

# Evolution of Human Parental Behavior and the Human Family

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## SYNOPSIS

**Objective.** To develop an evolutionary model that integrates human parenting and family formation with ideas about the evolved functions of distinctive human characteristics, such as concealed ovulation and sophisticated sociocognitive competencies. **Design.** Theoretical and empirical research across scientific disciplines is reviewed. The emphasis is on ecological and social conditions that covary, across species, with parenting, family formation, and potentially coevolving characteristics, such as a long developmental period. **Results.** For humans, social competition through coalition formation emerges as the key selective pressure that readily explains the coevolution of a constellation of characteristics that covary with parenting and family formation, including a lengthy developmental period, reduced sexual dimorphism, concealed ovulation, menopause, complex kinship networks, large brains, and sophisticated sociocognitive competencies. Individual and cross-cultural variations in patterns of parenting dynamics and family formation are viewed as adaptive phenotypic responses to different ecological and historical conditions. **Conclusions.** Human parenting and family formation are features of a coevolving suite of distinctive human characteristics, the evolutionary function of which is to facilitate the formation of kin-based coalitions for competition with other coalitions for resource control. In this view, a central function of human parenting and the human family is to provide a context for the development of socio-competitive competencies appropriate to the local ecology.

## INTRODUCTION

Parenting involves the protection and transfer of energy, information, and social relations (e.g., status) to offspring. Natural selection has fine-tuned the mechanisms that serve these ends for the specific demands of each species' ecology (e.g., Clutton-Brock, 1991). African hominoids, including chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), and humans (*Homo sapiens*; Gagneux et al., 1999), share a number of parenting mechanisms with other placental mammals, including internal gestation, lactation, and attachment mechanisms involving neuropeptides such as oxytocin. These

hominoids differ from most other mammals with respect to a life history strategy that involves intensive parenting over a long developmental period and, for some of these species, with respect to the importance of the social activities of males. As an example, for both gorillas and chimpanzees, the direct or incidental protection of offspring from infanticidal males is a critical component of these social activities (Goodall, 1986; Hrdy, 1999; Watts, 1989).

Whether or not human males are infanticidal, human beings take the general hominoid pattern to an extreme, in terms of intensive parenting over an extremely long developmental period, in terms of the critical importance of the social activities of men, and in terms of other later described features. The importance of social activities and especially social competition has, in fact, been emphasized in some models of hominoid evolution (Alexander, 1974, 1989; Byrne, 2000; Humphrey, 1976). The goal here is to take these ideas one step further by proposing a conceptual model that integrates social competition in hominoid evolution with patterns of parenting dynamics, family formation, and the broader suite of unusual human characteristics described in Table 1. The model is built around the basic evolutionary logic that selection pressures will result in the evolution of characteristics that covary with survival and reproductive outcomes (Price, 1970) and the assumption that at a social and behavioral level these characteristics function to allow individuals to attempt to gain access to and control of the associated resources, such as food, mates, and

**TABLE 1**  
Unique and Unusual Human Characteristics

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- (1) A very large brain and complex social competencies.
    - (A) The human neocortex is 35% to 60% larger than expected for a primate of the same overall body and brain size (Rilling & Insel, 1999).
    - (B) It appears that the neocortex is larger than that of other primates in those areas that support social competencies that are unique to humans (Rilling & Insel, 1999) — that is, theory of mind (Baron-Cohen, 1995) and language (Pinker, 1994).
  - (2) High levels of paternal investment.
    - (A) Paternal investment is only evident in 3% to 5% of mammalian species (Clutton-Brock, 1989).
    - (B) Even for these species, humans are unique in that paternal investment occurs in a social context of large multimale – multifemale communities, and where most adult members of these communities reproduce (Alexander, 1990; Geary, 2000).
  - (3) Concealed ovulation and continuous, nonreproductive sexual activity (Alexander, 1990).
  - (4) Children have a very long developmental period, relative to other comparably sized mammals and primates, and are highly dependent on adult caregiving (Bogin, 1997; McHenry, 1994a).
  - (5) Menopause (Alexander, 1990).
  - (6) There is only one species of *Homo* (Alexander, 1989; Wood & Collard, 1999).
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territory (Geary, 1998). At the core of the model is the proposal that the primary impediment to achieving control over these essential but limited resources is the conflicting interests of other human beings. In this view, competition with other human beings is an evolutionary force in and of itself and the key selection pressure driving the dynamics of human parenting, family formation, and the evolution of the suite of coevolving characteristics described in Table 1 (Alexander, 1990).

As a preview of our model, consider that an extended developmental period, a large brain, and complex social competencies tend to covary and vary with the complexity of the social ecology of primate species (Barton, 1996; Dunbar, 1993; Joffe, 1997). Complex social ecologies, in turn, are characterized by kin-based coalitions that compete and cooperate to facilitate access to and control of essential resources. As with these other species, human social competition is often coalitional, and the defining features of *H. sapiens* described in Table 1 are conceptualized as evolutionary adaptations that function to facilitate the formation of competition-related social networks, including families. Concealed ovulation, and nonreproductive sexuality, for instance, function to maintain extended male – female relationships and are features of human social dynamics that have coevolved with male parenting and the motivational disposition to form nuclear families (Alexander & Noonan, 1979; Dunbar, 1995; Geary, 2000; Pasternak, Ember, & Ember, 1997).

The family and wider kinship networks function to create a social ecology that facilitates the feeding and protection of children and that supports the long developmental period and activities (e.g., peer relationships) needed to acquire sociocompetitive competencies. In this view, the relations between parenting and child outcomes are predicted to be nuanced, varying from one child to the next and from one ecology to the next. The ultimate function of parental behavior is, however, the same: to provide a social context that enables the acquisition of sociocompetitive competencies. These competencies often involve social skills that enable the cooperative formation of coalitions, but this form of cooperation is ultimately a social strategy to facilitate competition with other coalitions and to gain access to and control over essential resources.

Because the model that integrates all of these human characteristics is based on a complex evolutionary scenario, we begin with a brief tour of the basics of evolutionary mechanisms and the logic of natural selection. The tour ultimately leads to discussion of evolutionary mechanisms and natural selection in a dynamic, complex social context. The next turn is to human evolution: In the second section, the focus is on evolutionary changes in social dynamics, as these might be inferred from patterns in the fossil record (e.g., sexual dimorphisms in physical size and change in brain size)

and patterns in extant primates. The goal is to develop a general picture of the evolution of human social dynamics, which then leads to the final destination: The dynamics of human parenting and family formation as seen today. The foci of this final section are on exploring the social and ecological moderators of family formation, elaborating the classic definition of parental investment (PI) in a way that incorporates aspects of social competition that appear to be uniquely human, and generating predictions to guide future research on parenting and families.

## EVOLUTIONARY LOGIC AND SOCIAL DYNAMICS

The goal of this section is to provide the background needed to comprehend the evolutionary process and the principles and patterns used to make inferences about the evolution of human parental behavior as well as other features noted in Table 1. The first part provides discussion of natural selection, and the second illustrates the process in a social context. The final parts provide overviews of the relation between evolution and development, and evolution and parenting.

### Natural Selection

The fundamental observations and inferences that led to Darwin's (and Wallace's) insights regarding natural selection and evolutionary change are shown in Table 2. One of these was with respect to the importance of individual differences. "These individual differences are of the highest importance for us, for they are often inherited, as must be familiar to every one; and they thus afford materials for natural selection to act on and accumulate" (Darwin, 1872, p. 34): Individual differences largely arise as a result of sexual reproduction (e.g., Hamilton & Zuk, 1982; Williams, 1975). The process of natural selection occurs when variability in a characteristic, such as degree of parental protection of offspring, covaries with variability in survival (e.g., of offspring) or reproductive outcomes (Price, 1970). If the characteristic is inherited, then the survivors will produce offspring who, as adults, will also have a behavioral tendency to provide greater rather than lesser degrees of parental protection of offspring. If the characteristic continues to covary with survival and reproductive outcomes in the offspring's generation, then the process will repeat itself. Over many generations and sometimes in a single generation there is a change in the selected characteristic such that the average individual in the population now shows greater levels of parental protection than did the average individual several generations earlier. This process of natural selection shapes species

TABLE 2  
Darwin's Observations and Inferences

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Observation

- (1) All species have such high potential fertility that populations should increase exponentially.
- (2) Except for minor annual and rare major fluctuations, population size is typically stable.
- (3) Natural resources are limited, and in a stable environment they remain constant.

Inference

- (1) More individuals are borne than can be supported by available resources, resulting in competition for those resources that covary with survival prospects.

Observation

- (1) No two individuals are exactly the same; populations have great variability.
- (2) Much of this variability, or individual differences, is heritable.

Inference

- (1) Prospects for survival are not random but covary with the heritable characteristics (genetics) of individuals. The resulting differential survival is natural selection.
  - (2) Over generations, natural selection leads to gradual change in the population — that is, microevolution — and production of new species — that is, macroevolution or speciation.
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*Note.* Observations and inferences are based on Darwin (1859) and Mayr (1982).

to their ecology and will occur whether the trait is physical, physiological, or behavioral.

Thus, heritable individual differences provide the grist for evolutionary selection. Given that nearly all features of human anatomy, physiology, behavior, and cognition show individual variability that is partly heritable, they are all potentially subject to selection pressures (e.g., Bouchard, Lykken, McGue, Segal, & Tellegen, 1990), including traits that can influence the dynamics of parenting and family formation (Geary, 2000; McGue & Lykken, 1992; Pérusse, Neale, Heath, & Eaves, 1994; Plomin, McClearn, Pedersen, Nesselroade, & Bergeman, 1989). The process of selection acting on variability can be complicated, however. Selection pressures can reduce or eliminate heritable variability and thus many traits that have undergone strong selection in the past no longer show heritable variability (e.g., all genetically normal human beings have two legs, an inherited but nonvariable characteristic). Selection pressures can also vary from one generation to the next or from one geographical region to the next. At times — when food is abundant and predators and parasites are scarce — selection pressures are weak, and individual differences do not covary with survival and reproductive outcomes. Strong selection results when competition is intense and individual variability in associated traits covaries strongly with survival and reproductive outcomes (e.g., Grant & Grant, 1989, 1993).

For all species there are many different forms of selection pressure, including parasites (e.g., those causing infectious disease), competition with other species (e.g., predators), and competition with conspecifics — that is, members of the same species. As noted, when resources are limited, competition with conspecifics can be understood as resulting from attempts to gain access to and control of the social (e.g., competition over mates), biological (e.g., food), and physical (e.g., nesting sites) resources that covary with survival and reproductive outcomes (Geary, 1998). Characteristics that result in the achievement of this control will enhance survival and reproductive prospects and thus evolve. In other words, Darwin's (1859) conceptualization of natural selection as resulting from a struggle for life is more precisely defined as a struggle to gain access to and control of the resources that support life and that allow one to reproduce.

### Evolution and Social Ecology

For species that live and evolved in complex social systems, survival and reproduction are highly contingent on the behavior of conspecifics (Maynard Smith & Price, 1973). Mating dynamics provide the clearest example and are termed *sexual selection* (see Andersson, 1994; Darwin, 1871; Geary, 1998). Sexual selection involves two general processes: intrasexual competition over access to mates, usually male – male competition, and intersexual choice of mating partners, usually female choice. In most mammalian species, males compete one-on-one for access to mates, but in a few species males form coalitions, or social networks, to enhance their competitive abilities (Wrangham, 1999). The Social Coalitions section illustrates coalition formation in the chimpanzee and describes how coalition formation covaries with reproductive outcomes. The second part sketches the fundamentals of coalition formation, or social networking, and provides a conceptual benchmark for later discussion of human social dynamics, the human family, and the functions of parenting.

*Social coalitions.* Chimpanzee communities are composed of coalitions of males and subgroups of females and their offspring (Goodall, 1986; Wrangham, 1986). Although social relationships among females can be quite intense (de Waal, 1993; Pusey, Williams, & Goodall, 1997), the focus here is the cooperative behavior of male coalitions, as related to the sexual politics of intra- and intercommunity relationships (de Waal, 1982; Goodall, 1986). Male coalitions are highlighted because they are unusual among primates and because they appear to be an important feature of human social evolution. Within communities, small coalitions of males cooperate to achieve social dominance over other males and coalitions and

thereby gain control over the social and sexual behavior of other community members (Mitani, Merriwether, & Zhang, 2000; Riss & Goodall, 1977). The function of this coalitional behavior is largely to control the mating activities of other community members and, through this, control of reproductive outcomes.

These smaller within-community coalitions will often cooperate and merge to form larger coalitions that then patrol the border of their territory and make incursions into the territory of neighboring communities (Goodall et al., 1979). When members of such patrols encounter one another, the typical response is pant-hooting (a vocal call) and physical displays on both sides, with the smaller group eventually withdrawing. At other times, meetings between patrols from one group and members of neighboring communities are deadly. Goodall (1986) described a series of such attacks by one community of chimpanzees on their southern neighbor. Over a 4-year period, the southern group was eliminated, one individual at a time, by the northern community, which then expanded their territory to include that of the now-extinct southern group. The result for the successful group was the acquisition of prime feeding areas and the recruitment of females into the community. In other words, coalitional aggression in the chimpanzee often results in increased levels of access to and control of the physical (territory), biological (e.g., fruit trees), and social (e.g., mates) resources that covary with survival and reproductive outcomes.

As with chimpanzees, social cooperation and competition appear to covary with survival and reproductive outcomes in other species in which coalitions form (e.g., Foley, 1996, 1999; Hamilton, 1964; Packer, Gilbert, Pusey, & O'Brien, 1991; J. E. Strassmann, Zhu, & Queller, 2000; Wrangham, 1999). For all of these species, coalitional behavior, or any form of social networking, can be readily understood as an aspect of the survival and reproductive strategies of each individual in the coalition and not as an adaptation for the species or even the wider group (Alexander, 1979; Williams, 1966). This is because individuals in successful coalitions achieve increased access to and control of essential resources — levels of access and control that would not be achievable if the individuals acted alone.

*Inclusive fitness, reciprocal altruism, and social dynamics.* The survival and reproductive benefits associated with the formation of coalitions result in the evolution of a form of social “deep structure.” The deep structure is expressed as a motivational and behavioral disposition to create a social organization that reflects the associated selection pressures (Foley & Lee, 1989). For coalitional species, the motivational disposition results in the attraction of individuals to one another and the resulting formation of social networks. The cooperative focus of these social networks will be on achiev-



ing the ends that resulted in the evolution of the deep structure, such as mate access in male chimpanzees. Across species, the degree of social attraction, or the extent to which one individual is likely to cooperate with another in coalition formation, is influenced by genetic relatedness and reciprocal altruism (Hamilton, 1964; Trivers, 1972; for examples and further discussion see Altmann et al., 1996; Caporael, 1997; de Waal, 1993).

The attractive force of genetic relatedness can be understood in terms of inclusive fitness (Hamilton, 1964). Here, the focus is on the reproductive success (i.e., number of offspring surviving to reproduce) of the individual and the individual's effect on the reproductive success of kin. This is because behaviors that benefit kin will necessarily contribute to the individual's overall genetic contribution to the next generation, which is represented by the combination of the individual's offspring and the offspring of kin. An important feature of this behavior is that it often does not result in a one-to-one exchange—that is, one member of a dyad (e.g., a parent) may invest more in the other member (e.g., offspring) than he or she receives in return. The degree to which an unequal degree of exchange is tolerated should be—and appears to be in those species in which it has been empirically assessed (e.g., Packer et al., 1991)—a direct function of degree of genetic relatedness (Hamilton, 1964; Trivers, 1974; West-Eberhard, 1975).

Reciprocal altruism, in contrast, involves exchanges between individuals who are not necessarily kin. Most basically, reciprocal altruism involves an exchange of information, resources, or social support that is beneficial from the perspective of both parties (Bugental, 2000; Trivers, 1971). The benefit of mutually cooperative behavior is the attractive force that results in the formation and maintenance of the relationship, termed *friendship* by psychologists (Hartup & Stevens, 1997). At the same time, these benefits, like those directed toward kin, are ultimately aspects of the survival or reproductive strategies of both parties.

There are also forces that repel and thus act to disrupt individual relationships and social networks. These forces are conflicts of interest (e.g., over the distribution of resources) and the cost of maintaining reciprocal relationships. Even among kin, the genetic interests of two individuals, such as a parent and offspring, will differ to some degree. Conflict arises as one individual attempts to get more resources from the other than the other is willing or able to give based on their best or self-interest (Trivers, 1974).

## Evolution, Sociality, and Development

When survival and reproduction are intimately linked to the development and maintenance of social networks, the complexity of daily living increases considerably. Not only does the individual have to become a



member of one such network, if not many such networks, the individual and the network must effectively compete or cooperate with other networks in the social ecology. The complexity results from the increase in the number of conspecifics the individual must come to know and maintain some form of relationship; the dynamics of the relationships among members of the network; and the politics, so to speak, of relations with other networks (Byrne, 1997; de Waal, 1982; Dunbar, 1998). Given this, it is not surprising that across species there is a direct relation between the species' social complexity (e.g., as indexed by average group size) and brain size (Barton, 1996; Dunbar, 1993, 1998; Sawaguchi, 1997). This finding suggests that brain and cognitive evolution have been, at least in part, a response to the complexities of social life (Alexander, 1989; Humphrey, 1976).

A complex social life and a large brain are also associated, at least across species of primates, with a long juvenile period (Joffe, 1997). Although there are several explanations for this relation (Charnov, 1993; Ross & Jones, 1999), it appears that one function of the developmental period is to learn about the complexities of social life, seek a niche in the wider social ecology, and test and refine the social strategies used to gain access to and some level of control of essential resources (Blurton Jones, Hawkes, & O'Connell, 1999; Geary, 1998; Mayr, 1974). The emergence of these social competencies must per force result from an interaction between genes and environment — that is, the result of an epigenetic process (Bornstein, 1989; Gottlieb, 1992). Genetic constraints ensure that infants and juveniles attend to and process the appropriate forms of social information (e.g., the faces of conspecifics) and engage in species-typical social behaviors (e.g., rough-and-tumble play). The potential for experience-driven modification of the supporting sociocognitive and emotional systems is likely, given the flux and dynamics of social relationships (e.g., MacDonald, 1992). Knowledge of the personality, social strategies, and so forth of other conspecifics in the local community as related to one's own personality, social skills, and so forth cannot be genetically prespecified. Rather, the knowledge and competencies needed to successfully compete in the local social ecology are predicted to be shaped through play, social discourse, and parental influence — activities constrained by species-typical patterns (e.g., Geary, 1999; Low, 1989).

A long developmental period has an inherent cost, however: the risk of death before the age of reproduction. In fact, evolution will relentlessly select for a short developmental period and thus a short reproductive cycle unless the benefits of delayed maturation outweigh the risks of dying before reproducing (Williams, 1957). One strategy for reducing the risk of premature death is to situate reproduction within a context that buffers infants and juveniles from potential threats. In many primate species this context is provided by female kin groups (Wrangham, 1980). These

kin-based female coalitions compete to secure and retain access to the resources, such as fruit trees, that covary with survival prospects. Offspring borne in coalitions that gain control of these resources are healthier and survive in greater numbers than do offspring borne in other networks (Silk, 1987). For these female-bonded primate species, the formation of stable social networks provides the context that reduces offspring mortality risks and allows for the long developmental period needed to learn the nuances of living in a complex social community, as well as other complex skills such as those involved in foraging (Barton, Purvis, & Harvey, 1995).

The evolutionary factors underlying the relations among social complexity, the length of the developmental period, and brain size are not fully understood (e.g., Ross & Jones, 1999) but are nonetheless consistent with coevolutionary processes. In theory, slight improvements in social networking reduce mortality rates to such a degree that offspring with somewhat larger brains, more sophisticated sociocognitive competencies, and a somewhat longer developmental period survive to adulthood in sufficient numbers. As adults, these individuals are more socially sophisticated and more likely to form effective competition-related coalitions than their faster maturing conspecifics, and they will likely have a survival and reproductive advantage, to the extent that social coalitions provide such an advantage. The more socially sophisticated adults form more complex social networks, which, in turn, further reduce offspring mortality rates. Over many generations, these coevolutionary processes can result in highly complex social systems, a long developmental period, large brains, and complex sociocognitive systems.

### Evolution and Parenting

Although Darwin (1871) identified and defined the principles of sexual selection (e.g., mate choice), he did not elaborate on the evolutionary origins of these principles. In fact, it is only recently that some level of consensus has been reached regarding the origins of intersexual choice and intrasexual competition (Cronin, 1991). Early contemporary models of the origins of these forms of sexual selection were provided by Williams (1966, 1975) and Trivers (1972) and focused on sex differences in parental care, specifically sex differences in the relative costs and benefits of producing offspring.

Trivers (1972) formalized these relations in his model of PI and sexual selection. In this model, each individual's overall reproductive effort is a combination of mating effort (e.g., time spent searching for mates) and parental effort, or PI. PI is any cost (e.g., time, energy) associated with raising offspring that reduces the parent's ability to produce or invest in other offspring (Trivers, 1974). Given that some level of PI is necessary for the re-

productive success of both parents, the nature of the PI provided by females and males creates the basic dynamics of sexual reproduction and sexual selection. In Trivers' (1972, p. 140) words

The sex whose typical parental investment is greater than that of the opposite sex will become a limiting resource for that sex. Individuals of the sex investing less will compete among themselves to breed with members of the sex investing more.

Stated somewhat differently, if one sex provides more than his or her share of PI, then members of that sex become an important reproductive resource for members of the opposite sex (Dawkins, 1989). Basically, the reproductive success of members of the lower investing sex is more strongly influenced by the number of mates that can be found than by investing in the well-being of individual offspring, whereas the reproductive success of members of the higher investing sex is more strongly influenced, in most cases, by investment in offspring than in finding mates.

In this view, the dynamics of sexual selection are influenced by the ways in which each sex distributes their reproductive effort across mating and parenting (Clutton-Brock, 1991), which, in turn, is influenced by a variety of factors. A full discussion of these factors is beyond the scope of this treatment (for reviews, see Andersson, 1994; Emlen & Oring, 1977; Geary, 1998, 2000), but one of these merits brief mention: the potential rate of reproduction (Clutton-Brock & Vincent, 1991). Across species, it is generally the case that the sex with the higher potential rate of reproduction invests more in mating effort than in parental effort, whereas the sex with the lower rate of reproduction invests more in parental effort than in mating effort. This is because, following mating, members of the sex with the higher potential rate of reproduction can rejoin the mating pool more quickly than can members of the opposite sex, and it is often in their reproductive best interest to do so, particularly when biparental care is not necessary for the viability of offspring (Clutton-Brock, 1991).

For mammalian species, internal gestation and obligatory postpartum female care result in a slower potential rate of reproduction for females than for males. At the same time, internal gestation and the need for postnatal care have resulted in an evolved female bias toward PI and a sex difference in the benefits of seeking additional mates (Trivers, 1972). Males can benefit, reproductively, from seeking and obtaining additional mates, whereas females cannot. Thus, a sex difference in reproductive rates, combined with offspring that can be effectively reared by the female, create the potential for large female – male differences in the mix of mating and parenting efforts, and this difference is evident in 95% to 97% of mamma-

lian species (Clutton-Brock, 1989). In these species, all of the PI is provided by females, either alone or as part of kin-based coalitions. Males, in turn, compete for access to mates or for control of the resources (e.g., territory) that females need to rear their offspring. The general pattern of PI in mammals highlights the unusual aspect of human parental behavior noted in Table 1 — that is, male parenting (Geary, 2000).

### Summary of the Evolutionary Basis of Sociality

Any social, behavioral, or psychological trait that is partly heritable is subject to selection pressures and will evolve to the extent that individual differences in the trait covary with individual differences in survival or reproductive outcomes (Price, 1970). On the basis of these relations it is necessarily true that traits that enable increased access to and control of the resources that covary with survival and reproductive outcomes will evolve. Social cooperation and coalition formation are readily understood as evolved strategies that allow individuals greater access to and control of essential resources than they could achieve alone. Consistent with evolutionary theory, coalitions are typically formed among kin and compete with other kin-based coalitions for control of essential resources (Hamilton, 1964). Traits that facilitate the formation and maintenance of competitive coalitions will coevolve with coalitional behavior — traits that are likely to include complex social competencies, a large brain, and long developmental period.

In humans, kin-based coalitions include nuclear and extended families, and as with other species, these coalitions compete for resource control and to create an environment that supports their children's long developmental period. Human families are unusual in that they are often composed of extended male kin-based coalitions — as contrasted with female coalitions in most other mammalian species where coalitions form — and often involve spousal cooperation in childrearing and other forms of male parenting. The next sections describe how these unusual features of the human reproductive strategy may have evolved and how they relate to the other unusual characteristics described in Table 1.

## HUMAN EVOLUTION

Constructing scientifically defensible models of human behavioral evolution is a difficult and often criticized endeavor (e.g., Eagly & Wood, 1999). Nonetheless, defensible models can be constructed when evolutionary principles are judiciously combined with reverse engineering and comparative studies (Byrne, 2000; Pinker, 1994, 1997). Reverse engineering in-

volves starting with functional behavioral or cognitive patterns and from there developing models of the selection pressures that likely contributed to the evolution of these traits (Mayr, 1983). The comparative method involves analyzing the relation between cross-species differences in behavioral strategies or cognitive and brain specializations and differences in ecological or social niche (e.g., Dunbar, 1993; Foley & Lee, 1989). This combined approach to constructing evolutionary models was followed in the next sections. The first part provides a primer on hominid evolution, and the second describes our model of social dynamics and the evolution of human parental behavior and family formation.

### Origins

Although much is known about many of the species composing the genus *Homo* and the predecessor genus *Australopithecus* (for accessible discussion, see Tudge, 2000), there is controversy with respect to the classification of these species (McHenry, 1994a, 1994b; Wood & Collard, 1999). Among these controversies are debates regarding whether variation in fossils presumed to represent a single species in fact represent two or more species, and regarding the evolutionary relatedness of various species (e.g., Aiello, 1992; McHenry, 1994a; Wood, 1992). There are, nonetheless, consistent patterns in the fossil record, such as sex differences in physical size. When these patterns are compared to similar patterns in extant primates, inferences can be drawn about aspects of the social behavior of species of *Homo* and *Australopithecus* and about potential changes in social dynamics (Foley, 1999; McHenry, 1994a, 1994b; Tudge, 2000; Wood & Collard, 1999).

As an example, in primates, the magnitude of the sex difference in physical size covaries with the intensity of one-on-one male – male competition over mates, with large differences associated with a polygynous mating system and, generally, with low levels of male parenting (Clutton-Brock, Harvey, & Rudder, 1977). More moderate sexual dimorphisms are associated with less intense male – male competition and higher levels of male parenting in some species, and with coalitional male – male competition in other species (Plavcan, 2000; Plavcan & van Schaik, 1997; Plavcan, van Schaik, & Kappeler, 1995). Males and females of monogamous species, in contrast, tend to be similar in physical size (e.g., Leigh, 1995). When these patterns are compared to patterns of sexual dimorphism in the fossil record, inferences about the reproductive strategies of extinct hominids can be drawn (Foley, 1999; Leakey, Feibel, McDougall, & Walker, 1995; Leakey, Feibel, McDougall, Ward, & Walker, 1998).

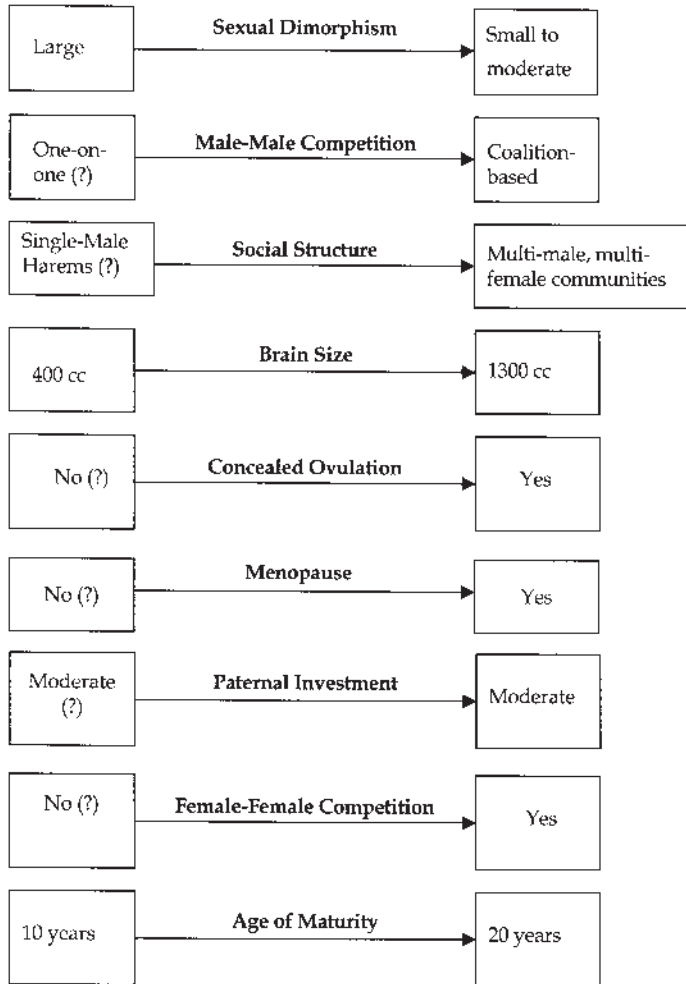
For australopithecine species dating from about 4 million years ago, including *A. afarensis* and *A. anamensis*, males are estimated to have weighed

from 60% to 100% more than females (e.g., Leakey et al., 1998; Ward, Leakey, & Walker, 1999). By, and perhaps with, the emergence of *H. erectus* about 1½ to 2 million years ago (Stringer, 1992), males were estimated to be about 20% heavier than females — a difference that is similar to what is seen in human beings today (McHenry, 1994a; Richmond & Jungers, 1995). In addition to this substantive change in the magnitude of the sexual dimorphism, there has been a dramatic increase in brain volume during hominid evolution. For instance, the cranial capacity, and brain size, of human beings is three times larger than that of *A. afarensis*. More important, when body size is controlled, australopithecine species appear to have had a relative brain size (i.e., encephalization quotient) similar to that found in chimpanzees (McHenry, 1994a). With the emergence of *H. erectus*, relative brain size substantially increased, and increased further with the emergence of *H. sapiens* (Ruff, Trinkaus, & Holliday, 1997); early modern humans appear to have emerged about 100,000 years ago, and maybe later than this (Stringer, 1992).

On the basis of the strong relation between adult size and age of physical maturity, McHenry (1994a) estimated that the age of maturation for australopithecines was very similar to that found in the modern chimpanzee — about 10 years. The age of maturation for *H. erectus* was estimated to be between 12 and 13 years, whereas that of modern human beings is as late as the early 20s (Tanner, 1990). The fossil record also indicates that *H. erectus* was the first hominid to expand out of Africa (Stringer, 1992) and may have survived in some parts of the world until about 26,000 years ago (Swisher et al., 1996). Neanderthals (*H. neanderthalensis*) also disappeared around that same time — that is, about 30,000 years ago (Stringer, 1992).

### Social Dynamics and Hominid Evolution

The fossil record indicates that during the past 4 million years there has been a significant reduction in the magnitude of the sex difference in physical size, a threefold increase in brain volume, a doubling of the length of the developmental period, and a disappearance of related species of *Homo*. Based on the covariation between these variables and social and ecological differences across living primates, defensible inferences can be drawn about the nature of social dynamics in early hominids (Alexander, Hoogland, Howard, Noonan, & Sherman, 1979; Clutton-Brock et al., 1977; Dunbar, 1998; Foley, 1999; Plavcan et al., 1995), although the associated models are not definitive (Plavcan, 2000). One framework for guiding these inferences is provided by contrasting likely characteristics of *A. anamensis* and *A. afarensis* with *H. sapiens*, as shown in Figure 1 and discussed in the respective next sections.



**FIGURE 1**

Significant Evolutionary Changes From *A. Anamensis* and *A. Afarensis* to *H. Sapiens*. Note that the suggestion of no concealed ovulation in these *Australopithecines* does not mean that females had conspicuous estrous swellings. Rather, if they followed the gorilla pattern, then small estrous swellings may have been present, and ovulation may have been signaled by means of pheromones. If male parenting in *Australopithecines* followed the gorilla pattern, then male-offspring affiliations would have been largely initiated by offspring rather than being a prominent feature of female – female competition, as it is in humans.



Before turning to this discussion, note that the most common alternative approach is to assume that the behavioral characteristics of the ancestor common to these australopithecine species and human beings were very similar to those observed in modern chimpanzees or bonobos (*Pan paniscus*; de Waal & Lanting, 1997; Kano, 1992; Wrangham, 1999; Wrangham & Peterson, 1996). This is a reasonable assumption in some respects. As noted, the encephalization quotient of chimpanzees, bonobos, australopithecines, and presumably the common ancestor are very similar (McHenry, 1994a, 1994b). However, the sexual dimorphism in chimpanzees and bonobos represents about a 20% to 25% weight advantage for males (Goodall, 1986; Kano, 1992). Although bonobo males do not show consistent coalitional aggression, male-on-male physical aggression is common and presumably a feature of the ancestor common to chimpanzees and bonobos. In any case, the degree of sexual dimorphism in chimpanzees and bonobos is considerably lower than that estimated for *A. anamensis* and *A. afarensis*. The contrast suggests that the reproductive strategy of male 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.

For reasons described next, we suggest that certain features of the social behavior of australopithecines may have been more similar to that seen in modern gorillas than in chimpanzees or bonobos. We are *not* arguing that australopithecines were gorilla-like in every sense, as they clearly were not (e.g., they were bipedal). Rather we believe that a gorilla-like model for australopithecine social dynamics provides an evolutionary launching point that more readily accommodates certain patterns of human parental behavior, such as male parenting, and family formation than does either a chimpanzee-like or bonobo-like social structure. At the same time, there are also similarities between human and chimpanzee behavior, especially male coalitions, and thus arguments can be made that australopithecines also evidenced this form of social competition. This is, of course, a possibility that cannot be ruled out. We are suggesting that an alternative be considered: Male coalitional behavior may have evolved independently in humans and chimpanzees and may not have been an important feature of the reproductive strategy of male australopithecines.

*Male – male competition, social structure, and brain size.* The degree of sexual dimorphism in *A. anamensis* and *A. afarensis* suggests intense one-on-one male – male competition and perhaps a gorilla-like social structure (Leakey et al., 1998). Although other social structures are, of course, possible (Plavcan, 2000), a gorilla-like social structure is consistent with many

features of human social organization. The modal social organization of both lowland gorillas (*Gorilla gorilla gorilla*) and mountain gorillas (*Gorilla gorilla beringei*) is single-male harems, which typically include one reproductive male, many females, and their offspring (Fossey, 1984; Stewart & Harcourt, 1987; A. B. Taylor, 1997). In lowland gorillas, several of these families may occupy the same geographical region and are often in proximity, whereas in mountain gorillas they are geographically isolated. In both cases, adult male and female gorillas often form long-term social relationships, and male gorillas, presumably due to high levels of paternity certainty associated with single-male harems, show high levels of affiliation with their offspring. "Associated males hold, cuddle, nuzzle, examine, and groom infants, and infants turn to these males in times of distress" (Whitten, 1987, p. 346).

The reduction in the magnitude of the sexual dimorphism, combined with coalitional aggression in extant human populations (e.g., Chagnon, 1988; Keeley, 1996), is consistent with the emergence of coalition-based male – male competition during hominid evolution, perhaps with the emergence of *H. erectus*. Still, coalitional behavior is more typical among female primates than among male primates. In these species, females are the philopatric sex — that is, the sex that stays in the birth group (Wrangham, 1980). Female-biased philopatry results in a degree of genetic relatedness among females that supports coalition formation when such behavior covaries with survival or reproductive outcomes (Sterck, Watts, & van Schaik, 1997). For human beings, chimpanzees, bonobos, and gorillas (sometimes sons inherit the harem), philopatry is male biased, not female biased, suggesting that the male-biased philopatry has a long evolutionary history in African hominoids (Ghiglieri, 1987; Pasternak et al., 1997; Stewart & Harcourt, 1987). Male-biased philopatry is important because it creates social conditions that can lead to the evolution of male kin-based coalitions (Foley & Lee, 1989). Unlike female coalitions, male coalitions are focused on competition for mates rather than competition for food (Wrangham, 1999). As described for chimpanzees, a coalition of male hominids would have had a competitive advantage over a lone male, even a larger male.

The social demands of coalition formation and competition should have resulted in an increase in social competency and a larger brain, in theory (Barton, 1996; Dunbar, 1998). Not only do males have to coordinate their activities regarding in-group and out-group competition, they need to compete with members of their own in-group for social dominance. One way to test this hypothesis and to provide a link to patterns in the fossil record is to compare the brain sizes and social competencies of chimpanzees and gorillas, and chimpanzees and baboons (*Papio*). The former contrast is

of interest because chimpanzees and gorillas are related species (Gagneux et al., 1999) and because male chimpanzees form coalitions unlike male gorillas. The latter contrast is of interest because both chimpanzees and baboons live in complex multimale, multifemale communities, but with the possible exception of hamadryas baboons (*P. hamadryas*; Sigg, Stolba, Abegglen, & Dasser, 1982), male baboons do not form substantial coalitions. The prediction is that chimpanzees will have a larger brain, once body size is controlled, than both gorillas and baboons.

Rilling and Insel's (1999) neuroimaging study confirmed that, once body size is controlled, chimpanzees have a larger brain and more cortical gyrification (i.e., more surface area) than gorillas and at least one species of baboon (i.e., *P. cynocephalus*). It is clear that chimpanzees outperform baboons on tasks that assess social competency, and there is some evidence that gorillas also perform more poorly than do chimpanzees on similar tasks (i.e., on proto theory of mind tasks; Parker & McKinney, 1999; Povinelli, 1993). The latter findings are not, however, conclusive (Byrne, 2000). The relation between these species differences in brain size and performance on social competency tasks is also not certain but is nonetheless suggestive (Dunbar, 1998; Pawlowski, Lowen, & Dunbar, 1998); an alternative explanation is that the differences are due to different foraging strategies (e.g., Barton et al., 1995).

Despite the ambiguities, when these patterns are combined with the evolutionary reduction in the size of the sexual dimorphism, it is plausible that a transition from a single-male to a multimale social system may have been the initial selection pressure that led to the threefold increase in brain volume during hominid evolution (see Figure 1). At some point during hominid evolution, average coalition size began to increase, presumably due to the competitive advantage associated with larger coalitions (Wrangham, 1999). An increase in coalition size would have necessarily resulted in an increase in the complexity of social dynamics, within and between coalitions, and an increased advantage of strong social competencies. These relations would have resulted in the further evolution of social competencies and brain size, as well as further decreases in the sexual dimorphism (i.e., "brain over brawn"; Pawlowski et al., 1998).

*Paternal investment, concealed ovulation, and female – female competition.* If the social structure of *A. anamensis* and *A. afarensis* was similar to that found in gorillas, then it would be possible that there are continuities in male parenting, male – female relationships, and family structure between these australopithecines and human beings. In fact, if the social structure of these australopithecines were similar to that found in gorillas, then the evolutionary emergence of human families would be straightforward.

Once lone males were replaced by kin-based multimale coalitions, the males and females of these species would likely maintain the preexisting social deep structure — a basic social organization that included one adult male, one or a few adult females, and their offspring, as well as long-term male – female relationships and male parenting (Lovejoy, 1981; Stewart & Harcourt, 1987). The primary difference is that these families would be nested within the larger community rather than being geographically (mountain gorillas) or socially (lowland gorillas) separated. As noted, lowland gorilla families are often in proximity, but they are not socially bonded together through a kin-based coalition or social network. In other words, human families are similar in many respects to gorilla families, with the addition that in most preindustrial societies human families are nested within a larger male kin-based community (Pasternak et al., 1997).

The emergence of male kin-based coalitions and thus multimale, multifemale communities with many reproductive males (see Table 1) would have resulted in an exponential increase in the complexity of social relationships relative to that evident in gorillas. In particular, this change in social structure increases the mating opportunities of both males and females, increases the risks of cuckoldry, and thus creates a social ecology that could potentially result in the evolution of reproductive dynamics similar to that found in other mammals — a male focus on mating and a female focus on parenting (Clutton-Brock, 1989). The issue is the mechanisms responsible for the maintenance of a family-focused social organization rather than the eventual evolution of the standard mammalian pattern.

We suggest that these mechanisms include concealed ovulation (where ovulation is not signaled to either the male or the female) and continuous, nonreproductive sexuality as well as pair bonding. The combination of concealed ovulation and nonreproductive sexuality is rare or perhaps unique in primates (Alexander, 1990; Alexander & Noonan, 1979; Geary, 2000; MacDonald, 1992). To be sure, a lack of estrous swelling at and around the time of ovulation also occurs in some other primates (e.g., gibbons, *Hylobatidae*, and marmosets, *Callitrichidae*), but this is not the same as concealing ovulation, which can be signaled in other ways (e.g., through pheromones). Across species, the lack of an estrous swelling covaries with infanticide risk and with monogamy (Dunbar, 1995; Hrdy, 1979, 1999; Sillén-Tullberg & Møller, 1993). When infanticide risk is high, females copulate with males who are likely to displace the dominant male and thus confuse paternity: Males generally do not attempt to kill the infants of females with whom they have copulated (Hrdy, 1979). Although infanticide risk may have been present during hominid evolution, it is not, in and of itself, a sufficient explanation of concealed ovulation in humans. This is be-

cause an evolved female strategy that confused paternity would be associated with little or no male parenting, which is inconsistent with the finding of male parenting in every human culture that has been studied (e.g., Geary, 2000; Hewlett, 1992; West & Konner, 1976) and with the possibility that australopithecine males parented (Lovejoy, 1981).

It is more likely that the evolutionary function of concealed ovulation, nonreproductive sexuality, and pair-bonding, combined with a female aversion to casual sex, is to increase in the length of affiliation between the adult male and the female or females in the family group and thereby maintain the family structure and male parenting (Alexander & Noonan, 1979; Miller, 1994; B. Strassmann, 1981). All of these mechanisms would be interrelated features of the evolving relationships between males and females. For instance, pair-bonding would be maintained, in part, through continuous, nonreproductive sexuality, result in male investment in relationships with individual females, and reduce the risks of female cuckoldry. Such mechanisms are necessary in multimale, multifemale communities because, as noted, in other primates and mammals living in such communities males focus their reproductive efforts on mating and show little PI. Without mechanisms to reduce the mating opportunities of hominid males and thus reduce the opportunity cost (i.e., the ability to sire offspring with many females) of male parenting, the sex difference in the potential rate of reproduction should eventually result in a male reproductive strategy similar to that seen in other mammals (Clutton-Brock, 1989). Even with mechanisms that maintain male parenting and a family organization, it should be noted that the sex difference in the potential rate of reproduction would still result in evolved sex differences in relative focusing on mating, favoring males, or parenting, favoring females (Geary, 1998).

Because males almost certainly differed on the dimensions that likely covaried with survival and reproductive outcomes, such as parental behavior (e.g., protection and provisioning) and social dominance, some males were of higher mate value than others. Individual differences in the mate value of males would have resulted in female – female competition over the development of a relationship with a preferable male and through this securing his social influence and PI (Geary, 2000; Symons, 1979; Trivers, 1972). Moreover, it is clear that women form social networks with other women in the wider community. These networks provide social support and alloparenting and appear to be a feature of the evolved female reproductive strategy (Geary, 2001; Irons, 1983; S. E. Taylor et al., 2000). Female – female competition over male parenting and the formation of female social networks indicate a level of social complexity beyond that found in gorillas, chimpanzees, or bonobos; female bonobos form social al-

liances, but they tend to be unstable (Hohmann, Gerloff, Tautz, & Fruth, 1999). It follows from these patterns that the likely changes in the nature of male – female and female – female relationships were part of the coevolutionary processes that contributed to the evolutionary increase in brain size and social competencies, in addition to the previously described changes in male – male relationships.

*Development.* An evolutionary increase in the complexity of male – male, male – female, and female – female relationships suggests a degree of social complexity in hominid evolution that is unique among extant primates. The covariation of social complexity, brain size, and the length of the developmental period in living primates is consistent with the position that the evolutionary increase in hominid brain size and the likely increases in social complexity are features of a coevolving suite of adaptations that included an increase in the length of the developmental period (Joffe, 1997; but see Ross & Jones, 1999). The flux and complexity of social relationships necessarily mean that only the skeletal structure of the supporting social competencies can be inherently prespecified. The fleshing out of these competencies results from an epigenetic process and a resulting adaptation of social and resource-acquisition (e.g., through hunting) strategies to the ecology of the local community (Flinn, 1997; Geary, 1998; Geary & Bjorklund, 2000; Gottlieb, 1992; MacDonald, 1992). In other words, an increasing complexity of hominid social dynamics would require a coevolving increase in brain size and cognitive competency (e.g., theory of mind) as well as a longer developmental period that would enable the acquisition of sociocompetitive or other (e.g., hunting) competencies appropriate to local conditions.

An increase in the length of the developmental period and corresponding changes in the complexity of social dynamics place a premium on parental behavior that fosters and enables the developmental acquisition of sociocompetitive or other competencies. From this perspective, the inclusive fitness of both males and females during hominid evolution was related to their offspring's ability to successfully reproduce in adulthood, and this, in turn, would have favored not only the maintenance of male parenting but also increased levels of cooperative parenting.

*Menopause.* Across extant primates, a long developmental period and intensive parenting are associated with a long lifespan (Allman et al., 1998). One unique feature of the life history and long lifespan of women is menopause. Although there is no current consensus regarding the evolutionary function (if any) of menopause, we suggest that it is a feature of the just mentioned suite of coevolving characteristics (see also Table 1). Ba-



sically, menopause results in an extended period during which women can invest in the well-being of their later-born children, as part of an adaptation that enables the long-term investment in a smaller number of children and other relatives, such as grandchildren. It allows them to focus on children they have already produced, avoiding the costs of additional pregnancies at a time when their health and the likelihood of their survival to the end of later-born children's dependency are diminishing (Alexander, 1974; Williams, 1957). A parallel is found in many preindustrial societies today, whereby parents will often commit infanticide to reduce the risks to their older children (Daly & Wilson, 1988b; Hill & Hurtado, 1996). In other words, infanticide, as well as reduced fertility associated with suckling (McNeilly, 1992), enables parents to reduce the number of dependent offspring and direct more PI to older children than would otherwise be the case. When this pattern is combined with a substantial increase in the length of the developmental period, menopause follows as a logical evolutionary adaptation that serves the same function — to reduce the number of dependent children and thus free parental resources that can be invested in a smaller number of children.

To the extent that menopause allowed more intense investment in a smaller number of children and thereby increased the survival rate and later competitiveness of these children, it would have covaried with reproductive outcomes and thus evolved. Men, with different, less risky parental activities, would not have been subject to the same selective pressures for stopping reproductive potential, although they too may have been selected to adjust reproductive behavior from mating to parenting with increased age (Draper & Harpending, 1988). From this perspective, older females must have had important effects on the success of their developing children, perhaps in part because of the importance of their accumulated knowledge for negotiating the social environment. Socially skilled and well-connected older mothers and grandmothers may have been especially valuable teachers of social and political wisdom, with associated reproductive benefits (Alexander, 1990; cf. O'Connell, Hawkes, & Blurton Jones, 1999). In short, the doubling of the maximum life span of humans, involving an increased period of prereproductive development on one hand, and an increased period of postreproductive parental and kin investment on the other, are indicative of the importance of parent – offspring relationships for acquiring and mastering sociocompetitive information.

*One species of Homo.* There is only a single remaining species of *Homo*, which is significant because many of our predecessors, such as *A. afarensis* and *H. erectus*, were ecologically well-adapted species that survived for hundreds of thousands of years (e.g., Wood, 1992; Wood & Collard, 1999).



An unresolved issue is, Why did *all* of these successful and well-adapted species disappear? We agree with Alexander (1989) that their disappearance is a direct consequence of the coevolutionary processes that resulted in an unprecedented level of cognitive and social complexity in modern human beings, which, in turn, resulted in a competitive advantage over related species, such as *H. erectus* and *H. neanderthalensis*. As noted, recent evidence suggests that *H. erectus* may have survived in some parts of the world until about 26,000 years ago, and Neanderthals survived in Europe until about 30,000 years ago (Stringer, 1992; Swisher et al., 1996). Fossils for both these species have been found in the same geographical areas as fossils of early modern humans, although it cannot be stated with certainty whether these species had contact with early humans. Contact, however, is plausible, and given that the evolution of many human competencies almost certainly occurred as a result of competition with other human beings (described next), there is no reason to believe that these competitive forces would not have been leveled against related species. Even without direct contact, the expansion and ecological dominance of early modern humans may have displaced related species and other populations of conspecifics.

*Evolution and human parental behavior.* The goal here is to understand the most critical evolutionary changes in social deep structure since *A. anamensis* and *A. afarensis* and to do so in a way that is plausible and parsimonious.

If we assume that the launching point was a gorilla-like social structure in *A. anamensis* and *A. afarensis*, then the evolution of current forms of human parental behavior requires fewer evolutionary changes than if the launching point was a chimpanzee-like or bonobo-like social structure. With a gorilla-like pattern, current patterns of human parenting and family structure (i.e., one adult male, one or several adult females and their children), as well as long-term male – female relationships, have been a feature of the hominid social deep structure for at least 4 million years. With a chimpanzee-like social structure, multiple evolutionary changes in a specific sequence, such as concealed ovulation evolving before male parenting, would have been necessary to create current patterns of human parental behavior, especially male parenting and male – female pair-bonding (Geary, 2000). A gorilla-like pattern, in turn, is similar in many respects to the polygynous and often times single-male harem social structure found in many mammalian species (Clutton-Brock, 1989). The primary difference is that gorilla families are socially isolated, and thus cuckoldry risks are low, and the benefits of male parenting are increased accordingly. In other words, a gorilla-like social structure with male parental behavior

is readily understandable within the broader range of mammalian reproductive strategies, especially if gorilla families were socially isolated.

Moving from a single-male harem to a multimale, multifemale community required the formation of male kin-based coalitions; stable multimale communities are not likely to evolve unless the males are genetically related. The first evolutionary step to multimale communities would simply involve greater stability and cooperation among adult males. Such coalitions could easily arise from a gorilla-like system, with the formation of father – son coalitions or coalitions among brothers, and the gradual increased tolerance of each other's mating relationships. Once formed, stable groups of cooperating males could easily displace a lone male (Packer et al., 1991; Wrangham, 1999). The transition would require only one change in hominid sociality, or social deep structure — an inherent tendency of males to form competition-related coalitions. As with chimpanzee coalitions, these early hominid communities were likely to have been characterized by coalitions of related males that defended a demarcated territory against groups of conspecific males (Barton, 1999; de Waal, 1993; Foley & Lee, 1989; Goodall, 1986). Unlike chimpanzee communities, the basic gorilla-like social structure — that is, families — would have been retained.

Rather than occurring before and being a necessary condition for the evolution of long-term male – female relationships and male parenting (Dunbar, 1995; Geary, 2000), concealed ovulation would function to maintain a gorilla-like family social structure, as described earlier. In fact, unlike female chimpanzees or female bonobos, female gorillas do not typically have conspicuous sexual swellings, although they often have minor swellings, and primarily solicit copulations behaviorally (Stewart & Harcourt, 1987). Thus, moving from a gorilla-like pattern of female sexual solicitation to the current human pattern requires fewer changes than if humans evolved from a more promiscuous chimpanzee-like or bonobo-like pattern. Still, there may have been a strengthening of male – female pair-bonds during hominid evolution, for reasons noted previously, to reduce cuckoldry risks and maintain male parenting in a multimale, multifemale community. Again, any such change would have evolved much more readily from a gorilla-like pattern of male – female relationships than from a chimpanzee-like or bonobo-like pattern, where long term male – female relationships are uncommon (Goodall, 1986): Male – female relationships are common in bonobos, but these tend to be mother – son pairs, not reproductive couples (Hohmann et al., 1999). Evolution from a gorilla-like pattern would simply require a quantitative change in the strength of the pair-bond, whereas evolution from a chimpanzee-like or bonobo-like pattern would require a more substantive and

qualitative change in the nature of male – female relationships. Moreover, it is likely that concealed ovulation, nonreproductive sexuality, and pair-bonding enabled female hominids to exert great social influence over male hominids than is currently found in gorillas and chimpanzees, where adult males dominate adult females (Goodall, 1986; Stewart & Harcourt, 1987).

Relationships among female gorillas vary from supportive grooming, which typically occurs among kin (e.g., mother – daughter), to competition over food (Stewart & Harcourt, 1987). Relationships among hominid females were likely to have been more complex than those seen among female gorillas, given the earlier described female – female competition over male parenting and other forms of investment (e.g., protection), as well as an increasing need for social support during the long developmental period of offspring. In fact, it has been argued that supportive relationships among females, even unrelated females, has been an important feature of hominid evolution and one that functions to provide social support during periods of stress and to assist with parenting (Geary, 2001; S. E. Taylor et al., 2000). The result would be an important change in the social deep structure of hominids — a strengthening of the inherent tendency of females to form social networks.

In this evolutionary scenario, male parenting, long-term female – male relationships, and a basic family structure following the gorilla-like pattern may have been in place since *A. anamensis* (Lovejoy, 1981). The move from a gorilla-like pattern to the current human pattern required only a few evolutionary changes, including the formation of male kin-based coalitions, a strengthening of the pair-bonds between males and females, the emergence of female bonding, and female – female competition.

Finally, as noted, *Australopithecus* was a well-adapted genus that existed for millions of years, and many individual australopithecine species survived for hundreds of thousands of years. During this time, there does not appear to have been substantive changes in brain volume, degree of sexual dimorphism, or length of the developmental period, suggesting little change in social deep structure. This long period of relative stasis began to change with the emergence of the genus *Homo*, and especially with the emergence of *H. erectus* and later of modern humans (McHenry, 1994a, 1994b; Ruff et al., 1997). In comparison to australopithecines, *H. erectus* is estimated to have had a substantially larger encephalization quotient, a longer developmental period, and a smaller sex difference in physical size, suggesting important shifts in the pattern and complexity of social dynamics. The emergence of archaic *H. sapiens* and modern human beings represents a very rapid increase in encephalization quotient (brain volume is estimated to have increased about 50% relative to *H. erectus*), a substantial

lengthening of the developmental period, and an increase in the complexity and size of social communities and relations between these communities (e.g., Keeley, 1996).

*Social competition and rapid evolution.* The factor that ties all of the previously described evolutionary changes together, especially the very rapid changes associated with the emergence of *H. sapiens*, is social competition (Alexander, 1990). However, the mechanisms by which social competition could have operated to produce these rapid evolutionary changes are in need of articulation. Although it cannot be known with certainty, the general mechanism appears to be competition for social status and power and the accompanying increase in the ability to gain access to and control of the resources that covary with survival and reproductive outcomes (Geary, 1998), although status striving in and of itself is an insufficient explanation for many uniquely human characteristics, such as a very large brain (see Table 1). This is because status striving and resource competition are not unique to human beings and, in fact, are a common feature of social life in many species (e.g., Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987; Wrangham, 1999). Human beings are, however, unique in that social competition occurs in the context of ecological dominance: In most ecologies, human groups have achieved a level of control over essential resources (e.g., food, use of land) that is not evident in other species (for further discussion, see Alexander, 1989). As noted by Alexander (1989, p. 458),

the ecological dominance of evolving humans diminished the effects of “extrinsic” forces of natural selection such that within-species competition became the principle “hostile force of nature” guiding the long-term evolution of behavioral capacities, traits, and tendencies, perhaps more than any other species.

In this view, once ecological dominance was achieved, the traits that began to strongly covary with individual differences in survival and reproductive outcomes were those that allowed hominids to socially “outmaneuver” other hominids. These traits would include sophisticated social competencies, such as language and theory of mind; an accompanying increase in brain size; and other adaptations that facilitated the formation and maintenance of kin-based social coalitions. The evolutionary changes associated with social competition might have been further accelerated if there were an inverse relation between the resulting individual differences in social status and mortality risks and regular but unpredictable population crashes (i.e., a rapid reduction in population size due to mortality; Boone & Kessler, 1999; Geary, 2000; Rogers, 1990). From this perspective, a

portion of the reproductive effort is diverted from simply producing children to investment that focused on achieving social status and through this greater social power (ability to influence others) and access to essential resources (e.g., food). Social status, in turn, enables parents to create an environment that reduces infant and child mortality risks, especially during population crashes, such as during an epidemic. In other words, social competencies and an increasing ability to exploit the ecology (e.g., through tool use) during hominid evolution reduced offspring mortality rates and resulted in temporary population increases (Lancaster & Lancaster, 1987). Competition within and between these communities was analogous to climbing a ladder, with each step up resulting in greater access to and control of essential resources. During population crashes, those on the bottom rungs of the ladder suffered disproportionate mortality. The result would be that individuals who were toward the middle rungs of the ladder before the population crash were now toward the bottom rungs of the ladder.

In keeping with this hypothesis, in extant preindustrial populations there is an inverse relation between social status and infant and child mortality rates (e.g., Boone & Kessler, 1999; Hill & Hurtado, 1996; United Nations, 1985). The relation between infant and child mortality risks during population crashes and social status has also been extensively studied for populations in preindustrial and industrializing Europe, and again the pattern supports the prediction. As an example, in an extensive analysis of birth, death, and demographic records from 18th-century Berlin, Schultz (1991) found a strong correlation,  $r = .74$ , between socioeconomic status (i.e., social status in industrial nations) and infant and child mortality rates. Infant (birth to 1 year) mortality rates were about 10% for aristocrats but more than 40% for laborers and unskilled technicians. "A senior official of the welfare authorities (*Armenbehörde*) observed in 1769 that among the poor weavers of Friedrichstadt 75 out of every 100 children borne died before they reached [adulthood]" (Schultz, 1991, p. 243). During the 1437–38 and 1449–50 epidemics in Florence, Italy, child mortality rates increased five- to tenfold, and these mortality rates varied inversely with socioeconomic status even at the high end of the continuum (Morrison, Kirshner, & Molho, 1977; for a review see Geary, 2000).

As found in these human populations and, in fact, many other mammalian species (Young, 1993), a similar pattern of population growth and punctuated crashes appear to have been features of hominid evolution (Rouhani & Jones, 1992). In an analysis of variation in the mitochondrial DNA (inherited from mother), Gagneux et al. (1999) found considerably less variability in human populations than in populations of other African hominoids. The restricted variability indicates that "something unusual happened in the early history of our species" (Gagneux et al., 1999, p.

5081), including the possibility of repeated bottlenecks and selective population sweeps — that is, repeated expansions and contractions of early human populations. This cyclical pattern operating in the context of the changes in hominid social structure (e.g., coalition-based male–male competition) creates a mechanism that could result in hand-over-hand coevolutionary change in traits that support social competition, including brain size, social competencies, length of the developmental period, and intensive parenting. Competition for social status, power, and access to and control of resources would favor a larger brain, greater social competencies, a longer developmental period, paternal investment, and so forth, and, as previously stated, population crashes would disproportionately affect those at the lower end of these correlated distributions. The result would be a shift in the distributions such that the mean brain size, length of the development period, and so forth increased relative to previous generations. Rapid cycles of these coevolutionary relations readily explain the rapid changes in brain volume, length of the development period, and so forth of *H. sapiens* and readily explain why parental behavior is such an integral aspect of the social life of women and men.

### THE DYNAMICS OF HUMAN PARENTING AND FAMILY FORMATION

The dynamics of human parental behavior and family formation are predicted to vary across socioecological context to the extent that the benefits of parenting covary with survival and reproductive outcomes across these contexts. The next first section provides a framework for understanding the dynamics of family formation across ecological and social conditions, and the second section provides a framework for understanding the dynamics of PI in a sociocompetitive context.

#### Ecological and Social Constraints on Family Formation

As noted, the modal family structure that emerged during the course of hominid evolution appears to be that of a male and one or several females and their offspring embedded in a larger male-biased kin group. Although this is a cross-culturally common form of family constellation (Brown, 1991), given the dynamic and unpredictable nature of social competition, a range of adaptive responses to ecological, historical, and social conditions is expected. Indeed, there is extraordinary intra- and intercultural variability in the dynamics of human parental behavior and family formation (Murdock, 1949).



With respect to the latter, the diversity of human family arrangements is not random noise or cultural helter-skelter. Consistent with the social-competition evolutionary scenario, several key environmental characteristics appear causally related to variations of marriage patterns and family structure (Flinn & Low, 1986), as described in Table 3. Key ecological variables include the quantity, type, and distribution of food and other material resources and whether these resources (e.g., cows or arable land) can be monopolized by male kin-based coalitions (e.g., sparse hunted game). Key social variables include rules for marriage, the extent of intragroup competi-

**TABLE 3**  
Marriage Patterns and Family Formation

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Polygyny

- (1) *Resource-based polygyny*. In resource-rich environments in which polygyny is not legally prohibited, male kin-based coalitions compete for control of these resources (e.g., land, cows), and dominant men in successful coalitions marry polygynously. A common family structure is a husband who lives separately (e.g., in a different hut) from his wives and their children (e.g., Borgerhoff Mulder, 1990; Draper, 1989).
- (2) *Social power polygyny*. In ecologies in which resources are abundant but not easily controlled by coalitions and in which polygyny is not prohibited, male kin-based coalitions compete for social dominance and power (e.g., through warfare). Dominant men in successful coalitions marry polygynously. A common family structure is a husband, two or three wives, and their children (e.g., Chagnon, 1988). Family units consisting of a husband, wife, and their children are common as well (e.g., Hames, 1996).

Monogamy

- (1) *Ecologically imposed*. In environments with sparse and widely distributed food sources, high levels of both maternal and paternal investment are needed to rear offspring successfully, and thus polygyny is rare. Monogamy and family units that consist of a husband, wife, and their children are common (Flinn & Low, 1986).
- (2) *Socially imposed*. Legal prohibition of polygamy in Western culture suppresses the male tendency to form polygynous marriages in resource-rich ecologies. Monogamy and family units consisting of a husband, wife, and their children are thus more common than would otherwise be the case. Serial monogamy and single-parent (typically mother) families are also common in these societies.
- (3) *Serial*. In resource-rich ecologies with socially imposed monogamy, men and women often have a series of legal marriages, although this pattern may also be found in other cultures (e.g., Hill & Hurtado, 1996). Men, but not women, who marry serially have, on average, more children than do their same-sex peers who stay monogamously married to one person (Buckle, Gallup, & Rodd, 1996; Johanna, Forsberg, & Tullberg, 1995).

Polyandry

- (1) *Fraternal polyandry*. Although rare, in societies in which land is of low fertility and thus yields poor crops, families tend not to divide inherited land (E. A. Smith, 1998). In these societies, brothers share the land — which can only support a small number of children — and marry polyandrously. In these cases, the family consists of two husbands, one wife, and their children. If one brother acquires additional wealth, he will often marry another women, who does not become the wife of his brother.
-



tion and warfare, and paternity certainty (e.g., D. R. White, 1988; D. R. White & Burton, 1988). A majority of preindustrial societies have marriage rules that allow polygynous or polyandrous unions, although the former is many times more common than the latter (Murdock, 1949). In these societies, coalitions of related males cooperate to gain access to and maintain control of the resources that women need to rear their children, or to control reproduction-related social dynamics. Control of material resources, such as land or cattle, results in resource-based polygyny (e.g., Borgerhoff Mulder, 1990), whereas control of social dynamics results in social power polygyny (Chagnon, 1977, 1988).

The material and social resources that are controlled by coalitions are not simply related to the mating efforts of the men, they are often times used to influence the social and reproductive interests of their children. With resource-based polygyny, the younger men in the coalitions are often dependent on the wealth of their father, uncles, and other relatives to pay the bride price needed to marry (e.g., Borgerhoff Mulder, 2000). At the same time, a young woman's parents and other relatives will often use their wealth and social power to facilitate her marriage to a wealthy or socially powerful man and kin group and to influence her treatment by the man and his kin after she has married. A similar pattern is found with social power polygyny, whereby male coalitions engage in negotiations with other coalitions to influence the reproductive prospects of their sons and daughters. In both forms of society, women almost always marry, some monogamously and some into polygynous unions (Hartung, 1982). High-status men typically have several wives, other men marry monogamously, and some men never marry (Murdock, 1949). Polyandry is found in less than 1% of human societies, and when it does occur, it is also related to resource control (e.g., E. A. Smith, 1998). Here, land tends to be inherited by sons but cannot be subdivided into smaller, functional plots (i.e., plots that can support a family). To keep this resource in the family and to provide sufficient resources to support children, brothers will marry the same woman and work the same land.

In all human societies, women and their children form the nucleus of the family, with men ranging from high to more distant levels of involvement with their wife (or wives) and children (Draper, 1989; Murdock, 1949). Men typically provide social protection and material resources to their wife (or wives) and children but may or may not reside with them. In any case, the families are typically embedded in a wider network of kin, who aid in the provisioning, protection, and socialization of children. Families embedded in a wider network of kin and other cooperating groups define, in essence, a collectivist society (for related discussion see Rothbaum, Pott, Azuma, Miyake, & Weisz, 2000).

Monogamous marriages and families consisting of a husband, wife, and their children who reside in the same household are particularly common in societies in which monogamy is ecologically or socially imposed (Alexander et al., 1979; Flinn & Low, 1986). Ecologically imposed monogamy is found in harsh ecologies, those in which the productive (e.g., hunting) activities of both parents are needed to keep children alive and developing normally, such as the !Kung san (Lee, 1979). Socially imposed monogamy is found primarily in Western societies where social tradition and formal laws prohibit polygamous marriages. The result is a suppression of polygynous marriages in higher status men, although serial monogamy is common in these societies, as are single-parent families (typically headed by mothers but often aided by maternal kin). In addition to the suppression of polygyny, these societies are unusual in that nuclear families are often physically isolated from the wider kin network, although kin are still a source of social and economic support; this isolation is more common in the professional classes, where jobs often require moving away from kin (Argyle, 1994). In societies with socially imposed monogamy, kin-based negotiations for marriage partners are uncommon, but intergenerational transfer of wealth (e.g., dowry) from parents to children, as related to their children's later marriage prospects or the well-being of the donor's grandchildren, is common (Gaulin & Boster, 1990), as are other forms of PI that influence children's later ability to acquire wealth (e.g., education).

The overall pattern indicates that, unlike most other mammals, both men and women are involved in family formation and PI, but the dynamics of these vary across differing physical and social ecologies. When it is not prohibited, men attempt to acquire the social and material resources needed to marry polygynously but must do so through cooperation with other male kin, and often through the cooperation of prospective brides (e.g., Chagnon, 1977). The combination of male coalitions and the distribution of resources in the wider ecology influences men's reproductive strategies and patterns of family formation, spousal warmth, and paternal investment. Women also influence these patterns, through attempting to influence men's negotiations for marriage of their daughters (e.g., Borgerhoff Mulder, 1990) to negotiating the nature of the spousal relationship, which, in turn, influences the nature of male parenting (Geary, 2000). All of these are variations on the same theme: Humans form complex kinship networks that cooperate to control social dynamics and gain access to material resources in the wider community. Various forms of family constellations are embedded within these networks, and parents and other kin expend considerable social and material resources on ensuring the growth, well-being, and normal development of a relatively small number of children.

## Dynamics of Parenting

Studies conducted on a wide range of species support the hypothesis that parenting evolved because the accompanying behaviors — providing food and protection from predators — covary with the likelihood that offspring will survive to adulthood (Clutton-Brock, 1991; Krebs & Davies, 1993; Trivers, 1972, 1974; Westneat & Sherman, 1993; Williams, 1966; Wolf, Ketterson, & Nolan, 1988). The same theoretical model and assumptions (e.g., the importance of calories) often guide the study of human parental behavior and family formation in preindustrial societies and the construction of models of their evolution (e.g., Hill & Hurtado, 1996; Lovejoy, 1981; Wrangham, Holland Jones, Laden, Pilbeam, & Conklin-Brittain, 1999). The approach taken in these studies is justified and well founded, as nutritional stress is common in these societies — predatory risks are less common, except from other humans — and almost certainly throughout much of hominid evolution (Hill & Hurtado, 1996; Mace, 2000). The approach is incomplete, however, as it does not fully consider the earlier described relations among social competition, parenting, and the function of childhood.

The latter illustrates the basic point: Children in these societies often engage in food-gathering activities — that is, securing calories (e.g., Blurton Jones, Hawkes, & O'Connell, 1997) — but they also engage in many social activities (e.g., rough-and-tumble play) that will facilitate their later socio-competitive competencies (see Geary, 1998). Engaging in social discourse and play necessarily entails caloric cost and risk of physical injury, and thus the accompanying motivational, affective, and behavioral tendencies would be eliminated by natural selection unless the acquisition and refinement of the associated skills provided some advantage in adulthood (P. K. Smith, 1982). Stated differently, if the evolutionary function of human parenting is simply the same as that found in most other species — that is, to provide calories and protection — then children would not be biologically primed to engage in activities that work against these ends (e.g., consuming calories through play).

On the other hand, if the unique features of the human species evolved as a result of status striving and social competition, and the function of social discourse and play is to refine sociocompetitive competencies, then these types of developmental activities would be expected to evolve as a feature of the suite of unique human characteristics described in Table 1 (Geary & Bjorklund, 2000; P. K. Smith, 1982). Indeed, some models of the function and evolution of human parenting focus on its relation to the later sociocompetitive competencies of children, but these models are underspecified — the dynamics of parenting as related to children's later social

skills and reproductive options are not fully delineated (Davis & Daly, 1997; Kaplan, Lancaster, & Anderson, 1998; Lancaster & Lancaster, 1987; MacDonald, 1997; Pleck, 1997). The parts described next address this limitation with discussion of the relation between parenting and status-striving and social competition. The first provides an elaborated definition of social resources, and the second provides an elaboration of the classic definition of PI. The final part overviews some empirical research on parenting, as related to predictions generated in the first two parts.

*Social resources.* If an essential evolutionary function of human parental behavior and family formation is related to status striving and social competition, then the definition of resources must be expanded beyond the tangible physical (e.g., land) and biological (e.g., cattle and calories) resources that often define PI and the dynamics of family formation in preindustrial and other societies (e.g., Borgerhoff Mulder, 1990; Flinn, 1986). In addition, social characteristics that potentially covary with survival and reproductive outcomes should be considered resources, such as a motivational disposition to share food with members of the local group (Hewlett, Lamb, Leyendecker, & Schölmerich, 2000). These social resources can be conceptualized in terms of social competency and social value, as shown in Table 4.

**TABLE 4**  
Concepts and Definitions of Social Competency and Social Value

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Social competency

- (1) *Social competency* is defined as the phenotypic characteristics of the individual, such as competencies in theory of mind, that facilitate social relationships, reciprocal or competitive.

Social value

- (2) *Social value* is defined as the summation of all of those characteristics that make the individual of value to the wider community or of value as a member of others' social networks. Social value is an emergent feature of complex social systems and can be achieved through many routes, including:
- (A) *Individual competencies.* These are defined as phenotypic competencies that are not directly social but have value to members of the community. These competencies would include, as examples, hunting skills in a preindustrial society and economically-important skills (e.g., the ability to set up computer networks) in industrial societies (Kaplan et al., 1998).
  - (B) *Individual social network.* The development of reciprocal relationships with individuals who are socially "well connected" are of value.
  - (C) *Family and kin status and social network.* As stated previously, the development of reciprocal relationships provides an egress to the family and kin network. Thus, individuals borne into high status and socially powerful families will by accident of birth be conferred with some level of social value.
-

Social competency refers to the constellation of temperamental, personality, and sociocognitive (e.g., theory of mind) characteristics that relate to social niche seeking and support reciprocal and competitive social strategies associated with status striving and resource competition (Buss, 1991; Byrne, 1997; Dunbar, 1998; Segal & MacDonald, 1998). Niche seeking and social strategies, in turn, are expected to coalesce around the foci of the social deep structure, such as the formation of female – female social networks as related to their evolutionary function — social support and alloparenting (Geary, 2001; S. E. Taylor et al., 2000). Although individual differences in these characteristics are moderately heritable, they are also influenced by ecological variance and thus potentially related to parenting strategies, as discussed next (Bouchard et al., 1990; Caspi, Taylor, Moffitt, & Plomin, 2000; MacDonald, 1992; Reiss, 1995; Rowe, Jacobson, & Van den Oord, 1999).

Social value is a less tangible concept but is captured by the implicit understanding of the importance of social attributes, such as reputation and social power (Boone & Kessler, 1999; Chagnon, 1977; Flinn & Low, 1986; Irons, 1979; Wedekind & Milinski, 2000). In theory, social value can be achieved through different means (see Table 4), which, in turn, results in a social ecology that supports the evolution and maintenance of individual differences in social competencies. However it is achieved, social value is defined as the summation of all of those characteristics that make the individual of potential benefit to others in the community and is an essential feature of the earlier described attractive forces underlying reciprocal altruism. These characteristics will include individual competencies and attributes (e.g., navigational abilities or mate value), interpersonal social network, and wider family and kin ties. As an example, the development of a reciprocal relationship with a member of a socially powerful kin group is expected to be a highly valued social asset, as these kin groups function to control the resources that covary with survival and reproductive outcomes in the local ecology (e.g., Chagnon, 1977). The development of a reciprocal alliance with such a kin group is basically a social strategy to help secure or maintain access to these resources. The willingness of members of such a kin group to develop reciprocal relationships will be related to the social and individual competencies of these nonkin individuals (e.g., hunting or fighting skills), as these competencies relate to resource control.

*Expanded definition of parental investment.* It follows from the previously described evolutionary model that social competencies and social value covaried with survival and reproductive outcomes during hominid evolution. It also follows that the evolved mechanisms that enhanced the ontogenetic expression of these traits involved a lengthening of the develop-

mental period and child-initiated play and social discourse that function to facilitate the acquisition of social competencies and enable the practice and refinement of social strategies related to resource competition (Geary & Bjorklund, 2000; Joffe, 1997). Of course many of these activities occur, and presumably evolved, within the context of peer groups (Harris, 1995). At the same time, a motivational disposition to provide PI that influenced social competency and social value would be expected to evolve, to the extent that the accompanying reproductive benefits (i.e., number of grandchildren) outweighed associated costs (e.g., fewer children; Hewlett et al., 2000; Low, 1989).

To fully explore this hypothesis, an expanded definition of PI is needed, and it is provided in Table 5. As shown, in evolutionary biology, PI is conceptualized in terms of the dyadic relationship between parent and offspring and parental provisioning of food and protection from predators (Clutton-Brock, 1991; Trivers, 1974). These aspects of PI are clearly important in human populations (e.g., Hill & Hurtado, 1996) but do not fully capture the complexity of human parental behavior. In addition, human PI is conceptualized in terms of direct and indirect investment and as often occurring across generations. Both direct and indirect PI are expected to be focused on enabling or fostering, to some degree, children's later social competitiveness, as this relates to relational dynamics and resource control in the ecology of the local community. Both forms of PI, however, are features of wider socialization influences on children, including peer relations, social organization (e.g., relations among kin groups), and social ideology (e.g., sanctioning of physical aggression as a means of conflict resolution; Collins, Maccoby, Steinberg, Hetherington, & Bornstein, 2000; Harris, 1995). As an example, direct PI is predicted to be reduced in social contexts in which kin or members of a social network provide some alloparenting.

Direct PI includes two components: immediate-generational and multi-generational. Immediate-generational PI occurs in the context of parent – child relationships or the wider context of the family, and it is predicted to have features common to all children in the family and to interact with the social and individual competencies of individual children — that is, to reflect shared and nonshared environmental processes, respectively. Shared environmental processes would include features of parenting that are common to all children, as such a tendency to supervise their activities, and parental characteristics that influence the wider family environment, such as making books available in the household. Evolutionary logic also leads to the prediction that a motivational disposition for parents to provide nonshared or discriminant PI is likely to evolve (Daly & Wilson, 1980). When siblings differ in social and individual competencies and in person-



**TABLE 5**  
 Classic and Elaborated Definitions of Parental Investment

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Classic definition

- (1) Parental investment (PI) is conceptualized as occurring within the context of the parent – offspring dyad (Clutton-Brock, 1991; Trivers, 1972, 1974; Williams, 1966).
- (2) PI is “defined as anything done by the parent for the offspring that increases the offspring’s chance of surviving while decreasing the parent’s ability to invest in other offspring” (Trivers, 1974, p. 249).
- (3) PI is typically conceptualized as involving provisioning (i.e., providing calories) or providing protection, usually from predators (Clutton-Brock, 1991).

Elaborated definition

- (1) For humans, PI is focused to some degree on fostering sociocompetitive competencies in children (Davis & Daly, 1997; Kaplan et al., 1998; MacDonald, 1997).
  - (2) If so, then PI should covary with the survival rate of children, as in the classic definition, and with children’s later social competencies and value (Boone & Kessler, 1999; Geary, 2000).
  - (3) Within a sociocompetitive context, the nuances of PI require a distinction between two general forms of investment: direct and indirect.
    - (A) *Direct PI* Includes two forms: immediate-generational and multigenerational.
      - (i) *Immediate-generational PI*. Parental behaviors that are directed toward children, occur within the context of the parent – offspring dyad, involve a cost to the parent, and can increase the survival chances as well as the social competencies and social value of children.
      - (ii) *Multigenerational PI*. Parental behaviors that influence children’s later ability to invest in the donor’s grandchildren, or direct investment in grandchildren. This is essentially investment that functions to increase or maintain the social status of the lineage.
    - (B) *Indirect PI* is defined as parental behaviors that occur outside the context of the parent – child dyad but can effect the survival chances, social competencies, or social value of children. Indirect PI includes the following:
      - (i) *Reciprocal investment*. Parental reciprocal social relationships and behaviors that are directed toward nonkin, who, in turn, provide social support and other behaviors that directly benefit the parents’ children.
      - (ii) *Community investment*. Parental behaviors that improve the infrastructure, material and social, of the wider community into which their children and grandchildren will live (e.g., Caspi et al., 2000).
      - (iii) *Lineage status, or “family name.”* Children’s social value, in the context of the wider community, is influenced by status of the lineage or family into which they are born. Here, investment is multigenerational. The costs include maintenance of “family name,” such as inhibiting behavior (e.g., short-term mating) that might have long-term social costs (e.g., to reputation) and, where possible, the accumulation of material resources that are invested in later generations (e.g., through inheritance). As stated previously, this is status-oriented lineage investment.
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ality and temperament, and individual differences in these competencies covary with later social competitiveness, then the most effective overall parenting strategy is to focus on the strengths of individual children; effectiveness is understood in terms of parents' later inclusive fitness (i.e., having grandchildren; Boone & Kessler, 1999; Irons, 1979; Voland, 1988). The function of such PI would be to enhance competencies that enable individual children to maintain or enhance social status and resource control as adults. The nature of this PI would typically vary from one child and one ecology to the next: Direct PI that enhanced a child's inherent competency that is of little competitive value in the social ecology of the local community would be "wasted effort."

Multigenerational PI is status-driven lineage investment and can involve resources invested in individual children that can directly influence the well-being of grandchildren, or direct investment in grandchildren (e.g., inheritance). The former is complicated, however, as it can have elements of immediate-generational PI. As an example, consider that when it occurs, dowry is typically found in societies with socially imposed monogamy and high levels of paternal investment. Dowry can be viewed as immediate-generational PI that enhances the social value of daughters, as related to their ability to attract high-status and high investing mates (Gaulin & Boster, 1990). Investment that enhances the quality of children's later mating options can also be viewed as a form of multigenerational PI because such investment can be used to secure both ties to socially influential kin groups, and thus a larger network of kin to provide support to grandchildren, and higher quality genes for one's grandchildren. Most important, such investment increases the likelihood that the donor's descendants will maintain or increase their social status and thus achieve enhanced mating opportunities and avoid excess mortality during population crashes (Boone & Kessler, 1999; Geary, 2000; Klindworth & Voland, 1995).

Indirect PI could only evolve in a species with a well-defined and stable social structure and thus can only be understood in terms of the wider social ecology. Indirect PI includes behaviors that occur outside of the context of direct PI but nonetheless directly influence the individual's inclusive fitness. Women, for instance, spend considerable effort on developing and maintaining intimate relationships with one another, suggesting that this behavior has covaried with survival and reproductive outcomes during hominid evolution (Geary, 2001; S. E. Taylor et al., 2000). Geary (1998, 2001) argued that these relationships result in greater social stability in the women's social network, with social stability, in turn, being correlated with their children's physical health (e.g., Flinn, 1999). In other words, the function of these relationships is to create a stable social environment that, in turn, reduces health risks to children. Investment in the wider commu-

nity can be viewed in the same way. Investment in lineage status is also an indirect form of PI (Boone & Kessler, 1999; Chagnon, 1977; Davis & Daly, 1997). The associated activities, such as accumulation of wealth (e.g., rather than using it for mating effort) and development and maintenance of family reputation, will influence the social value and social power of kin, sometimes even distant kin (as in many of I. Newton's kin; M. White, 1997) and can result in multigenerational control of the resources that covary with survival and reproductive outcomes. Such investment is thus readily understood as an aspect of the human reproductive strategy, but a strategy that should only be expressed in social contexts where this form of investment covaries with reproductive outcomes.

More practically, the nuanced forms of PI defined in Table 5 provide a framework for conceptualizing the function of human parenting and the human family and for guiding future research on parenting and the family, as illustrated in the next section.

*Evaluation of direct and indirect PI.* The basic predictions that follow from the status striving and social competition model of the evolution human parental behavior and family formation are presented in Table 6. An exhaustive review of the associated parenting and family literature is beyond the scope of this treatment, but an overview is in order.

**TABLE 6**  
Predictions of the Social Competition Model of the  
Human Family and Parenting

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- (1) The relation between parental behavior and children's social competencies and social value should reflect both shared and nonshared environmental variance. For the latter, direct PI is predicted to be discriminant, to some degree, and interact with inherent characteristics of the child, such as temperament and cognitive profile, as these relate to social competitiveness in the local ecology (Kaplan et al., 1998).
  - (2) Paternal investment should be correlated with children's later social competitiveness. If paternal investment evolved as part of the suite of human characteristics described in Table 1 and these, in turn, are an evolved reflection of social competition, then male parenting should be at least as strongly, perhaps more strongly, related to children's later social competitiveness than female parenting (Geary, 2000; Lancaster & Lancaster, 1987).
  - (3) Investment in lineage status should be associated with fewer, more competitive children. Such investment is predicted for contexts in which mortality risks are relatively low, and this investment covaries with children's later social status. It is also predicted that the tendency to invest in fewer children will be more strongly expressed in societies with socially imposed monogamy, at least with respect to men's reproductive strategies. In these contexts, lineage investment should be related to higher long-term reproductive success (e.g., more grandchildren) than a low PI, high-fertility reproductive strategy for both men and women (Boone & Kessler, 1999; Davis & Daly, 1997).
-

The first prediction relates to the core of current controversy and debate on the relation between parenting and child outcomes — that is, the degree to which parents influence children's behavior, personality, and cognitive ability (Collins et al., 2000; Harris, 1995; Hewlett et al., 2000; Rowe, 1994). Behavioral genetic studies suggest that individual differences in all of these characteristics are moderately to strongly heritable and only weakly related to gross indicators of family environment (Rowe, 1994), although the methodological complexities of deriving estimates for genetic and shared and nonshared environmental effects make definitive conclusions untenable at this point (e.g., Stoolmiller, 1999; Turkheimer & Waldron, 2000). The complexity of these issues is illustrated by a recent large-scale twin study of vocabulary IQ (Rowe et al., 1999). Vocabulary IQ is of theoretical interest because it covaries with social competency and occupational success in industrialized nations; that is, IQ is related to the ability to acquire social value (e.g., through education) and to the ability to gain access to important resources (Gottfredson, 1997; Legree, 1995).

Across this large and varied sample of twin and sibling adolescents, individual differences in vocabulary IQ were estimated to be moderately related to individual differences in the supporting genes (the heritability estimate was .57) and weakly related to individual differences in shared family environment (estimate was .13); shared environment was indexed by parental education (Rowe et al., 1999). However, the estimates for the relative contributions of genes and the shared environment varied by level of parental education. For well-educated parents, individual differences in their children's vocabulary IQ were estimated to be strongly related to genetics (estimate of .74) and not related to shared family environment (estimate of .00). For poorly educated parents, in contrast, individual differences in their children's vocabulary IQ were estimated to be related to both genetics (estimate of .26) and shared family environment (.23).

The pattern suggests that families that provide an intellectually stimulating environment (e.g., more complex parent – child language discourse, availability of books) allow all of their children to develop their full intellectual potential. The beneficial effects of such family contexts are not detected in behavioral genetic studies, as these studies focus on individual differences, and in optimal environments individual differences are more strongly related to genetic variability than to variability within this restricted range of environments (Scarr, 1992). Such environments, however, will result in improvements in mean levels of competency, even when individual differences are more strongly related to genetics (Rowe et al., 1999; Stoolmiller, 1999). In any case, the finding for poorly educated parents provides more direct evidence for the importance of the shared family envi-

ronment for the acquisition of an important, theoretically and practically, sociocompetitive competency.

Behavioral genetic studies also suggest that nonshared environmental factors — that is, factors unique to individual children — contribute to much of the nonheritable differences in sociocompetitive competencies, although these effects can be related to parents, teachers, peers, and other factors (Turkheimer & Waldron, 2000). In fact, some theorists argued that these effects are largely due to the nature of children's relationships with their peers and to other extrafamily groups (Harris, 1995). Other theorists have emphasized the complex interactions between children's individual phenotypes (and genotypes) and family environment, shared and nonshared (Collins et al., 2000; Reiss, 1995). The prediction that direct, immediate-generational PI will, in part, be discriminant and interact with the phenotype of individual children suggests more subtle relations between parenting and child outcomes than are testable with most current research designs (but see Reiss, 1995). To be sure, there is considerable evidence that parents will treat one child differently from another, as frequently demonstrated with the comparison biological and stepchildren (Daly & Wilson, 1980, 1988a; Flinn, 1988, 1992), but these studies typically focus on conflict, not on parental enhancement of children's social competitiveness and social value based on the phenotype of individual children.

In one study that is relevant to the prediction, Kaplan et al. (1998) found that fathers invested more education-related time with children whom they perceived as being more intelligent and thus most likely to benefit — in terms of academic achievement and later occupational and social competitiveness — from this investment. The interpretation of this pattern is not straightforward, however, as the accompanying father – child interactions are likely to be influenced by child evocative effects and shared genes for intelligence, intellectual motivation, and so forth (Scarr & McCarthy, 1983). Despite these potential confounds, the results of Kaplan and his colleagues suggest that PI can influence their children's social value and that the nature of such investment may differ from one child to the next (also see Kaplan, Lancaster, Bock, & Johnson, 1995). Although the magnitude of any such differential PI on child competencies is not known, cross-cultural studies of parental contributions (e.g., helping with homework) to children's academic achievement support a similar conclusion (Stevenson & Stigler, 1992). Specifically, that PI is often focused on and enhances children's sociocompetitive competencies and that these parental activities are often sensitive to the competencies needed to succeed in the local ecology.

The research of Flinn and his colleagues also suggests child-specific effects of family relationships and parenting on children's endocrine and immune systems (Flinn, 1999; Flinn & England, 1995, 1997; Flinn, Quinlan,

Decker, Turner, & England, 1996), variables that traditionally have not been assessed in psychological studies of the relation between parenting and child outcomes. In this 14-year study, the family environment along with cortisol (a primary stress hormone in primates) and testosterone profiles were assessed for children and adults in a rural village in Dominica, in the West Indies. Analyses of data indicated that children living in households with intensive, stable caregiving usually had moderate cortisol levels, low frequency of illness, and appropriate immune response. Children living in households with nonintensive, unstable caregiving were more likely to have abnormal (usually high and variable, but sometimes low) cortisol levels. Traumatic family events were associated temporally with elevated cortisol levels. Some children with caregiving and growth problems during infancy had unusual cortisol profiles. These associations indicated that family environment was a significant source of stress and illness risk for children. The variability of stress response, however, suggested a complex mix of each child's perceptions, neuroendocrinology, temperament, developmental history, and specific context.

Another pattern of results indicated that the presence or absence of father was related to the cortisol and testosterone levels of boys, but not girls. In comparison to boys residing with their biological father, father-absent boys and boys living with a stepfather had either unusually low or highly variable cortisol levels and weighed less. An analysis of adults who grew up in father-present or father-absent households also revealed significant differences: As adults, father-absent men had higher cortisol levels and lower testosterone levels than did their father-present peers. The endocrine profile of father-absent men suggests chronically high stress levels, which can significantly increase the risk for a number of physical disorders (e.g., Sapolsky, 1986). For males, both physical size and physical health influence their desirability as mates. Thus, developmental factors, such as parenting and the family environment (e.g., levels of conflict), that covary with these physiological and health outcomes can potentially influence men's social value in adulthood.

The second prediction specifically concerns the evolutionary function of men's parenting and is highlighted because male parenting is unusual in mammals and is especially uncommon for species that live in multimale, multifemale communities, as noted in Table 1. If our previously described evolutionary model is correct, then men's parenting, in and of itself, readily follows from the presumed gorilla-like social structure of australopithecines. In this view, men, as a group, have an evolved motivational disposition to provide some degree of investment in their children, although there will be considerable individual differences in this regard, of course (Flinn, 1981; Geary, 2000). Moreover, if social competition was the

driving force in hominid evolution with the emergence of the genus *Homo* and the maintenance and modification of male PI as part of the broader suite of adaptations described in Table 1, then men's parenting might be more strongly related to their children's later sociocompetitive competencies than women's parenting.

In other words, given the basic pattern of mammalian reproduction (e.g., the sex difference in the potential rate of reproduction and in focus on mating or parenting), male parenting would have persisted during hominid evolution only to the extent that the reproductive benefits of paternal investment outweighed the benefits of focusing resources on mating efforts. Furthermore, if hominid evolution was characterized by ever-increasing levels of social competition, then male parental activities that fostered the competitiveness of their offspring would be more likely to result in a reproductive advantage than other forms of male parenting. Female parenting may have been at least as important as male parenting for fostering offspring's competitiveness, but in theory relatively more maternal than paternal investment would be focused on the physical well-being of offspring.

The assessment of the influence of men's parenting and the evaluation of the second prediction is confounded by assortative mating. Men of higher social competency and social value tend to marry similarly competent women, and thus paternal correlates of child outcomes are confounded by maternal characteristics (Geary, 2000). In the few studies that have explicitly controlled for this confound, paternal influences on child outcomes remain significant (e.g., Kaplan et al., 1998), and across cultures, the withdrawal of paternal investment through death or divorce is generally associated with poorer child outcomes (Hill & Hurtado, 1996; United Nations, 1985). In further support of the second prediction, in industrial societies, paternal investment of time (e.g., help with homework) and income (e.g., tutors) is associated with upward social mobility of children, even after controlling for maternal characteristics (Amato, 1998; Kaplan et al., 1998). MacDonald (1993) found that father – child play is correlated with children's later social competencies with peers, and Ellis, McFadyen-Ketchum, Dodge, Pettit, and Bates (1999) found that paternal warmth and investment in the family are associated with delayed pubertal onset in daughters (see also Belsky, Steinberg, & Draper, 1991). Delayed pubertal onset, in turn, increases the length of the developmental period, delays onset of sexual activity, and is often associated with higher educational attainment and thus improved sociocompetitive competencies in adulthood (Parke & Buriel, 1998). Although not definitive, these studies are consistent with the hypothesis that men's parenting is as strongly, perhaps more strongly, related to children's later social competitiveness (e.g., educational outcomes) as women's parenting (e.g., Kaplan et al., 1995).



The third prediction is related to the demographic shift — a secular reduction in infant and child mortality risks followed by a reduction in the number of children born per family and often times increased investment per child (Boone & Kessler, 1999; Hed, 1987). The pattern has been interpreted in different ways, from a refutation of sociobiological principles (Vining, 1986) to the effects of the “unnaturalness” of modern society (Kaplan et al., 1995). The third prediction is that the demographic shift is a reflection of an evolved motivational disposition to invest in children’s later social competitiveness, which often occurs at a cost of fewer children. It follows, however, that this motivational disposition is most likely to be facultatively expressed in environments with relatively low infant and child mortality rates where investment in lineage enhancement is possible (e.g., through accumulation of wealth passed across generations) and when children have the opportunity to improve their later social status (Chisholm, 1993; Geary, 2000; Lancaster & Lancaster, 1987; Pleck, 1997).

Although the evidence is not yet definitive, reduced fertility is commonly found in societies where infant and child mortality rates are comparatively low and where there is opportunity for improving children’s later social status (e.g., Hed, 1987; Perrenoud, 1991; Schofield, Reher, & Bideau, 1991). Direct multigenerational PI that will enhance the socio-competitive abilities of children, and indirect PI associated with lineage investment often emerge in these populations as well (e.g., through dowry or educational investment; Geary, 2000; Kaplan et al., 1998; Lynn, 1996) and are often associated with greater long-term reproductive fitness in comparison to a higher fertility, low-PI reproductive strategy (e.g., Klindworth & Volland, 1995).

It should be noted, however, that these patterns have been found in societies with socially imposed monogamy, which, in turn, appears to shift men’s reproductive effort from mating to parenting, at least to some degree (Geary, 2000). Therefore, the third prediction, as well as the results regarding the second prediction, need to be qualified: Any motivational disposition of men to focus their parenting on increasing the sociocompetitiveness of their children and, as a corollary, preferring fewer children may be expressed more strongly in societies with socially imposed monogamy than in other societies. In societies in which men’s reproductive potential is not restricted by ecologically or socially imposed monogamy, their reproductive strategies can entail more complex trade-offs between investing resources in mating effort versus parental effort. The latter often involves marrying as many women as possible and thus maximizing the number of children they sire. The former involves investing these resources in a smaller number of wives and children and thus freeing resources to invest in the competitiveness of these children.

Borgerhoff Mulder (2000) conducted a relevant analysis of the reproductive strategies of Kipsigis men and women, a pastoral society in Kenya in which men are allowed to marry as many women as they can support. In this society, the most important material resource is land, which is controlled by male-dominated kin groups. When men marry, they provide to their wife (or wives) and their children a specific amount of land, which is then used for small-scale agricultural production. The land will also be inherited by sons, who, in turn, will use it in their attempts to marry. Social custom dictates that the land should be divided evenly among sons, and thus if a woman has too many sons, then none of these men will have enough land to marry and reproduce. Borgerhoff Mulder (2000) confirmed that the optimal reproductive strategy for women, as indexed by the number of surviving grandchildren, is to invest (land in this case) in a smaller number of sons — that is, to have fewer children than their biological potential. In other words, women who had fewer children than her land could support had more surviving grandchildren than did women who had as many children as their land could support. By having fewer children, each of their sons inherited more land and thus were better able to attract wives.

Men in this society are faced with more complex reproductive decisions. If they marry as many women as they can support and thus maximize the quantity of children, then their sons will inherit less land on average than if they married fewer women. Borgerhoff Mulder's (2000) analysis indicated that men, on average, followed the reproductive strategy that maximized the quantity of children and did not divert resources from their mating effort to provide their sons with more heritable land. In this society, men invested resources, land in this case, that influenced the well-being of their children but did not divert resources from their mating efforts to enhance the later competitiveness of these children. The finding is in keeping with the prediction that any motivational disposition for men's parenting to be focused on enhancing children's later social competitiveness is more likely to be expressed in societies with socially imposed monogamy than in other societies, as monogamy frees resources that might otherwise be used to attract additional wives. Note that if men did not have a presumably evolved motivational potential to shift resources from mating efforts to parenting efforts, then intense male parenting would not be evident in any type of society and social prohibitions against polygynous marriages would not be effective.

In summary, although parenting and family formation are variable among and within human societies, associations with social and ecological parameters such as subsistence practices, group size, land ownership, and social status suggest that humans have evolved phenotypic flexibility for

responding to factors affecting reproductive competition (Flinn & Low, 1986; Low, 1999). In all of these different contexts, the social dynamics of reproductive decisions (e.g., marriage decisions, investment in children) are influenced by issues related to increasing access to and control of the resources that covary with survival (e.g., access to arable land) and reproductive (e.g., ability of a man to pay bride price) outcomes in the local ecology. Although to varying degrees, in all societies these social dynamics are embedded in the context of cooperating and competing kin groups.

## CONCLUSIONS

Nuclear and extended families, and accompanying levels of investment of parental time and resources in children, are found in one form or another in all human societies; thus, is it reasonable to conclude that these are a reflection of evolved features of the social deep structure of *H. sapiens* (Bugental, 2000; Caporael, 1997; Pasternak et al., 1997). The apparent naturalness of human parental behavior and families has left the true uniqueness of this social organization largely unexamined, from an evolutionary perspective. To be sure, there are thoughtful evolutionary analyses of the human family and the dynamics of human parenting (e.g., Belsky et al., 1991; Draper & Harpending, 1988; Hewlett, 1992; Hewlett et al., 2000), but, with the exception of Alexander (1990; Alexander & Noonan, 1979), these have not been considered in terms of their comparative uniqueness or in terms of the suite of the other unusual features of *H. sapiens* (see Table 1). Among these unusual features are male parenting — humans are the only species of terrestrial primate that lives in multimale, multifemale groups with fathers — and a development period that is considerably longer than would be expected based on life history parameters of other mammals and primates (Bogin, 1997; Geary, 2000; Hill & Hurtado, 1996; Hill & Kaplan, 1999; Lancaster & Lancaster, 1987). Accompanying the long developmental period, of course, is extended and oftentimes extensive levels of PI, although in many preindustrial societies much of this investment is provided by the extended kin network, not simply the biological parents (Pasternak et al., 1997).

The position here is these features of human parenting, families, and development are coevolutionary aspects of a wider suite of characteristics that define the uniqueness of *H. sapiens* (Alexander, 1990). As noted, these other features include concealed ovulation, menopause and continuous, nonreproductive sexual activity (supporting extended female – male relationships; Dunbar, 1995; Geary, 2000); an unusually large brain and highly sophisticated sociocognitive competencies (i.e., language and theory of mind); and the absence of related species of *Homo*. Although it cannot be

stated with complete certainty at this time, all of these characteristics are parsimoniously explained by a single selective force — social competition through coalition formation. Among the supporting evidence is the finding that the complexity of a species' social organization, as indexed by group size, is related to brain size, to length of the developmental period, and almost certainly to sociocognitive competency (Barton, 1996; Humphrey, 1976; Joffe, 1997; Povinelli, 1993). The organization into social groups is consistently related to competition for control of the resources that covary with survival and reproductive outcomes, and these groups, in turn, are most typically composed of kin (Goodall, 1986; Hamilton, 1964, 1975; Packer et al., 1991; Sterck et al., 1997).

It follows from these patterns that the human nuclear and extended family are a reflection of an evolved motivational disposition to form social groups with kin and that the function of these groups is to cooperate so as to facilitate competition with other kin groups for access to and control of the resources that covary with survival and reproductive outcomes in the local ecology. The large brain and long developmental period of humans are largely to support the acquisition of supporting sociocompetitive competencies (e.g., social strategies for influencing other people or for acquiring resources, such as through hunting), and families and kin groups function to provide the necessary context for acquiring these skills (Geary & Bjorklund, 2000). Of course, many of these competencies are acquired in peer groups (Harris, 1995), but engagement in peer activities is possible only through extensive PI during this developmental period. Sheltering during a long developmental period also allows child-directed niche seeking; that is, it allows children to experiment, often in the context of peer relationships, with different social roles and strategies while being sheltered from adult-like competition. Moreover, parenting activities, such as the nature of parent – child play or attachment patterns, may influence relationships with peers and later relationships in adulthood (Belsky, 1997; Hewlett et al., 2000; MacDonald, 1993).

When considered in terms of direct and indirect PI, it follows that the evolutionary function of human parents is not simply to have as many children as is biologically possible. Although birth rates would be expected to vary with infant and child mortality risks in the local community (Chisholm, 1993; Wilson & Daly, 1997), many unique features of humans — menopause, paternal investment, extensive PI during a prolonged developmental period, and so forth — indicate adaptations associated with having fewer children than is biologically possible and investing considerable social and material resources in these children. A corollary prediction is that the nature of this investment, at least in part, will be unique to individual children and reflect an interaction between the temperament, personality, and cognitive

competencies of individual children, as these are related to resource acquisition and other forms of social competition in the wider ecology (Collins et al., 2000; Reiss, 1995). Furthermore, in contexts in which wealth can be accumulated and controlled across generations, PI can take the form of multigenerational lineage investment — that is, investment that functions to maintain the social competitiveness of the donor's descendants.

Although the social landscape and the social dynamics of preindustrial societies are generally in keeping with this view (Chagnon, 1977, 1988; Pasternak et al., 1997), much research will be needed to test the many nuances of our proposed theory (see Table 6). The basic thesis is that the human family and the dynamics and function of human parenting will only be fully understood when viewed from an evolutionary perspective, but one that considers features of kin relationships and parenting that are common across species (e.g., Trivers, 1974) and one that considers families and parenting in the context of the uniqueness of the human species (Alexander, 1990). The one factor that ties together cross-species patterns and the suite of uniquely human characteristics, including extensive and prolonged parenting in the context of families, is social competition. It is perhaps an irony that the aspects of human social relationships that are most closely associated with nurturing and cooperation appear, ultimately, to be an evolved feature of a competitive social strategy, but parsimony and the confluence of evidence described herein allow us no other conclusion.

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