoting enduring social relationship between a man and a woman. Such relationships, as current divorce records make clear, are not something that comes naturally to humans. Moral systems, across cultures, provided step-by-step procedures for maintaining enduring social relationships (Edel & Edel, 1959). If the ecological dominance–social competition scenario is correct (Flinn, Geary, & Ward, 2005), fathers may often have been absent, with the mother largely responsible for the development of social competence favored by intense pressure for within-group cohesion. If we wish to understand human families, we must understand how mothers prepared their altricial children for a "world that [was becoming] socially complex" (Coe, 2003, p. 110).

## Kin Networks and Multiple Caretakers

All human societies recognize kinship (Brown, 1991) as a key organizational principle. All languages have kinship terminologies and concomitant expectations of nepotism (Fortes, 1969; Murdock, 1949). Human kinship systems appear unique in the consistency of both bilateral (maternal and paternal) and multigenerational structure. These aspects of human kinship link families into broader cooperative systems and provide additional opportunities for alloparental care during the long social childhood. Human grandparents stand out as unusually important in this regard (Flinn & Leone, 2006, 2007; Hrdy, 2005).

Grandparents and grand-offspring share 25% of their genes (identical by descent), a significant opportunity for kin selection. Few species, however, live in groups with multiple overlapping generations of kin. Fewer still have significant social relationships among individuals two or more generations apart. Humans appear rather exceptional in this regard. Grandparenting is cross-culturally ubiquitous and pervasive (Murdock, 1967; Sear, Mace, & McGregor, 2000). Our life histories allow for significant generational overlaps, including an apparent, extended post-reproductive stage facilitated by the unique human physiological adaptation of menopause (Alexander, 1987; Hawkes, 2003).

The neuroendocrinological mechanisms guiding attachment processes in grand-relationships are uncertain. The maternal neuropeptide oxytocin and dopamine system is a likely candidate (for review, see Fleming, O'Day, & Kraemer, 1999; Insel, 2000). Regardless, the significance of emotional bonding between grandparents and grandchildren is beyond doubt. The evolved functions are uncertain but likely involve the exceptional importance of long-term extensive and intensive investment for the human child. The emotional and cognitive processes that guide grand-relationships must have evolved because they enhanced the survival and eventual reproductive success of grandchildren. In addition to the physical basics of food, protection, and hygienic care, development of the human child is strongly influenced by the dynamics of the social environment (Dunn, 2004; Hetherington, 2003a, 2003b; Konner, 1991). Grandparents may have knowledge and experience that are important and useful for helping grandchildren and other relatives succeed in social competition (Coe, 2003). Humans are unusual in the role of kin in alloparental care and group coalitions. We term this evolutionary puzzle "extended kin networks."

## OUR ARGUMENT: THE SOCIAL ENVIRONMENT AS A KEY SELECTIVE PRESSURE

### Information Processing Is a Core Human Adaptation

Children are especially tuned to their social world and the information it provides. The social world is a rich source of useful information for cognitive development. The human brain appears designed by natural selection to take advantage of this bonanza of data (Belsky, 2005; Bjorklund & Pellegrini, 2002; Tooby & Cosmides, 1992). "Culture" may be viewed as a highly dynamic information pool that co-evolved with the extensive information-processing abilities associated with our flexible communicative and socio-cognitive competencies (Alexander, 1979). With the increasing importance and power of information in hominin social interaction, culture and tradition may have become an arena of social cooperation and competition (Baumeister, 2005; Coe, 2003; Flinn, 2004, 2006a).

The key issue is *novelty.* One of the most difficult challenges to understanding human cognitive evolution and its handmaiden culture is the unique informational arms race that underlies human behavior. The reaction norms posited by evolutionary psychology to guide evoked culture within specific domains may be necessary but insufficient (Chiappe & MacDonald, 2005). The mind does not appear limited to a pre-determined Pleistocene set of options—such as choosing mate *A* if in environment *X*, but choose mate *B* if in environment *Y*—analogous to examples of simple phenotypic plasticity (MacDonald & Hershberger, 2005).

Keeping up in the hominin social chess game required imitation. Getting ahead favored creativity to produce new solutions to beat the current winning strategies. Random changes, however, are risky and ineffective. Hence the importance of cognitive abilities to hone choices among imagined innovations in ever-more-complex social scenarios. The theater of the mind that allows humans to "understand other persons as intentional agents" (Tomasello, 1999, p. 526) provides the basis for the evaluation and refinement of creative solutions to the never-ending novelty of the social arms race. This process of filtering the riot of novel information generated by the creative mind favored the cognitive mechanisms for recursive pattern recognition in the "open" domains of both language (Nowak, Komarova, & Niyogi, 2001; Pinker, 1994) and social dynamics (Flinn, 2006a; Geary, 2005). Cultural "traditions" passed down through the generations also help constrain the creative mind (Coe, 2003; Flinn & Coe, 2007). The evolutionary basis for these psychological mechanisms underlying the importance of social learning and culture appears rooted in a process of "runaway social selection" (Alexander, 2005; Flinn & Alexander, 2007).

## Runaway Social Selection

Darwin (1871) recognized that there could be important differences between (1) selection occurring as a consequence of interaction with ecological factors such as predators, climate, and food, and (2) selection occurring as a consequence of interactions among conspecifics, that is, members of the same species competing with each other over resources such as nest sites, food, and mates. The former is termed "natural selection" and the latter "social selection," of which sexual selection may be considered a special subtype (West-Eberhard, 1983). The pace and directions of evolutionary changes in behavior and morphology produced by these two types of selection—natural and social—can be significantly different (Fisher, 1930; West-Eberhard, 2003).

Selection that occurs as a consequence of interactions between species can be intense and unending—for example with parasite-host red-queen evolution (Hamilton, Axelrod, & Tanese, 1990) and other biotic arms races. Intra-specific social competition may generate selective pressures that cause even more rapid and dramatic evolutionary changes. Relative to natural selection, social selection has the following characteristics (West-Eberhard, 1983): (1) The intensity of social selection (and consequent genetic changes) can be very high because competition among conspecifics can have especially strong effects on differential reproduction. (2) Because the salient selective pressures involve competition among members of the same species, the normal ecological constraints are often relaxed for social selection. Hence, traits can evolve in seemingly extreme and bizarre directions before counterbalancing natural selection slows the process. (3) Because social competition involves *relative* superiority among conspecifics, the bar can be constantly and consistently raised generation after generation in an unending arms race. (4) Because social competition can involve multiple iterations of linked strategy and counterstrategy among interacting individuals, the process of social selection can become autocatalytic, its pace and directions partly determined from within, generating what might be termed "secondary red queens." For example, reoccurrence of social competition over lifetimes and generations can favor flexible phenotypic responses such as social learning that enables constantly changing strategies. Phenotypic flexibility of learned behavior to contend with a dynamic target may benefit from enhanced information-processing capacities, especially in regard to foresight and scenario building.

Human evolution appears characterized by these circumstances generating a process of runaway social selection (Alexander, 2005; Flinn & Alexander, 2007). Humans, more so than any other species, appear to have become their own most potent selective pressure via social competition involving coalitions (Alexander, 1989; Geary & Flinn, 2002), and dominance of their ecologies involving niche construction (Laland, Odling-Smee, & Feldman, 2000). The primary functions of the most extraordinary and distinctive human mental abilities—language, imagination, self-awareness, theory of mind, foresight, and consciousness—involve the negotiation of social relationships (Flinn, Geary, & Ward, 2005; Siegal & Varley, 2002; Tulving, 2002). The multiple-party reciprocity and shifting nested sub-coalitions characteristic of human sociality generate especially difficult information-processing demands for these cognitive facilities that underlie social competency. Hominin social competition involved increasing amounts of novel information and creative strategies. Culture emerged as a new selective pressure on the evolving brain.

## Evolution of the Cultural Brain

As noted above, the human brain is a big evolutionary paradox. It has high metabolic costs, takes a long time to develop, evolved rapidly, enables behavior to change quickly, has unique linguistic and social aptitudes, and generates unusual levels of informational novelty. Its primary functions include dealing with other human brains (Adolphs, 2003; Alexander, 2005; Amodio & Frith, 2006). The currency is not foot-speed or antibody production, but the generation and processing of data in the social worlds of the human brains' own collective and historical information pools. Some of the standout features of our brains that distinguish us from our primate relatives are asymmetrically localized in the prefrontal cortex, including especially the dorsolateral prefrontal cortex and frontal pole (Ghazanfar & Santos, 2004; for review, see Geary, 2005). These areas appear to be involved with "social-scenario building" or the ability to "see ourselves as others see us so that we may cause competitive others to see us as we wish them to" (Alexander, 1990b, p. 7) and are linked to specific social abilities such as understanding sarcasm (Shamay-Tsoory, Tomer, & Aharon-Peretz, 2005) and morality (Moll, Zahn, Oliveira-Souza, Krueger, & Grafman, 2005). An extended childhood seems to enable the development of these necessary social skills (Joffe, 1997).

## Evolution of the Human Family as a Nest for the Child's Social Mind

To summarize our argument, we view the human family as the nexus for the suite of extraordinary and unique human traits. Humans are the only species to live in large multi-male groups with complex coalitions and extensive paternal and alloparental care, and the altricial infant is indicative of a protective environment with intense parenting and alloparental care in the context of kin groups (Chisholm, 1999). The human baby does not need to be physically precocial, instead, 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, 1990a; Bjorklund & Pellegrini, 2002; Fisher, 2005; Geary & Bjorklund, 2000). In contrast to the slow development of the ecological skills of movement, fighting, and feeding, the human infant rapidly acquires skill with the complex communication system of human language (Pinker, 1994; Sakai, 2005). 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 (Deacon, 1997; Dunbar, 1998) and provides a new mechanism for social learning and culture.

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. Ecologically related play and activities (e.g., exploration of the physical environment) are also important (see Geary, Byrd-Craven, Hoard, Vigil, & Numtee, 2003) but appear similar to those of other primates. The unusual scheduling of human reproductive maturity, including an "adrenarche" (patterned increases in adrenal activities preceding puberty) and a delay in direct mate competition among men 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). 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 men, 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 men can identify their offspring with sufficient probability to offset the costs of investment, although reciprocity with mates is also likely to be involved (Geary & Flinn, 2001; Smuts & Smuts, 1993). Humans exhibit a unique "nested family" social structure, involving complex reciprocity among men and women to restrict direct competition for mates among group members.

Foraging men "provide a considerable portion of the energy consumed by juveniles and reproductive-aged women.... It is the partnership between men and women that allows long-term juvenile dependence and learning and high rates of survival" (Kaplan et al., 2000, p. 173). Bi-parental care may be particularly important during the period of lactation that coincides with attachment, a key component in the development of social competence. Among the Hadza foragers of Tanzania, Marlowe (2003) found that husbands appear to compensate for their wives' diminished foraging return when they have young children. Similarly, among the Ache and Hiwi foragers, women's time spent foraging and in childcare were inversely related; nursing women spent less time foraging than did non-nursing women, and women's foraging time was inversely related to their husbands foraging (Hurtado, Hill, Kaplan, & Hurtado, 1992). Based on these findings Marlowe (2003) suggests that pair bonds in human evolution may function to provisiona mate and children during a "critical period" coinciding with lactation.

Among foragers "divorce or paternal death leads to high rates of child mortality among the Ache, the Hiwi, and the !Kung, but not the Hadza" (Kaplan et al., [2000], p. 173). Similar to findings for foragers, in the world's large-scale "industrial" populations, public health studies consistently find that single mothers tend to wean their children earlier than do women living with a mate (Bar-Yam & Darby, 1997; Pande, Unwin, & Haheim, 1997). This association is probably related to the tradeoff between breastfeeding and women's work (Arlotti, Cottrell, Lee, & Curtin, 1998) that may be particularly pressing among single mothers. Prolonged nursing may have a positive influence on long-term psychomotor and neural development in well-nourished populations (Clark et al., 2006; Horwood, Darlow, & Mogridge, 2001). Breastfeeding duration has also been associated with long-term reduction in children's stress-hormone levels (Quinlan, Quinlan, & Flinn, 2003), and increased "developmental stability" (Leone, Quinlan, Hayden, Stewart, & Flinn, 2004). Nursing can be important to the mother–child bond, associated with positive emotions and attachment linked to maternal hormones, including prolactin and oxytocin (Ellison, 2001, pp. 83–126). Maternal responsiveness, related to nursing, appears to influence the development of children's attachment styles and later conjugal relations as an adult (Belsky, 1997; Chisholm, 1999). Ecological exigencies for social competence may drive the evolution of human pair bonds and regulate pair-bond stability in contemporary populations.

It is difficult to imagine how this system could be maintained in the absence of another unusual human trait: concealed, or "cryptic," ovulation (Alexander & Noonan, 1979). Human groups tend to be male philopatric (men tend to remain in their natal groups), resulting in extensive male-kin alliances, useful for competing against other groups of male kin (LeBlanc, 2003; Wrangham & Peterson, 1996). Women 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). Parents and other kin may be especially important for the child's mental development of social and cultural maps because they can be relied upon as landmarks to provide relatively honest information. From this perspective, the evolutionary significance of the human family in regard to child development is viewed more as a nest from which social skills may be acquired than merely an economic unit centered on the sexual division of labor (Flinn, Ward, & Noone, 2005).

## Evolution of the Human Family: The Fossil Evidence

A prolonged childhood in the latter part of human evolution can be seen in delayed dental maturation rates occurring after the early evolution of *Homo*. The teeth of early *Homo erectus* (1.6 million years) developed at similarly relatively rapid rates as those of apes and australopithecines (Dean et al., 2001; Smith, 1993). However, they are modern in pattern by 800,000 years ago (Bermudez de Castro, Rosas, Carbonell, Nicolas, Rodriguez, & Arsuaga, 1999), and certainly in rate by 150,000 years ago (Guatelli-Steinberg, Reid, Bishop, & Larsen, 2005; see also Dean et al., 2001). Thus, by the appearance of *Homo sapiens*, at least, rates of juvenile development appear to have slowed to modern human levels.

During this time period, brain size increased roughly 50%, from 800–900 cc to 1,200–1,600 cc. At this same time, female body size increased markedly from about three to four feet in stature to four to five feet, with a corresponding estimated 50% increase in body mass (McHenry 1992a, 1992b; Ruff, Trinkaus, Walker, & Larsen, 1993). These brain size increases were associated with a change in pelvic structure permitting the birth of larger-brained infants (Ruff, 2002). It may be that this change in body size and pelvic structure permitted the initial brain size increase without altering selection on timing of birth and rate of brain growth. Subsequent brain size increase, then, would have necessitated more altricial infants with a greater percentage of brain growth occurring post-natally (Portman, 1941). This, and the slowing rates of development during this period, may reflect intensified selection for a long period of dependency and learning throughout the evolution of *Homo erectus*, appearing in roughly modern human form by the appearance of *Homo sapiens*.

With the origins of *Homo*, female body size increased dramatically, and although men increased in size, the change was not as pronounced, resulting in a decrease in sexual dimorphism (McHenry 1992a, 1992b; Ruff et al., 1993). Selection for larger women may have been due to increasing fecundity and the ability to produce larger, higher-quality infants, perhaps facilitated by increasing ability to extract higher-quality resources from the environment more consistently (Ungar, Grine, Teaford, & El Zaatari, 2006). A lack of concomitant selection for a similar magnitude of increasing male size is what probably reflects changing male reproductive strategies. Although its magnitude is the subject of current debate, most indications are that *Australopithecus* species were more dimorphic in body mass than later hominins (Cunningham, Cole, Jungers, Ward, & Wescott, 2005; Plavcan, Lockwood, Kimbel, Lague, & Harmon, 2005; but see Reno, Meindl, McCollum, & Lovejoy, 2005). This change in dimorphism likely reflects changing patterns of social behavior (e.g., Plavcan & Van Schaik, 1997a, 1997b). High levels of sexual dimorphism are associated with extensive and intense mate competition in extant primates (Plavcan, 2000). Reduced dimorphism in hominoids is associated with stable male–female mating relationships (hylobatids, humans) (Plavcan, 2000; Plavcan & Van Schaik, 1997a) and also with male–male coalitions (chimpanzees, humans) (Pawlowski, Lowen, & Dunbar, 1998; Plavcan & Van Schaik, 1997a, 1997b). Both of these systems offer less relative advantage for large male size than do other hominoid social systems. It is reasonable to hypothesize that either, and perhaps both, of these social changes were taking place early in the evolution of *Homo*. An increase in infant altriciality necessitates greater social support for women, and almost certainly paternal and alloparental care. Fairly exclusive mating relationships and cooperative kin networks would have permitted both of these changes.

## Ecological Variation in Parenting, Pair Bonds, and Life-History Development

Social competence is developmentally expensive in time, instruction, and parental care. Costs are not equally justified for all expected adult environments. The human family may help children adjust development in response to environmental exigencies for appropriate tradeoffs in life-history strategies. Life history reflects two basic "decisions" (see Roff, 2002): whether to reproduce now or later, and how much to invest in each offspring. If all else is equal, then organisms should begin to reproduce as soon as possible to maximize fitness. But when fitness hinges on accumulation of resources and skills (including social skills), delaying reproduction is appropriate (Roff, 2002; Geary & Bjorklund, 2000). Long delays, however, can reduce fitness through a shortened reproductive span, discounted reproduction, and mortality exposure. Parental care in early childhood appears to affect life-history strategies in humans (Chisholm, Quinlivan, Petersen, & Coall, 2005; Draper & Harpending, 1982; Quinlan, 2003), suggesting a "rule of thumb" for development (Belsky, Steinberg, & Draper, 1991). Direct parental care received during childhood may determine whether development continues or not and indicates appropriate adult strategies. If a child perceives that "parental investment" (PI) is consistent and forthcoming, then she should delay reproduction and emphasize high levels of PI herself. High levels of PI indicate an environment in which offspring success is sensitive to parental care, and a long developmental period should improve offspring social competency. Delayed reproduction coupled with high parental investment is called a "parenting-effort strategy." If PI is not forthcoming, then the child should accelerate reproductive development. Low levels of PI may indicate that success is not dependent on parenting, because environmental risks cannot be avoided through additional parental care (Chisholm, 1999; Quinlan, 2003, 2006). If PI is not forthcoming, then delaying reproduction may reduce fitness. Therefore, limited PI should predict accelerated maturation. A strategy characterized by early maturity coupled with low parental investment is called "mating effort."

The nature of risk in an environment should influence strategic choices. "Risk" can be defined as "unpredictable variability in the outcome of an adaptively significant behavior" (Winterhalder & Leslie, 2002, p. 61). If risk is high, then parental effort might be wasted because child outcomes are determined by chance rather than parenting (Quinlan, 2007; see also Scheper-Hughes, 1992). Hence, high fertility and lower levels of parental investment per child are predicted to enhance parents' fitness. But if extrinsic risk is low, then more children survive to reproduce, and responsive parenting can promote children's ultimate success as members of their society. If knowledge, skill, and social competence lead to success (Flinn, 2004; Kaplan et al., 2000), then low fertility and higher levels of parental investment are predicted to enhance parents' long-term fitness (Mace, 2000). The nature of parental care during childhood may indicate appropriate adult strategies and affect developmental pathways tuned to socio-environmental risk.

The quality of pair bonds is a key feature in theories of human life-history development. Pair-bond stability and father involvement may be reliable indicators of local resource stability and the long-term benefits of parental care.

This hypothesis is based in parental investment theory (Clutton-Brock, 1991; Trivers, 1972). Parental investment is defined as expenditures (cash, time, attention, etc.) benefiting one offspring at a cost to parents' ability to invest in other offspring or reproductive opportunities (Clutton-Brock, 1991, p. 9). The theory predicts father abandonment in environments where paternal care does not benefit men's fitness (Trivers, 1985). "Aloofness" between women and their mates may influence socialization practices that shape adult behavior (Draper & Harpending, 1982).

Stress response systems may link parenting to reproductive development (Cameron, Champagne, Parent, Fish, Ozaki-Kuroda, & Meaney, 2005; Chisholm, 1999; Ellis, 2004). Unresponsive parenting is positively associated with children's stress-hormone levels (cortisol) (Ellis, Essex, & Boyce, 2005; Flinn, 2006b) and autonomic reactivity (reviewed in Boyce & Ellis, 2005). Early life stress has been associated with difficulty in bonding and "affiliative" behavior as adults (Henry & Wang, 1998). Although pathologically high stress may significantly delay reproductive development (Henry & Wang, 1998), moderately stressful family environments are associated with accelerated maturation in healthy, well-nourished populations (Ellis & Garber, 2000; Moffitt, Caspi, Belsky, & Silva, 1992). Timing of stressful family events may influence the strength of developmental effects because organizational influences are strongest in early childhood (West-Eberhard, 2003).

Rodent models of adaptive stress-response systems and related behavioral and reproductive strategies have identified maternal behavior as a mechanism that communicates ecological conditions to offspring (e.g., Cameron et al., 2005). Children's experience of maternal behavior throws regulatory switches associated with a developmental cascade, including sympathetic adrenomedullary (autonomic) and adrenocortical (cortisol) reactivity, timing of puberty, defensive responses, and reproductive behavior.

Among humans, warm and supportive family environments have been found to predict heightened autonomic reactivity (Ellis et al., 2005), early puberty (reviewed in Ellis, 2004), and development of high parenting-effort life-history strategies (Quinlan, 2003). Pair bonds apparently support warm, affectionate family environments (Quinlan, 2003). Mothers often face a critical choice between childcare and work. Tradeoffs between parenting and production create pressure for cooperative childrearing among humans. Nursing often taxes mothers' time and energy in ways that other childcare does not; hence, parental cooperation may be particularly important during lactation (Marlowe, 2003). A child's father may be especially well situated to assist the nursing mother because he and the mother share identical genetic interest in their children's success. Other potential helpers may not share such "symmetrical" interests with a child's mother.

## SUMMARY AND CONCLUDING REMARKS

Human childhood is a life-history stage that appears 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. Mastering the social environment presents special challenges for the human child. Social competence is difficult because the target is constantly changing and similarly equipped with theory of mind and other cognitive abilities. Here we suggest that family environment, including care from fathers and grandparents, is a primary source and mediator of the ontogeny of social competencies.

Following the ecological-dominance/social-competition model, human family systems and child-development strategies may have evolved in response to a cycle of inter-group conflict on a multigenerational time scale. Human developmental plasticity appears consistent with cycling on "cultural" time scales—that is, over the course of generations that coincide with violent population expansions followed by periods (generations) of stasis in which competition becomes more subtle and social rather than violent. Bi-parental care enhances children's social competence during non-warfare periods, but mothers may take on increased socialization responsibilities, perhaps with the help of grandmothers, during times of intense inter-group conflict.

An evolutionary developmental perspective of the family can be useful in these efforts to understand this critical aspect of a child's world by integrating knowledge of physiological causes with the logic of adaptive design by natural selection. Human biology has been profoundly affected by our evolutionary history as unusually social creatures, including, perhaps, a special reliance upon smart mothers, cooperative fathers, and helpful grandparents. Indeed, the mind of the human child may have design features that enable its development as a group project, guided by the multitudinous informational contributions of its ancestors and co-descendants (Coe, 2003).

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