

# SEXUAL SELECTION AND HUMAN LIFE HISTORY

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### **I. Introduction**

What is the evolutionary *raison d'être* of lifetimes and effort?

-R. D. Alexander, *The biology of moral systems* (1987, p. 38)

Sexual selection and life history are firmly established disciplines in evolutionary biology, and associated theory and research are focused on determining the ultimate and proximate causes of sex differences and developmental patterns, respectively

(Andersson, 1994; Charnov, 1993; Darwin, 1871; Roff, 1992). Research in human developmental science in general and human developmental sex differences in particular has not been informed by this wealth of empirical and theoretical work, with a few exceptions (Archer, 1992; Bjorklund & Pellegrini, 2002; Bogin, 1999; Freedman, 1974; Hill & Kaplan, 1999; Kenrick & Luce, 2000). As a redress, the general focus here is on relating human developmental sex differences to sexual selection and life history (Geary, 1999). In particular, I describe theory and evidence regarding the view that many human life history traits and developmental sex differences have evolved as a result of various forms of social competition (Alexander, 1987, 1989; Geary & Flinn, 2001).

To provide the necessary background and to introduce human developmental scientists to relevant work in evolutionary biology, in the next three sections I review research on life history, sexual selection, and their relation in nonhuman species. Then I relate the basic patterns and principles described in the first three sections to human developmental sex differences, with a focus on the relation between the social competition inherent in the dynamics of sexual selection and the evolution of sex differences in human life history traits (e.g., adult size, maturational patterns) and in developmental activity (e.g., play).

## II. Natural Selection and Life History

I begin by describing the basic mechanisms of natural selection along with the basic principles of life history and sexual selection. Then I meld the principles of life history and sexual selection to provide the theoretical foundation for interpreting research on human developmental sex differences.

### A. NATURAL SELECTION

The fundamental observations and inferences that led to Darwin's and Wallace's (1858; Darwin, 1859) insights regarding natural selection and evolutionary change are shown in Table I. Of particular importance are individual differences, which largely result as a consequence of sexual reproduction (Hamilton & Zuk, 1982; Williams, 1975). The process of natural selection occurs when heritable variability in a trait, such as age of reproductive maturity, covaries with variability in survival or reproductive outcomes (Price, 1970). As an example, if age of maturation is heritable and early maturing individuals survive to maturity and thus reproduce more successfully than later maturing individuals, then after many generations, the mean age of maturation for this population will shift downward (see Reznick & Endler, 1982).

The strength of selection pressures can vary such that individual differences in some traits strongly influence the probability of survival or reproduction (e.g., to next breeding season), whereas other traits are only weakly related to or are

TABLE I  
Darwin's and Wallace's Observations and Inferences

Observations	Inferences
<ol style="list-style-type: none"> <li>1. All species have such high potential fertility that populations should increase exponentially.</li> <li>2. Except for minor annual and rare major fluctuations, population size is typically stable.</li> <li>3. Natural resources are limited in a stable environment they remain constant.</li> </ol>	<ol style="list-style-type: none"> <li>1. More individuals are born than can be supported by available resources, resulting in competition for those resources that covary with survival prospects.</li> </ol>
<ol style="list-style-type: none"> <li>1. No two individuals are exactly the same; populations have great variability.</li> <li>2. Much of this variability appears to be related to inheritance that is passed on from parents to offspring.</li> </ol>	<ol style="list-style-type: none"> <li>1. Prospects for survival are not entirely random but covary with inherited characteristics. The relation between these characteristics and differential survival is natural selection.</li> <li>2. Over two generations, natural selection leads to gradual change in the population, that is, microevolution, and production of new species, that is, macroevolution or speciation.</li> </ol>

*Note:* Observations and inferences are based on Darwin and Wallace (1858), Darwin (1859), and Mayr (1982). Although genetics were not yet understood, Darwin inferred that traits were passed on from parent to offspring through, among other things, what was known about the effects of selective breeding (artificial selection) on the emergence of various domestic species.

unrelated to survival or reproductive prospects. If strong selection is maintained across many generations, then heritable variability should be reduced to zero, and it has been for some traits (e.g., all genetically normal humans have two legs, a heritable trait that shows no variability across individuals). However, for a variety of reasons many of the traits that covary with survival and reproductive outcomes show heritable variability and are thus subject to evolutionary change (see Roff, 1992, for a discussion of why heritable variability is maintained). Mousseau and Roff (1987) conducted a comprehensive review of the heritable variability of the morphological, behavioral, physiological, and life history phenotypes (i.e., measurable traits) that covary with survival and reproductive outcomes in wild,

outbred animal populations. The analysis included 1120 heritability estimates—the proportion of variability across individuals that appears to be due to genetic variability—across 75 invertebrate and vertebrate species. Although there was considerable variation ---across species, contexts, and phenotypes--- in the magnitude of the heritability estimate, their analysis indicated that “significant genetic variance is maintained within most natural populations, even for traits closely affiliated with fitness” (Mousseau & Roff, 1987, p. 188). The median heritability estimates were .26 for life history traits (e.g., age of maturation), .27 for physiological traits (e.g., cardiovascular capacity), .32 for behavioral traits (e.g., mating displays), and .53 for morphological traits (e.g., body size), values that are similar to those found in human populations (Plomin, DeFries, McClearn, & McGuffin, 2001).

Kingsolver and colleagues (2001) reviewed field studies of the relation between the types of traits analyzed by Mousseau and Roff (1987) and survival and reproductive outcomes in wild populations (see also Endler, 1986). Across species and traits, the median effect size indicated that being one standard deviation above (e.g., late maturation) or below (e.g., early maturation) the mean was associated with a 16% increase in survival (e.g., surviving to next breeding season) or reproductive (e.g., number of offspring) fitness. If the heritability of any such trait was only .25, “then selection of this magnitude would cause the trait to change by one standard deviation in only 25 generations” (Conner, 2001, p. 216), or in 12-13 generations with a heritability of .50.

The basic point is that the principles of natural selection have been empirically evaluated in many species and for many different traits. Many of these traits both show heritable variability and covary with survival and reproductive outcomes, the conditions needed for natural selection and thus evolutionary change to occur (see Table I).

## B. LIFE HISTORY

As aptly described by Alexander, “lifetimes have evolved to maximize the likelihood of genic survival through reproduction” (Alexander, 1987, p. 65), and the focus of life history research is on the suite of phenotypic traits that defines the species’ maturational and reproductive pattern (Charnov, 1993; Roff, 1992). A *suite* of traits must be considered because of the trade-offs involved in the expression of one phenotype versus another (Williams, 1957). The trade-offs are commonly conceptualized in terms of a competitive allocation of resources (e.g., calories) to somatic effort or reproductive effort, as shown in Figure 1 (Alexander, 1987; Reznick, 1985, 1992; Williams, 1966). Somatic effort is traditionally defined as resources devoted to physical growth and to maintenance of physical systems during development and in adulthood (see West, Brown, & Enquist, 2001), although growth also involves the accumulation, as in increases in body size, of reproductive potential. Reproductive effort is expended during adulthood and is distributed

Life History					
Somatic Effort			Reproductive Effort		
Infancy and Juvenility		Life Span	Adult Reproductive Years		
Growth	Developmental Activity	Maintenance (Survival)	Mating	Parenting	Nepotism

Fig. 1. Components of life history. Development activity refers to social, behavioral, and cognitive activities during juvenility that promote survival and increase reproductive potential (see Figure 6). Nepotism refers to activities that promote the somatic or reproductive efforts of kin, such as nephews and nieces.

among mating, parenting, and in some species nepotism, that is, investment in kin other than offspring (Emlen, 1995; Hamilton, 1964).

In addition to these traditional components of life history, Figure 1 includes developmental activity as a feature of somatic effort during infancy and juvenility. Some developmental activities will promote survival during development (e.g., predator avoidance), whereas others are analogous to the relation between physical growth and the accumulation of reproductive potential. The latter developmental activities result in the refinement of behavioral (e.g., practicing mating displays), cognitive (e.g., birdsong), and physical (e.g., improving cardiovascular capacity) competencies that will later influence reproductive prospects (Geary & Bjorklund, 2000), and presumably result in somatic changes (e.g., modification of neural systems supporting birdsong) during infancy and juvenility. In other words, the results of many developmental activities are incorporated into the developing soma---for instance, distribution of slow and fast muscle fibers as related to physical activity (Byers & Walker, 1995)---and facilitate later reproductive activities. Lifetimes are thus conceptualized as involving the accumulation of reproductive potential---captured by growth and developmental activity during infancy and juvenility---and then the expenditure of this potential on reproductive effort in adulthood (Alexander, 1987).

The clearest examples of this view of lifetimes are found in many species of *Insecta* where distinct morphs are associated with different life history stages. An illustration is provided in Figure 2 for the tomato hornworm moth (*Manduca quinquemaculata*), where the behavior of the larvae (caterpillars) is focused on somatic effort---to avoid predation and to grow---but the behavior of the adult (moth) is focused on reproductive effort. In fact, the caterpillar morph cannot reproduce and in some species of *Insecta* the adult morph does not eat; that is, the sole function of the moth or butterfly is to reproduce (Alexander, 1987).

Although life history traits will sometimes fall into more than one of the categories shown in Figure 1---sex hormones, for---instance, may influence growth as

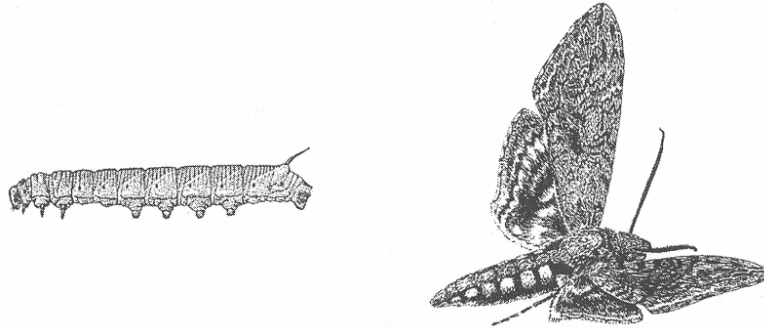


Fig. 2. Two life history stages of the tomato hornworm moth (*Manduca quinquemaculata*). To the left is the larval stage during which the caterpillar's behavior is focused on somatic effort, that is, avoiding predation and growth. To the right is the adult stage during which the moth's behavior is focused on reproductive effort. United States Department of Agriculture, public domain illustrations.

well as allocation of reproductive effort into mating or parenting---these categories nonetheless provide a useful heuristic for conceptualizing trade-offs. Within finite lifetimes, trade-offs between the different components of somatic and reproductive effort can be conceptualized in terms of the relative size of the corresponding rectangles in Figure 1. As examples, traits that facilitate predator avoidance (e.g., dull coloration, a feature of somatic effort) may be negatively correlated with mating success (e.g., attracting mates), or traits that facilitate mating activities (e.g., testosterone) may negatively affect health (Folstad & Karter, 1992). Thus the selective advantage for expressing one trait often has an associated cost in terms of other selection pressures or in terms of the expression of other traits (Williams, 1966).

Because of these trade-offs, selection pressures do not commonly operate such that a single trait is optimally expressed (e.g., having the brightest possible plumage within physiological constraints). Rather, selection will result in an evolved combination of traits that minimize costs (e.g., predation risks) and enable---within trade-off and ecological (e.g., food) constraints---producing the optimal number of offspring that are likely to survive to adulthood and reproduce themselves (Roff, 1992). A full discussion of the complexity of life history trade-offs is beyond the scope of this treatment (see Charnov, 1993; Roff, 1992; Stearns, 1992), but in the pages that follow I describe some of the most basic of these trade-offs as well as the related issue of phenotypic plasticity.

### 1. Lifetime Pattern of Reproduction

Reproductive activity takes on two general forms: in semelparity all reproductive potential is spent in one breeding episode, but in iteroparity reproductive potential is allocated across more than one breeding episode. Semelparity is a more risky strategy because reproduction during poor ecological conditions could result in extremely high offspring mortality rates, with no opportunity to reproduce under

more favorable conditions. Semelparity is, however, favored when adult mortality is high and thus the probability of surviving to the next breeding season is low. Under these conditions, individuals that devote minimal resources to somatic effort in adulthood and maximal resources to reproductive effort will produce more offspring than individuals that do not. In contrast, iteroparity is favored when juveniles and adults are likely to survive from one breeding season to the next (e.g., due to low predation risks) and juveniles are unlikely to reproduce successfully (Roff, 1992; Wittenberger, 1979). For these species, the current reproductive effort is balanced against the costs of this effort with respect to survival and future reproductive potential. As a result, during each breeding season iteroparous species invest more in maintenance and less in reproduction than semelparous species (Roff, 1992).

A comparison of female Pacific salmon (*Salmo gairdneri*) and female Atlantic salmon (*S. salar*) illustrates how selection pressures can influence the evolution of a semelparous or iteroparous reproductive strategy. Female Pacific salmon experience intense competition for suitable nesting sites and must guard these sites after depositing their eggs (de Gaudemar, 1998). The intensity of the competition favors expending all resources in one reproductive episode. Females that do not incur the costs of competition will not obtain a suitable nesting site or will have their site destroyed by other females, and thus they will not reproduce at all. The result of this competition has been the evolution of a life history strategy such that resources that could be used for maintenance and survival---females die at the end of the first breeding episode---are expended on behavioral competition for nesting sites and on the development of eggs. The latter results in the production of several--fold more eggs than the iteroparous Atlantic salmon (Roff, 1992). In contrast, competition among females for suitable nesting sites is less intense in Atlantic salmon. In this species, females devote more resources to maintenance and less to reproduction during each breeding season and thus survive to reproduce over many breeding seasons (Roff, 1992). The advantage of distributing reproduction over several seasons is to counter year-to-year fluctuations in predation or other risks (e.g., lack of food) to offspring survival. Although female Atlantic salmon produce fewer eggs during any single season than do female Pacific salmon, the number of viable offspring produced during the reproductive life span of these two species is comparable.

There are also variations in life history traits (e.g., age of maturation) across semelparous species and across iteroparous species. These cross-species differences are understandable in terms of differences in selection pressures in each species' specific ecology. As an example, consider Reznick and Endler's (1982) study of the influence of predation on growth and reproductive patterns in iteroparous guppies (*Poecilia reticulata*). Here, three populations of the same species were studied under three patterns of predation risk: high risk (predators feeding on large adults), medium risk (predators feeding on juveniles), and low risk (few predators). When risk was high, females matured more rapidly and were smaller

as adults, two factors that lowered their risk of being eaten by predators before reproducing. In addition, they allocated more reproductive effort to initial breeding episodes, producing two to three times as many offspring in these breeding episodes than did females in less risky environments. In locales where predation was less severe and adult mortality rates were lower, individuals grew more slowly, attained a larger adult size, and females allocated their reproductive effort over more breeding episodes. Follow-up studies revealed that these differences in life history pattern were due to a combination of genetic differences between these populations and phenotypic plasticity (discussed later, Reznick & Bryga, 1987, 1996; Reznick, Shaw, Rodd, & Shaw, 1997; Rodd, Reznick, & Skolowski, 1997). In sum, Reznick and colleagues' studies empirically demonstrate systematic relations between predation risks and life history and reproductive parameters in three populations of the same species of guppy and thus illustrate the conditions that could ultimately lead to the emergence of different species of guppy with different life history and reproductive traits (Darwin, 1859).

## 2. Reproductive Costs

Reproduction involves costs associated with mating (e.g., finding mates), producing gametes and offspring (e.g., eggs), and for many species parental care (Roff, 1992). Mechanisms underlying the cost/benefit trade-offs involved in reproducing may be genetic or social/environmental, or they may represent a genotype by environment interaction (Reznick, Nunney, & Tessier, 2000). Social costs include those incurred during intrasexual competition over mates and are described later. Genetic trade-offs arise when the same gene or genes affect two or more life history traits (Williams, 1957). In many species, reproducing earlier in life is associated with a shorter life span (Reznick, 1992). The same genes that promote early reproduction have the negative consequence of accelerating the onset of senescence and reducing the life span.

Life span is also influenced by more proximal reproductive costs, such as producing eggs, competing for mates, and caring for offspring, which can compromise the physical health and oftentimes the survival prospects of parents (Clutton-Brock, 1991; Steams, 1992). The underlying physiological mechanisms governing these cost/benefit trade-offs are not fully understood, but include the energetic demands of reproduction (e.g., parental care) and associated hormonal changes (Sinervo & Svensson, 1998). For example, the development of male secondary sexual characteristics needed to compete with other males (e.g., antlers) or to attract females (e.g., a bright plumage) requires an increase in testosterone levels which in turn can compromise the immune system and survival prospects of unhealthy males (Folstad & Karter, 1992; Saino & Møller, 1994; Saino, Møller, & Bolzern, 1995). Similarly, in the female collard flycatcher (*Ficedula albicollis*) large brood sizes are associated with a reduced production of antibodies for a common parasite; the result is increased infection rate and mortality rate (Nordling, Andersson, Zohari, & Gustafsson, 1998).

### 3. *Growth and Development*

All other things being equal, evolution should result in a life history pattern in which females produce many, fast maturing offspring, that have an increased probability of surviving to reproduce (Williams, 1966). The fact that many species do not show this life history pattern indicates that the associated trade-offs are costly. These trade-offs include smaller and less competitive offspring that in turn suffer high mortality rates (Stearns, 1992). Across species of plant, insect, fish, reptile, and mammal, offspring that are larger at time of hatching or birth have increased survival rates due, in part, to decreased predation risk and decreased risk of starvation (Roff, 1992). The trade-off is that females of these species produce fewer offspring than do females of related species that produce many smaller offspring. Thus fast maturation and large numbers of offspring are associated with low-quality offspring (i.e., high mortality risks and low competitiveness). High-quality--larger and more competitive---offspring come at a cost of fewer offspring produced during a reproductive life span. Many factors will influence whether a species tends toward a low-quality/high-quantity or high-quality/low-quantity reproductive pattern, including age-specific mortality risks (e.g., through predation), population stability or expansion, and intensity of competition with conspecifics (Mac Arthur & Wilson, 1967; Stearns, 1992; Roff, 1992).

Species that produce fewer and larger offspring also tend to have slower rates of growth, higher levels of parental care, and longer life spans in comparison to related species that produce smaller but more offspring (Roff, 1992; Shine, 1978, 1989; Stearns, 1992). This life history pattern is more common in iteroparous than in semelparous species and is associated with relatively low juvenile mortality rates and a low probability of reproducing at an early age (Roff, 1992). Low juvenile mortality is related to larger size at hatching or birth as well as to parental protection and provisioning (Clutton-Brock, 1991; Shine, 1978). As described later, a low probability of reproducing at an early age can result from reproductive competition with more mature individuals in the population. In this situation, delayed maturation can improve reproductive prospects through, for instance, an increase in body size. Large body size enables females to give birth to larger and thus more competitive offspring, and for males it facilitates male-male competition in adulthood (Carranza, 1996; Stearns, 1992). In some species, developmental activity during the maturational period enables improvements in survival- and reproduction-related behavioral/cognitive competencies. Slow maturation and growth thus allows for the accumulation of more reproductive potential, through physical development and developmental activity, than is possible with faster maturing species.

### 4. *Phenotypic Plasticity*

Phenotypic plasticity refers to the potential for the modification of survival- and reproduction-related phenotypes in response to social and ecological (e.g., food) conditions, but within genetically based constraints (Roff, 1992). The potential

to modify the expression of life history traits presumably evolved as an adaptation to variability across seasons and generations in the ecologies in which the species evolved. Phenotypic plasticity enables a more optimal expression of life history traits as these relate to survival and reproductive demands in the local ecology. The mechanisms associated with plasticity include hormonal and/or other endocrine responses as well as ecological conditions (e.g., water availability) that affect the physical and behavioral condition of the individual (McNamara & Houston, 1996; Sinervo & Svensson, 1998). Phenotypic plasticity has been empirically demonstrated in a wide range of plant species (Fenner, 1998; Sultan, 2000) as well as in a diversity of other species ranging from plankton to primates (Alberts & Altmann, 1995; McLaren, 1966; McNamara & Houston, 1996; Mиаud, Guyétant, Elmberg, 1999; Roff, 1992). In all of these species, phenotypic plasticity is expressed within the constraints of norms of reaction (Stearns & Koella, 1986). Norms of reaction represent a genotype whose phenotypic expression varies with ecological conditions, but only within a genetically constrained range.

Consider field voles as one example (*Microtus agrestis*; Ergon, Lambin, & Stenseth, 2001). In this species, populations residing in different locales vary significantly in two life history traits, adult body mass and timing of yearly reproduction. On one hand, if the population differences reflect genetic variance then individuals transplanted from one population to the other will show the body mass and reproductive timing of their natal group. On the other hand, if the population differences reflect variation in local ecologies, such as quality and availability of food, then, in the season following transplantation, body mass and reproductive timing of transplanted individuals should be the same as that of the local community. In fact, the life history traits of transplanted individuals were indistinguishable from those of the local community and differed significantly from those of their natal community. Regardless of natal community, individuals living in richer ecologies developed a higher wintering body size and as a result were able to reproduce earlier. Individuals living in poorer ecologies needed to devote added time to foraging and growth---somatic effort---and thus experienced a delay in the onset of reproduction---reproductive effort.

Phenotypic plasticity in growth and reproductive timing has also been demonstrated for many other species, including humans (Stearns & Koella, 1986), as well as for many other life history traits (Roff, 1992). For some species, cross-generational plasticity has been demonstrated, whereby the ecological conditions experienced by the mother influence life history trade-offs in offspring (Hofer, 1987). For example, offspring of nutrient-deprived plants allocate more growth-related resources to root production, whereas offspring of light-deprived plants allocate more resources to leaf production (Sultan, 2000; see also Alekseev and Lampert, 2001, for an analogous mechanism in the crustacean *Daphnia*). In mammals, maternal condition during pregnancy and during offspring suckling can

have long-term reproductive consequences. Healthy mothers give birth to heavier offspring and they provide more milk, both of which promote early growth and this, in turn, is associated with larger adult size and higher breeding success (Clutton-Brock, 1991). As an example involving social dynamics, testicular maturation and achievement of social dominance are accelerated in male baboons (*Papio cynocephalus*) borne to high-ranking females, thereby enhancing the males' reproductive prospects (Alberts & Altmann, 1995).

### 5. Conclusion

From plankton to primates, considerable empirical evidence supports the position that age of maturation, reproductive pattern, number of offspring, extent of parenting, and length of the developmental period are evolved features of the species' life history (Williams, 1966; Roff, 1992; Stearns, 1992). The accompanying suite of developmental and reproductive traits essentially involves the respective accumulation and expenditure of reproductive potential, within the constraints imposed by external conditions, such as parasites and predators, and social competition, including sexual selection (Alexander, 1987).

## III. Sexual Selection

Sexual selection refers to the processes associated with mating competition with members of the same sex and species (intrasexual competition) and the processes associated with choosing mates (intersexual choice; Darwin, 1871). Sexual selection is related to sex differences in hundreds of species and most typically includes male-male competition over access to mates and female choice of mating partners (Andersson, 1994). As I describe in the first part of this section, the dynamics of sexual selection turn on the degree to which members of each sex allocate their reproductive effort to competing for mates or investing in parenting. In the second and third parts of this section, I illustrate the evolutionary influences of intrasexual competition and intersexual choice, respectively.

### A. MATING OR PARENTING?

As shown in Figure 1, reproductive effort is distributed between mating (e.g., time spent searching for mates), parenting, and occasionally nepotism. Nepotism is less central to the later discussion of human life history and is not considered further (see Emlen, 1995); this is not to say that humans do not engage in significant levels of nepotism--they do (see Geary & Flinn, 2001; Pasternak, Ember, & Ember, 1997). The distribution of reproductive effort across mating and parenting is, however, central to the later discussion, and it turns on the extent of each sexes' parental effort or parental investment (Trivers, 1972; Williams, 1966).

Parental investment is any cost (e.g., time) associated with raising offspring that reduces the parents' ability to produce or invest in other offspring (Trivers, 1974). Given that some level of parental investment (even if it only involves producing eggs) is necessary for the reproduction of both parents, the nature of the investment provided by females and males creates the basic dynamics of sexual reproduction and sexual selection. If one sex provides more than his or her share of parental investment, then members of that sex become an important reproductive resource for members of the opposite sex (Dawkins, 1989; Trivers, 1972). The reproductive success of members of the lesser 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 more highly investing sex is more strongly influenced, in most cases, by investment in offspring than in finding mates.

In most species, the sexes differ in the degree to which the reproductive effort is allocated to competition for access to mates or to parental investment (Andersson, 1994; Trivers, 1972; Williams, 1966). These differences, in turn, are related to the potential rate of reproduction and to social and ecological influences on mating opportunities, in particular, the operational sex ratio (OSR; Clutton-Brock & Vincent, 1991; Emlen & Oring, 1977; Krebs & Davies, 1993). Reproductive rates and the OSR are related but described separately.

### *1. Reproductive Rates*

A sex difference in potential rate of reproduction can create a sex difference in relative emphasis on mating or on parenting. Most generally, 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 (Clutton-Brock & Vincent, 1991). This pattern arises because 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. Under these conditions, individuals of the sex with the faster rate of reproduction will typically have a higher lifetime reproductive success if they rejoin the mating pool and compete for mates than if they parent (Parker & Simmons, 1996).

For species with internal gestation and obligatory postpartum female care (e.g., suckling in mammals), the rate at which females can produce offspring is considerably lower than the potential rate of reproduction of conspecific males (Clutton-Brock, 1991). In addition, internal gestation and the need for postnatal care results in a strong bias in mammalian females toward parental investment and results in 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. In other words, males that compete for additional mates typically have more offspring than do males that do not compete and instead invest in parenting. Thus, the sex difference in reproductive rate, combined with offspring that can

be effectively raised by the female, creates the potential for a large female--male difference in the mix of mating and parenting, and this difference is realized in 95-97% of mammalian species (Clutton-Brock, 1989). In these species, females can effectively provide the majority of parental care and do so. Female care, in turn, frees males to invest in mating effort, which typically takes the form of male--male competition over access to mates or for control of the resources (e.g., territory) that females need to raise their offspring.

## 2. Operational Sex Ratio

The OSR is defined as the ratio of sexually active males to sexually active females in a given breeding population at a given point in time and is related to the rate of reproduction (Emlen & Oring, 1977). In a population where the number of sexually mature females equals the number of sexually mature males---an actual sex ratio of 1:1---any sex difference in the rate of reproduction will skew the OSR. As noted, mammalian males have a faster potential rate of reproduction than conspecific females, which typically results in more sexually receptive males than sexually receptive females in most populations. This biased OSR creates the conditions that lead to intense male-male competition over access to a limited number of potential mates. Although these patterns are most evident in mammals, they are also found in many species of bird, fish, and reptile (Andersson, 1994). And they are not limited to males: When females have a faster rate of reproduction than males (e.g., when males care for eggs), female-female competition is often more salient than male-male competition (e.g., Reynolds, 1987).

The sex difference in potential reproductive rate and a skewed OSR appear to be the ultimate sources of the male focus on mating effort and the female focus on parental effort in the vast majority of mammalian species (Emlen & Oring, 1977; Parker & Simmons, 1996). The biology of internal gestation and suckling are not the only factors that influence the potential rate of reproduction and the OSR in mammals; social and ecological factors are sometimes important as well. As an example, male callitrichid monkeys (*Callithrix*) have a higher potential rate of reproduction than conspecific females do. However, shared territorial defense, female-on-female aggression that drives away the males' potential mating partners, and other factors negate this physiologically based sex difference and result in a more balanced OSR, monogamy, and high levels of paternal investment (see Dunbar, 1995).

## B. INTRASEXUAL COMPETITION

Intrasexual competition over mates, whether male--male competition or female-female competition, will result in the evolutionary emergence of sex differences for those traits that facilitate this competition (Andersson, 1994; Darwin, 1871). Studies of intrasexual competition have revealed that the associated sex differences

can be physical, behavioral, or cognitive (including neural) and typically only affect those features actually involved in the competition (Andersson, 1994; Geary, 1998). One of the more common expressions of intrasexual competition involves physical threats and fights over access to mates or for control of the territory that members of the opposite sex need to raise offspring (e.g., nesting spots). A common result is that physically larger, healthier, and more aggressive individuals (typically males) monopolize the reproductive potential of members of the opposite sex (typically females). The accompanying individual differences in reproductive success---some individuals have many offspring, others have few or none---result in the evolution of sex differences in physical size and aggressiveness. The polygynous ruff (*Machetes pugnax*) provides one example of such competition among males. As described by Darwin, males are considerably larger and more aggressive than females and physically compete for sexual access to females. These physical and behavioral sex differences evolved in the ruff, and many other species, because of the reproductive advantages associated with larger size and pugnacity in males (Darwin, 1871).

Sometimes the competition is more behavioral or cognitive (e.g., spatial cognition, as in searching for mates) than physical (Gaulin & Fitzgerald, 1986, 1989; Gilliard, 1969). In these situations, behavioral and cognitive traits that facilitate intrasexual competition will evolve in the same way that physical traits evolve (see Geary, 1998, for elaboration). When males parent (e.g., incubate eggs), females may compete more intensely for mates than males; that is, physical female-female competition is more intense than male-male competition. In these species, females are larger and more aggressive than males (see Reynolds, 1987).

### C. INTERSEXUAL CHOICE

The sex that invests more in parenting tends to be more choosy with regard to mating partners than the other sex (Trivers, 1972). Because females tend to invest more in parenting than males, female choice is predicted to be and is more common than male choice. Male choice is predicted for species with paternal investment, although this prediction has not been as thoroughly tested as female choice. In any case, female choice has been studied most extensively in birds, although it is also evident in insects, fish, reptiles, and mammals, including humans (Andersson, 1994; Buss, 1994). Several examples of male traits that have been shaped by female choice are shown in Figures 3 and 4; in some species these traits may also be involved in male-male competition, as in dominance displays. These traits often involve elaborate physical displays, as in the crest along the back and tail of the male crested newt (*Triturus cristatus*; Figure 3), the dorsal fin of the male dragonet (*Callionymus lyra*; Figure 3), and the comb of the male hoopoe (*Upupa epops*; Figure 4). In many species, males are often more elaborately colored than females. The comb of the male hoopoe is a bright orange, and the male dragonet has a brilliant yellow body of varying shades, whereas the female dragonet is a "dingy reddish-brown" (Darwin, 1871, Vol. II, p. 8).

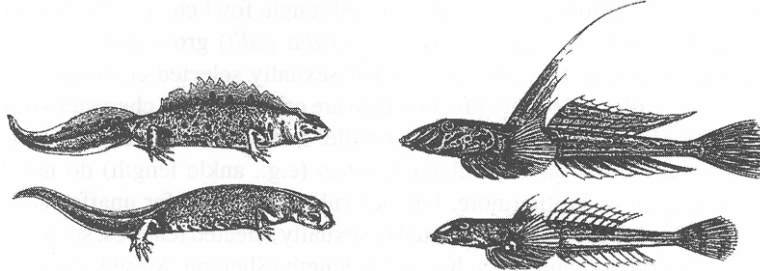


Fig. 3. Indicators of male fitness shaped by female choice for selected species of amphibian and fish. To the left are male (top) and female (bottom) *Triturus cristatus* (from *The Descent of Man, and Selection in Relation to Sex, Part II*, p. 24, by C. Darwin, 1871, London: John Murray). To the right are male (top) and female (bottom) *Callionymus lyra* (from *The Descent of Man, and Selection in Relation to Sex, Part II*, p. 8, by C. Darwin, 1871, London: John Murray).

Traits such as those shown in Figure 3 are indicators of the physical, genetic, or behavioral fitness (e.g., ability to provide) of the male. These traits are honest indicators of male fitness, as they commonly are not expressed in unfit males (Zahavi, 1975). As an example, in some species of bird the coloration of male plumage covaries with physical health, in particular, resistance to infection by local



Hoopoe

Fig. 4. The size and coloration of the comb of the male hoopoe (*Upupa epops*) are indicators of male fitness shaped by female choice (from *A History of British Birds*, p. 50, by F. O. Morris, 1891, London: Nimmo).

parasites (see Hamilton & Zuk, 1982). In red jungle fowl chicks (*Gallus gallus*), males infected with a parasitic worm (*Ascaridia galli*) grow more slowly than their healthy peers, and, in adulthood, their sexually selected characteristics are more adversely affected by the infection than are other physical characteristics. For instance, the comb of affected males is smaller and duller than that of unaffected males but many other physical characteristics (e.g., ankle length) do not differ across these groups. Furthermore, females substantially prefer unaffected males (by two to one), and preference is related to sexually selected features, such as comb length, but not other features, such as ankle length (Sheldon, Merilä, Qvarnström, Gustafsson, & Ellegren, 1997; Zuk, Thornhill, & Ligon, 1990).

Related studies have demonstrated that unfit males cannot tolerate the hormonal changes needed for the expression of sexually selected traits. Experimentally increasing male testosterone levels to induce the expression of secondary sexual characteristics results in increased mortality in unhealthy males, perhaps due to suppression of immune functions (Folstad & Karter, 1992). In series of field experiments, Siano and colleagues assessed the effect of testosterone implants on mortality rates in the barn swallow (*Hirundo rustica*; Saino *et al.*, 1995; Saino, Bolzern, & Møller, 1997). In this species, female choice is influenced by the length and symmetry of the male's tail features (Møller, 1994). Testosterone implantation suppresses the immune system in males with shorter tail feathers more severely than in males with longer tail feathers and results in increased parasite loads and higher mortality rates in shorter tailed than in longer tailed males. The pattern indicates that males with long tail feathers can support high testosterone levels---and thus more effectively compete for mates---without compromising their immune system, suggesting that their immune system is well adapted to local parasites or that they are in better general physical condition than are males with short tail feathers. The pattern also illustrates an important life history trade-off for shorter tailed males. Resources (e.g., calories) that could be used for the development of a sexually selected trait must be diverted to immune functions. The cost is an inability to attract mates during the current mating season, and the benefit is increased survival prospects and thus an opportunity to mate in subsequent seasons.

#### IV. Life History and Sexual Selection

Sexual selection and life history have been linked theoretically and empirically, although the extent of the interrelation is not fully understood (Andersson, 1994). Predation risks, for example, may indirectly influence the opportunities for intrasexual competition or intersexual choice to operate and thus evolve (Partridge & Endler, 1987; Winemiller, 1992). More relevant to the current treatment is the prediction that social dynamics inherent in intrasexual competition and intersexual choice can influence and be influenced by life history traits (Höglund &

Sheldon, 1998; Kokko, 1997; Svensson & Sheldon, 1998). In fact, competition among members of the same species should, in theory, favor life history traits that include fewer, more competitive offspring (Mac Arthur & Wilson, 1967), which favors the evolution of iteroparity, a longer developmental period, higher levels of parental investment, and other traits that support social competition (Roff, 1992). Empirically, many of the hormonal mechanisms that influence the expression of life history traits (e.g., maturational timing) and trade-offs (e.g., mortality risks) also influence expression of secondary sexual characteristics involved in intrasexual competition and intersexual choice (Sinervo & Svensson, 1998).

The full extent of the relation between sexual selection and life history remains to be determined. For now, in the parts that follow I illustrate how intrasexual competition and intersexual choice appear to relate to the evolution and phenotypic expression of life history traits and trade-offs. In the final part, I address the issue of phenotypic plasticity.

#### A. INTRASEXUAL COMPETITION

Studies of the relation between intrasexual competition and life history have focused largely on males (Stearns, 1992), presumably because male-male competition is more common than female-female competition (Darwin, 1871; Andersson, 1994).<sup>1</sup> The relation between male-male competition and a few life history traits (e.g., age of maturation) have been studied in a variety of mammalian and bird species (e.g., Clinton & Le Boeuf, 1993; Harvey & Clutton-Brock, 1985; McElligott & Hayden, 2000; Rohwer, Fretwell, & Niles, 1980; Wiley, 1974) as well as in some other species (Stamps, 1995). I first illustrate the relation between physical male-male competition and sex differences in life history traits and then consider the relation between behavioral competition and sex differences.

##### *1. Physical Competition*

Males of many species of insect, reptile, fish, bird, and mammal show little or no parental investment and compete intensely for access to females (Andersson, 1994; Clutton-Brock, 1989; Darwin, 1871). One result is that only a minority of males reproduce, thereby creating strong selection pressures for the evolution of traits that support competitive ability (e.g., Clinton & Le Boeuf, 1993; McElligott & Hayden, 2000; Plavcan & van Schaik, 1997a). Among these traits are physical size and aggressiveness such that larger, more aggressive males are

<sup>1</sup>When it occurs, female-female competition should relate to life history traits in many of the same ways as male-male competition. Social dynamics in polyandrous shorebirds, for instance, include intense female-female competition for access to males to brood their eggs. Although the issues have not been thoroughly studied, females of these species show some of the same life history patterns common for males of other species in which male-male competition is intense (Reynolds, 1987; Reynolds & Székely, 1997).

typically more competitive than smaller, less aggressive males. In theory, these conditions could result in the evolution of growth rates such that males grow faster than females and achieve large size at progressively younger ages. However, the calories needed to achieve large size and the lost opportunity to practice fighting before reproductive maturity place formidable constraints on the evolution of such a life history pattern. A more common pattern is for males to grow more slowly and mature later than females and to engage in play fighting during juvenility (Smith, 1982; Stearns, 1992).

As an example, the mating dynamics of primates are consistently related to sex differences in maturational patterns (e.g., duration, growth spurt) and physical size (Leigh, 1995). Polygynous species with physical male-male competition are characterized by consistent sex differences, whereby males grow more slowly and evidence both a longer period of rapid growth (i.e., the growth spurt), and a longer overall developmental period than females. The result is larger males than females. In these species, both males and females are physically aggressive, but male-on-male physical aggression is related to competition for mates and is more severe and deadly than female-on-female aggression, which is related to competition for food (Smuts, 1987).

Further evidence that the sex differences in life history pattern are related to male-male competition comes from comparisons of evolutionarily related (i.e., having a recent common ancestor) monogamous and polygynous species. Intrasexual competition is less intense in monogamous species and thus the selective advantages for physical size and aggressiveness are considerably less relative to polygynous species (Clutton-Brock, Harvey, & Rudder, 1977). Among monogamous species of primate, the sexes rarely differ in adult size or maturational pattern (Leigh, 1995).

For mammalian species in which physical male-male competition is found, the development period of males can range from moderately longer (e.g., 2.8 vs 3.5 years in the patas monkey, *Erythrocebus paras*) to more than twice as long as that of females (e.g., 3.0 vs 8.0 years in the northern elephant seal, *Mirounga angustirostris*; Le Boeuf & Reiter, 1988; Harvey & Clutton-Brock, 1985; Stearns, 1992). Males may weigh slightly more than females (e.g., 19% heavier in colobus monkeys, *Colobus angolensis*) or can weigh more than double that of females (e.g., 120% heavier in mandrills, *Mandrillus sphinx*, another monkey; Harvey & Clutton-Brock, 1985). Intrasexual competition and accompanying reductions in parental investment (Trivers, 1972) are also related to average length of the life span (Allman, Rosin, Kumar, & Hasenstaub, 1998). The lesser investing sex shows more intense intrasexual competition and has a shorter life span on average than does the more highly investing sex, whether the latter is female or male. The sex difference in life span appears to be a consequence of the higher nutritional demands needed to grow larger, the injuries associated with male-male competition, and the immunosuppressive effects of testosterone (Clinton & Le Boeuf, 1993;

Clutton-Brock, Albon, & Guinness, 1985; Folstad & Karter, 1992). The advantage of physical size also creates a selective advantage for larger offspring and an accompanying increase in the size of females, but with the trade-off of fewer offspring (Carranza, 1996; Roff, 1992).

The overall pattern is consistent with predictions noted earlier regarding social competition and life history evolution (MacArthur & Wilson, 1967; Roff, 1992). The features of primate life history and particularly that of humans (described later) and related species (e.g., chimpanzees, *Pan troglodytes*) appear to be especially in keeping with this hypothesis. Across species of primate, larger and fewer offspring, are associated with the predicted life history patterns of longer interbirth intervals, higher levels of maternal investment, larger brains, longer developmental periods, and longer maximum life spans (Allman, McLaughlin, & Hakeem, 1993; Harvey & Clutton-Brock, 1985). Across these species, the length of the developmental period and brain size covary positively with the species' social complexity, the intensity of intrasexual competition, and with foraging complexity (Allman *et al.*, 1993; Dunbar, 1993; Joffe, 1997; Sawaguchi, 1997), suggesting that a long maturational period is not simply about producing a larger body size, at least in primates. Presumably, a long developmental period and a large brain enable the practice and refinement of sociocompetitive and foraging skills---accumulation of reproductive potential---before engaging in actual (potentially life threatening) competition and unsupported (by parents) food acquisition.

## 2. Behavioral Competition

Intrasexual competition with a strong behavioral component can result in alternative reproductive strategies and life histories for one or both sexes or in an exaggeration of the behavioral and associated life history traits. The different reproductive strategies and life histories of smaller jack and larger hooknose male salmon (*Oncorhynchus kisutch*) provide a clear example of the former (Gross, 1985). Hooknose males mature later and compete physically for access to eggs laid by females, whereas jack salmon are specialized to hide among rocks and furtively spawn while hooknose males are fighting. The smaller and earlier maturing jacks are just as reproductively successful, on average, as larger hooknose males, and thus early maturity and furtive mating represents a successful life history strategy for males of this species (Gross, 1985).

Studies of bowerbirds provide some the best examples of how intrasexual competition and intersexual choice can involve behavioral competition and result in the evolution of behavioral sex differences (Gilliard, 1969). In most of these species, the principal focus of competition and choice is the bower, a structure made of tree boughs and vines shown in Figure 5 (Darwin, 1871). A female bowerbird's choice of mating partners is strongly influenced by the complexity and symmetry of the male's bower as well as by the number of decorations around the bower. Males thus compete with one another through bower building and through the destruction of

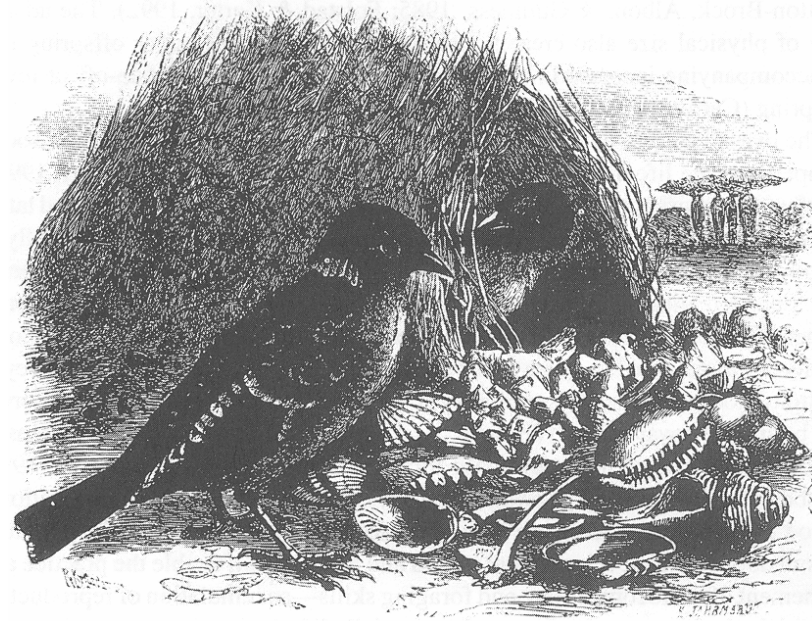


Fig. 5. Bower building and behavioral male--male competition in the bowerbird (*Chlamydera maculata*) (from *The Descent of Man, and Selection in Relation to Sex, Part II*, p. 70, by C. Darwin, 1871, London: John Murray).

their competitors' bowers (Borgia, 1985a, 1985b; Collis & Borgia, 1992), although courtship displays, calls, and physical fights among males are also components of male--male competition and female choice (Borgia & Coleman, 2000).

As with species in which physical male--male competition is prevalent, sex differences in the life history traits of one well-studied bowerbird, the satin bowerbird (*Ptilonorhynchus violaceus*), are evident, including differences in growth patterns and developmental activity. Female satin bowerbirds begin to reproduce at 2 years of age, whereas males do not produce sperm until they are 5 years of age and do not achieve an adult-male plumage until they are 6- or 7-years-old (Vellenga, 1980). Even then, most males that hold bowers do not mate until 10 years of age, if they mate at all (Borgia, personal communication, August 24, 2001). During development, young males watch older males at their bower and imitate bower building and courtship displays when the older male leaves the bower (e.g., to feed; Collis & Borgia, 1992). Young males also engage in play fighting, which provides the experience needed for dominance-related encounters in adulthood.

Although the degree to which bower building is genetically or experientially based is not yet certain, the delayed maturation of male satin bowerbirds almost

certainly provides an opportunity to practice and refine the bower construction and physical competition skills that will be needed in adulthood. In this circumstance, the later reproductive advantage of bower building and other competition-related skills will---when combined with low juvenile mortality risks---provide a selective advantage for delayed maturation in males. In other words, delayed maturation enables males through developmental activities to accumulate the reproductive potential needed to compete with other males and to attract female mates in adulthood.

#### B. INTERSEXUAL CHOICE

The relation between intersexual choice---typically female choice---and sex differences in life history traits has received less attention than the relation between intrasexual competition and life history. One difficulty is that many traits that influence female choice are also related to male-male competition, as in dominance displays (e.g., birdsong often has this dual function; Borgia & Coleman, 2000). An important window into the likely influence of female choice on the evolution of life history traits in males comes from studies of lekking species (Höglund & Alatalo, 1995; Wiley, 1974). Leks can be areas in which males gather together during the mating season to strut, display plumage, or engage in other activities that function to attract mating partners, or they can be more dispersed areas in which single males display. In both situations, females will survey a number of males and will then mate with one or a few of them. The result is a minority of males copulate with most of the females that visit the lek. The satin bowerbird provides one example of a lekking species. The delayed maturation of male bowerbirds and the sex difference in developmental activities (i.e., bower building) are likely the evolutionary result of male--male competition and female choice, although the relative contribution of these different components of sexual selection are not known. Whatever the relative contribution, female choice has contributed to the evolution of sex differences in the life history of bowerbirds.

Peacocks (*Pavo cristatus*) provide another example of a lekking species but one in which male--male competition is minimal and female choice largely determines which males reproduce and which do not (Höglund & Alatalo, 1995; Petrie, 1994; Petrie, Halliday, & Sanders, 1991). Unlike peahens, peacocks develop large tail trains with varying numbers of eyespots. Males display unfolded trains to females, and females choose mates on the basis of the length of the train and the number of eyespots (Petrie *et al.*, 1991). Train length and number of eyespots are reliable predictors of the growth and survival rate of the males' offspring and are thus honest (i.e., cannot be faked; Zahavi, 1975) indicators of the genetic quality of the male (Petrie, 1994). As with bowerbirds, sex differences in life history traits are found. Peahens begin to reproduce at 2 years of age, whereas males do not develop their full trains until 3 years of age and do not establish a lekking display site until 4 years

of age (Manning, 1989; Petrie, personal communication, August 28, 2001). Some males successfully mate at age 4, whereas other males do not mate until later years and some not at all. In this species, the development of the sexually selected traits that females use in mate choice decisions has resulted in accompanying changes in the life history of males, including a lengthening of the developmental period and an increase in size at maturity (for related discussion see Brooks & Kemp, 2001; Wiley, 1974).

### C. PHENOTYPIC PLASTICITY

Phenotypic plasticity is a common feature of life history traits. That is, the ontogenetic expression of life history traits is influenced by ecological conditions within the constraints of reaction norms (Stearns, 1992). Plasticity of life history traits is often conceived in terms of nonsocial factors, such as predation, food availability, or rainfall (e.g., Stearns & Koella, 1986; Sultan, 2000). Life history traits that have been shaped by sexual selection are also likely to show phenotypic plasticity, but the ontogenetic expression of these traits should be more strongly influenced by social competition and dynamics than by nonsocial conditions (Rohwer *et al.*, 1980; Selander, 1965). In fact, the relation between many ecological variables, such as food availability, and the plastic expression of life history traits may be moderated by social competition. The age of reproductive maturity in many species is influenced by access to high-quality foods (Stearns & Koella, 1986), which in turn is often influenced by social competition. In many species of primate, coalitions of related females compete for access to high-quality food sources, such as fruit trees (Wrangham, 1980). Socially dominant coalitions gain access to these foods, and the combination of dominance and better nutrition is related to a number of indices of reproductive maturity and success, including age at first conception and number of offspring surviving to maturity (Silk, 1993).

The dynamics of sexual selection also appear to influence the ontogenetic expression of many life history traits. As with bowerbirds, males are often physiologically able to reproduce many years before they actually reproduce (Wiley, 1974). The reproductive delay can be due to competition with older and more dominant males or a female preference for older males (Brooks & Kemp, 2001; Selander, 1965). In many lekking species, for instance, males must establish and defend a display territory, and older males typically have an advantage over younger males in competition for these sites (Wiley, 1974). In some species, the physiological stress associated with male-male competition and the behavioral subordination to more dominant males, as well as other forms of social competition, can delay physiological maturation or reduce reproductive potential (e.g., reduce size of testes) in adult males (Dixon, Bossi, & Wickings, 1993; Walter & Dittami, 1997; Walters & Seyfarth, 1987). As noted earlier, testicular maturation in male baboons is related to the social rank of their mother (Alberts & Altmann, 1995).

In short, the presence of dominant males often results in the inhibition of competitive behavior in younger males and can delay the onset of reproductive maturity and inhibit the expression of traits associated with female choice. Note also that nonsocial influences on the expression of life history traits, such as food availability in the absence of social competition, can strongly influence the later ability to compete for mates or attract mating partners (e.g., Nowicki, Peters, & Podos, 1998).

## V. Human Developmental Sex Differences

A comprehensive understanding of human developmental sex differences can only be achieved through consideration of the evolution and proximate functions of life history traits (Bjorklund & Pellegrini, 2002; Bogin, 1999; Geary & Bjorklund, 2000; Hill & Kaplan, 1999; Kaplan, Hill, Lancaster, & Hurtado, 2000; Kenrick & Luce, 2000; Lancaster & Lancaster, 1987). Current models of human life history focus on the complexity of the foraging demands in traditional societies (Kaplan *et al.*, 2000) or on social competition (Alexander, 1987, 1989; Geary & Flinn, 2001). In fact, both forms of selective pressure are likely to have been important. In many traditional societies, men provide---through hunting---the majority of calories and protein consumed by their social group (Ember, 1978; Kaplan *et al.*, 2000). The acquisition of hunting skills requires many years of practice and experience, which has been interpreted as a selective pressure for an increase in the length of the developmental period during which hunting (and foraging for females) skills are practiced (Kaplan *et al.*, 2000). The proceeds of hunts are also related to male--male competition (social status) and female choice of mating partners (Hill & Hurtado, 1996), components of sexual selection. Moreover, the extraordinary hunting and foraging skills of humans in traditional societies, and presumably during human evolution, contribute to the ecological dominance of most human groups, which in turn significantly alters the pattern of selective pressure, 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.

With the achievement of ecological dominance, natural selection becomes a struggle with other human beings for access to and control of the social (e.g., competition for mates), biological (e.g., food), and physical (e.g., territory) resources that covary with survival and reproductive outcomes (Geary, 1998). Elaborating on Alexander (1989), Geary and Flinn (2001) argued that the resulting social competition was the primary selective pressure driving the coevolution of a suite of

human characteristics, including several life history traits described in Table II. In this view, the hunting and foraging demands described by Kaplan *et al.*, (2000; Hill & Kaplan, 1999) are intertwined within a broader suite of social–competitive selection pressures, including intrasexual competition and intersexual choice.

My goal in the remainder of this chapter is to extend the social competition model to provide a theoretical frame for understanding sex differences in human life history and for organizing psychological research on sex differences in developmental activities, such as play patterns; implications for understanding sex differences in human cognition and cognitive development are described elsewhere (Geary, 1998, 2002). In the first two parts, I provide sketches of sexual selection in humans and sex differences in life history traits, respectively. In the third part, I describe the framework for and research on developmental activities. The behavioral and social activities described in all parts are more strongly influenced by inherent and implicit processes than by conscious choice. In other words, as with other species, children and adults are inherently biased to engage in activities that covaried with survival and reproductive outcomes during human evolution, whether or not they are consciously aware of the proximate function (e.g., to attract mates) of the activities (Geary, 1998).

TABLE II  
Unique and Unusual Traits Related to Social Competition and Human Life History

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*I. Large brain and complex social competencies*

1. The human neocortex is 35-60% larger than expected for a primate of the same overall body and brain size (Rilling & Insel, 1999).
2. The neocortex apparently 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).

*II. High levels of paternal investment*

1. Paternal investment is only evident in 3-5% of mammalian species (Clutton-Brock, 1989).
2. 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).

*III. Long developmental period and adult life span*

1. Relative to other mammals and primates, children have a very long developmental period characterized by slow development during middle childhood and high dependency on adult caregiving (Bogin, 1999).
2. Relative to other great apes, humans have a very long adult life span, and low juvenile and adult mortality rates (Allman *et al.*, 1993; Hill *et al.*, 2001).

*IV. Menopause*

1. Menopause may enable women to heavily invest in their later born children or in grandchildren (Hawkes *et al.*, 1998; Williams, 1957).
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## A. SEXUAL SELECTION DURING HUMAN EVOLUTION

Unlike most other mammals, both women and men invest in parenting, although men on average do not invest as much as women (Geary, 2000). In natural environments, paternal investment supports the intensive parenting and long developmental period that is characteristic of humans and appears to allow parents to successfully raise more children than would otherwise be the case (see Table II; Geary & Flinn, 2001; Lancaster & Lancaster, 1987; Kaplan *et al.*, 2000). In addition, paternal investment complicates the dynamics of sexual selection, resulting in male choice and female-female competition, on top of the standard components of male-male competition and female choice. Intensive parenting and the complexity of sexual selection create six interrelated classes of social relationship that involve conflict and competition, as described in Table III. These forms of social relationship capture the within-species competition noted by Alexander (1989) and are likely to have been (and continue to be) important forces in human cognitive, brain, and social evolution, as well as potent influences on evolutionary change in human life history and developmental activity. Extended spousal and parent-child relationships create conditions that favor the evolution of complex sociocognitive competencies, as both forms of relationship involve not only cooperation but also manipulation and deception as related to attempts to gain access to resources that covary with survival and reproductive outcomes (e.g., Geary, 2000; Trivers, 1974). Further discussion of these relationships is beyond the scope of this article, but here I summarize work on intrasexual competition and intersexual choice.

*1. Intrasexual Competition*

On the basis of the fossil record, males apparently were larger than females throughout hominid evolution, suggesting physical male-male competition and a sex difference in parental investment (e.g., McHenry, 1991). The fossil record does not provide insights into the intensity or form of this male-male competition (Plavcan & van Schaik, 1997b), but patterns throughout human history and in extant cultures suggest competition involving male coalitions and one-on-one competition for status and dominance within coalitions (Chagnon, 1988; Geary, 1998; Geary & Flinn, 2002; Horowitz, 2001; Wrangham, 1999). To illustrate, for forest dwelling Ache (hunter-gatherer society, Paraguay) coalitional warfare with non-Ache accounted for 36% of all adult male deaths, and an additional 8% of men died during status-oriented club fights with other Ache men (Hill & Hurtado, 1996). This pattern of coalitional and within-coalition male-male competition is common in traditional societies (Keeley, 1996) and has evolutionarily significant survival and reproductive consequences. Dominant men in dominant coalitions typically have more wives and more surviving children than do other men (e.g., Chagnon, 1988). In addition to facilitating male-male competition, men's coalitions also enable them to achieve ecological dominance, that is, to efficiently extract resources

TABLE III  
Forms of Social Conflict and Competition

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Intrasexual competition
<p><i>I. Male--male competition</i></p> <p>1. In traditional societies, men form coalitions that compete for control of mating dynamics (e.g., exchange of brides) and for control of the resources that covary with survival and reproductive outcomes in the local ecology (Chagnon, 1988; Geary, 1998). Men also form dominance hierarchies within the in-group coalitions and compete for position (and thus influence) in the hierarchy. Competition is often physical and deadly (Keeley, 1996).</p>
<p><i>II. Female--female competition</i></p> <p>1. Women compete for access to resources, including access to resource-holding or socially influential men. Relative to men, this competition is less physical (Campbell, 1999) and involves subtle manipulation of social relationships, with the goal of organizing these relationships to maximize the woman's access to resources that covary with survival and reproductive outcomes in the local ecology (Geary, 2002).</p>
Intersexual choice
<p><i>I. Male choice</i></p> <p>1. Paternal investment leads to the prediction that men will be selective in their mate choices (Trivers, 1972), and this is the case. Men's mate choices are influenced by fertility cues (e.g., age) as well as by indicators of women's social and maternal competence (Geary, 1998).</p>
<p><i>II. Female choice</i></p> <p>1. Women's mate choices are influenced by men's social and parental competence. More so than men, women also focus on men's social status, including material resources, social influence, and cues to their ability to acquire and maintain these resources (Buss, 1989, 1994). Women are also sensitive to their ability to influence potential mates and thus gain access to their resources.</p>
Family conflict
<p><i>I. Spousal</i></p> <p>1. Spouses, of course, cooperate in raising children, but extended maternal and paternal investment also results in strong potential for conflicts of interest (Kaplan <i>et al.</i>, 2000; Svensson &amp; Sheldon, 1998). Conflicts are predicted to center on (1) extent of maternal versus paternal investment, (2) resource control (e.g., spending on children or status-oriented objects), and (3) marital fidelity.</p>
<p><i>II. Parent--offspring and sibling</i></p> <p>1. Across species, conflicts of interest are endemic to parent--offspring relationships (Trivers, 1974). Parents, of course, invest time and resources to promote the well-being of offspring, but offspring often press for additional resources, sometimes with accompanying morbidity and mortality costs to parents (Westendorp &amp; Kirkwood, 1998). The long developmental period of humans results in an extended parent--child relationship and thus the potential for extended conflicts over parental allocation of resources. In the context of these relationships, children are predicted to attempt to secure from parents (and to a lesser degree kin) resources that facilitate (1) growth and maintenance and (2) reproductive potential.</p> <p>2. Siblings will also compete for parental resources.</p>
<p>from the environment through hunting and to maintain a comparatively risk-free (e.g., low predation risk) territory for their social group (Tiger, 1969).</p> <p>These male coalitions consist of related men and define the basic social structure of the group. Women tend to emigrate into the group of their husband, although in many societies they maintain ties to their kin (Pasternak <i>et al.</i>, 1997; Seielstad,</p>

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Minch, & Cavalli-Sforza, 1998). In any case, male coalitions provide protection from other coalitions, and provision their wives and children, although women also provide food through gathering (Ember, 1978; Geary & Flinn, 2001; Kaplan *et al.*, 2000). Within these groups, women form a small network of relationships with other women and provide social and emotional support to one another (Taylor *et al.*, 2000). Women also work to organize social relationships within the wider group to divert additional resources to themselves and to their children (Geary, 2002; Geary & Flinn, 2002). One result is conflicts of interest with other women. The resulting female-female competition focuses on disrupting the social network of their female competitors (often co-wives), as well as competing for the attention and resources of men within the group. This form of interpersonal competition has been termed relational aggression by Crick and her colleagues (Crick, Casas, & Mosher, 1997).

The function of male-male (achieving status and cultural success; Irons, 1979) and female-female (control of interpersonal relationships; Geary, 2002) competition is the same from one society or historical period to the next: to gain access to and control of the resources that covary with survival and reproductive outcomes in the local group and ecology. However, the form of intrasexual competition shows considerable phenotypic plasticity, varying with cultural mores (e.g., prohibitions against polygyny) and social conditions, such as the operational sex ratio (Flinn & Low, 1986; Geary, 1998, 1999; Low, 1989). In some societies, men achieve cultural success by killing other men, whereas in other societies they achieve cultural success by obtaining an education and securing a high-income job. The underlying motive is always the same, however: to achieve dominance over other men and thus increase access to culturally important resources and, through this, reproductive opportunity (Perusse, 1993). Patterns of intrasexual choice also show phenotypic plasticity, as illustrated by cross-cultural variability in women's preference for husbands who have or have not killed other men (preference varies with whether or not killing confers social status; Geary, 1998).

## 2. *Intersexual Choice*

Patterns of intersexual choice can influence the form and intensity of intrasexual competition. As an example, men's focus on physical attractiveness (e.g., fertility cues) in choosing a spouse intensifies female-female competition in this area, with women competing by highlighting or manipulating (e.g., through makeup or padded bras) these cues (Buss & Shackelford, 1997). Similarly, women's preference for culturally successful and resource-holding men intensifies male-male competition for control of culturally important resources, especially in cultures where female choice is not suppressed (Geary, 1998). The reproductive preferences of men and women conflict directly in other ways (Buss & Schmitt, 1993). As with other mammalian males, men can reproduce without paying the cost of parental investment, but women do not have this option. The result is men, on average, are more interested in casual sexual relationships than are women and

will sometimes manipulate women into sexual relationships and then abandon them if a pregnancy occurs (Oliver & Hyde, 1993; Symons, 1979). Men face a different issue. When they invest in children, the paternity of these children is never certain. Although firm estimates are not yet available, perhaps 10-15% of children are sired by a man who is not the women's husband and putative father (Geary, 2000). In these situations, the man is being manipulated by his spouse into raising the children of another man.

#### B. SEX DIFFERENCES IN LIFE HISTORY

A relation between heritable variability in life history traits (e.g., parenting) and survival and reproductive outcomes in human populations has been inferred in many analyses (Geary, 2000; Kaplan *et al.*, 2000), but, unfortunately, rarely evaluated in genetic studies of reproductive fitness. In one such twin study, the relation between lifetime reproductive fitness (number of surviving children) and three life history traits—age at menarche, at first reproduction, and at menopause—was assessed for Australian women over the age of 45 (Kirk *et al.*, 2001). Age at first reproduction (early 20s vs late 20s) was significantly related to reproductive fitness (controlling for educational level and religious affiliation), with earlier reproduction resulting in more children during the reproductive life span. The covariation between age of first reproduction and reproductive fitness was due, in part, to shared genetic influences, indicating that a subset of genes influences both age of first reproduction and lifetime reproductive fitness in the Western women assessed in this study.

Similar studies have not yet been conducted for all of the life history traits described in Table II, although individual differences in many of these traits (e.g., life span) have been shown to be related to both heritable and environmental factors (e.g., Herskind *et al.*, 1996). In any event, these traits suggest that selection favored a life history pattern whereby humans invested heavily in a small number of offspring, presumably so that these offspring acquire sophisticated social, behavioral, and cognitive skills, that is, acquired reproductive potential. An unresolved issue is the selection pressures that contributed to the evolution of this suite of life history traits. As stated, theoretical models tend to focus on ecological (e.g., food acquisition, predation) pressures, social pressures (e.g., between group competition), or some combination. To the extent that social competition contributed to the evolution of human life history, sex differences in the associated traits should vary in ways consistent with sexual selection and other forms of social competition. In Table IV, I present a series of predictions regarding how sexual selection might have influenced the evolution of sex differences in human life history. Many of the empirical studies cited therein and described in the following sections are consistent with the predictions, but definitive tests will require the type of analysis conducted by Kirk *et al.*, (2001). Before proceeding to the discussion of sex differences, I provide a general outline of human life history in the first part.

TABLE IV

## Predicted Influence of Sexual Selection on Human Life History

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Women's life history
<p><i>I. Female--female competition</i></p> <p>1. Female-female competition is highly social, involving the manipulation and disruption of the relationships of other girls and women as related to mating dynamics and resource control (Crick <i>et al.</i>, 1997). Based on the relations among social competition, length of the developmental period, and brain size in primates (Joffe, 1997), human female--female competition is predicted to favor delayed maturation and developmental activities that involve the practice and refinement of competition-related social competencies.</p>
<p><i>II. Male choice</i></p> <p>1. Due to menopause and women's declining fertility beginning in the late 20s (Menken <i>et al.</i>, 1986), men base mate choice decisions, in part, on physical indicators of fertility. These indicators, such as large eyes, are correlated (across species) with youth. Male choice is thus predicted to favor earlier maturation in women and thus retainment of these cues, although selection for earlier maturation is balanced by the conflicting benefits of larger size and thus delayed maturation (Kirk <i>et al.</i>, 2001; Stearns &amp; Koella, 1986).</p>
Men's life history
<p><i>I. Male--male competition</i></p> <p>1. Men are predicted to have and evidence the same life history pattern found in other mammalian species with physical male--male competition. Included among these traits are, in comparison to women, a shorter life span, slower growth and longer developmental period, larger adult size, higher mortality rate at all ages, and higher levels of risk taking and intrasexual violence (e.g., Allman <i>et al.</i>, 1998; Wilkins, 1996; Wilson &amp; Daly, 1985).</p> <p>2. In relation to other mammals, the previously noted pattern has likely been mitigated by paternal investment, resulting in an evolutionary reduction in the magnitude of the sex differences in many life history traits (e.g., maximum life span).</p> <p>3. Coalitional male-male competition is necessarily a complex and highly social activity (Geary &amp; Flinn, 2002). As with women, social competition should favor delayed maturation and developmental activities that involve the practice and refinement of associated competencies.</p>
<p><i>II. Female choice</i></p> <p>1. Female choice is related, in part, to the physical and social cues associated with male--male competition and should thus intensify these aspects of male--male competition, such as the tendency toward behavioral risk taking (Buss, 1989; Kelly &amp; Dunbar, 2001).</p> <p>2. Female choice is also related to physical indicators of health (e.g., Gangestad, Bennett, &amp; Thornhill, 2001), and the expression of these indicators may be costly for many men (Shackelford &amp; Larsen, 1997). For instance, the androgens that result in the development of physical traits (e.g., masculine jaw) associated with female choice are predicted to compromise the immune system (Folstad &amp; Karter, 1992) and thus the physical health and development of some males (Geary, 1998).</p>

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*1. Pattern of Human Life History*

The focus of human life history research conducted by biologists and anthropologists is largely on the growth component of somatic effort shown in Figure 1 as well as reproductive correlates. These studies reveal that in traditional societies and in preindustrial Europe, a typical life history pattern involves women achieving menarche at about 15-16 years of age, marrying soon thereafter, and having their first child between 18 and 22 years of age (Kaplan *et al.*, 2000; Korpelainen, 2000;

Stearns & Koella, 1986). For women, peak fertility is achieved in the mid- to late 20s and gradually declines to near zero by age 45 (Menken, Trussell, & Larsen, 1986; Wood, 1994), resulting in a 25-year reproductive span. During this span, a common interbirth interval is 2-4 years and a common pattern is for women to have four to six children before the onset of menopause, although one to three of these children do not survive to adulthood (Blurton Jones, 1986; Hill & Kaplan, 1999; Lummaa, 2001). Women and men who survive to age 15 years will, on average, live to their mid-50s (e.g., Hill & Hurtado, 1996). In many traditional societies, socially dominant men will have several wives, but often do not marry their first wife until their 20s or later; many other men will never marry (e.g., Borgerhoff Mulder, 1990; Chagnon, 1988; Murdock, 1949).

Relative to current industrial society, a 30-40% mortality rate before the age of 15 and an average life span of 55 for those who survive to adulthood seems rather dismal. However, in comparison to other apes and mammals, the human pattern represents comparatively low infant and child mortality risks (Lancaster & Lancaster, 1987) and a comparatively large number of children surviving to adulthood relative to other apes (Hill *et al.*, 2001). The achievement of comparatively low infant and child mortality risks and a comparatively large number of surviving children is not likely to be achievable without men's parental investment, at least in traditional societies, whether the tendency to provide this investment evolved primarily for the provisioning of women and dependent children (Kaplan *et al.*, 2000) or to facilitate a broader suite of sociocompetitive competencies (Alexander, 1989; Geary, 2000; Geary & Flinn, 2001; but see Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998).

As with other species, both heritable and environmental factors appear to contribute to individual differences in human life history traits (de Bruin *et al.*, 2001; Kirk *et al.*, 2001), and apparently within the constraints of norms of reaction (Stearns & Koella, 1986). As an example, Kirk *et al.* found that individual differences in women's life history traits were influenced, in part, by genetics, with heritability estimates ranging from .51 for age of menarche to .21 for age at first reproduction. Stearns and Koella demonstrated that well nourished and healthy girls achieve menarche earlier than other girls, indicating an important environmental component to the expression of this life history trait. At the same time, there are genetic constraints such that age of menarche is not typically achieved earlier than age 11 years, with a mean of 13 years, even in well-nourished and healthy populations (Kirk *et al.*, 2001).

## 2. *Sexual Selection and Women's Life History*

Whatever the primary selective advantage, paternal investment necessarily coevolved with women's life history traits. The trade-offs associated with paternal investment are female--female competition over this investment and male choice (Trivers, 1972), along with the compromises needed to maintain a long-term

spousal relationship. As noted earlier and in Table IV, social competition covaries with a longer developmental period and a larger brain, at least in primates (e.g., Joffe, 1997). The longer developmental period presumably allows juveniles to practice and refine sociocompetitive competencies, that is, to improve their reproductive potential. If so, then female-female competition would have contributed to the long juvenile period found in humans and girls' developmental activities should involve, in part, a preparation for this competition in adulthood as well as preparation for family life as a parent and spouse, as described later.

Across societies, male choice is related to physical indicators of female fertility as well as to personal and social indicators of fidelity and thus certainty of paternity (Buss, 1994; Buss, Larsen, Westen, 1996; Geary, 1998). Physical indicators of fertility include age, the hip-to-waist ratio, breast symmetry, and a youthful appearance (Cunningham, 1986; Kenrick & Keefe, 1992; Møller, Soler, & Thornhill, 1995; Singh, 1993). The hip-to-waist ratio is a natural consequence of birthing children with large brains, but also influences male choice and may have been exaggerated as a result (Singh, 1993). Enlarged breasts in the absence of lactation is unusual in mammals and may have been shaped by male choice. Moreover, men's rating of women's physical attractiveness is related to breast symmetry, that is, similarity in the size of the two breasts. Breast symmetry, in turn, is a reliable indicator of women's fertility (Møller et al., 1995). A focus on youthful appearance follows from the age-related decline in women's fertility and appears to have influenced the evolution of certain facial characteristics in women. These characteristics are cross-species indicators of youth, including relatively large eyes and a small chin (Cunningham, 1986). In short, male choice may have been influenced by the life history pattern of women (e.g., menopause) and may have influenced the evolution of certain aspects of women's physical development.

As noted in Table V, phenotypic plasticity in some aspects of women's life history is related to social conditions and to female hormones (Ellis, McFadyen-Ketchum, Dodge, Pettit, & Bates, 1999; Flinn & Low, 1986; Wilson & Daly, 1997). For example, girls with a warm relationship with their father and a father who is highly invested in the family experience menarche later than do girls living in father-absent homes or with an emotionally distant father (Ellis *et al.*, 1999). Relationship with father may be a proximate indicator of the stability and warmth of the girls' later spousal relationships as well as an indicator of mortality risks in adulthood (a deceased father cannot be invested or warm; Belsky, Steinberg, & Draper, 1991; Chisholm, 1993; Draper & Harpending, 1988). These cues in turn are presumed to influence women's reproductive pattern in adulthood, such that paternal warmth is associated with delayed maturation. Delayed maturation, in turn, should enable the acquisition of additional sociocompetitive competencies and greater reproductive potential. The reproductive potential may involve the acquisition of social and emotional traits that support high cooperation with a spouse and high investment in a small number of children (MacDonald, 1992).

TABLE V

## Phenotypic Plasticity in Human Life History

*I. Family functioning and wealth*

1. Family functioning can influence the phenotypic expression of some life history traits in both men and women. As examples, psychosocial stressors during childhood are associated with smaller adult size and lower testosterone levels in adulthood for men (e.g., Flinn *et al.*, 1996) and a warm relationship with father is associated with later maturation for women (Ellis *et al.*, 1999).
2. Wealth of the family and kin group can influence nutritional and physical health during development and result in an earlier age of maturation, larger adult size in women and men, and lower infant and child mortality risks (Herman-Giddens, Wang, & Koch, 2001; Korpelainen, 2000; Stearns & Koella, 1986).

*II. Culture and the operational sex ratio*

1. In ecologies with high adult mortality (often due to male-on-male violence) women and men have an earlier age of reproduction and have more children during the reproductive life span (Chisholm, 1993; Wilson & Daly, 1997). In ecologies with high infant and child mortality risks, women and men have more children during their reproductive life span (Korpelainen, 2000).
2. Socially imposed monogamy, as in Western culture, moderates the dynamics of intersexual choice and intrasexual competition. The intensity of male-male competition decreases and the standards of male choice increase, whereas the intensity of female-female competition increases but female choice does not appear to be as strongly affected (Geary, 1998). As an example, in these societies men's mate choices are influenced by women's material resources (e.g., dowry, income; Gaulin & Boster, 1990). As a result, the marriage and reproduction of women may be delayed while these resources are accrued by women and/or their families.
3. The intensity of competition for cultural resources and social status is predicted to result in corresponding delays in men's reproductive opportunities beyond the age of physical maturation, as younger men will typically be disadvantaged in comparison to older men, both in terms of female choice and male-male competition (e.g., Borgerhoff Mulder, 1988). One possible result is age-related difference in men's reproductive strategies, with younger men engaging in more opportunistic mating and older men investing in children (Draper & Harpending, 1988).
4. The operational sex ratio moderates the dynamics of intersexual choice and intrasexual competition. When the number of marriage-age men is lower than marriage-age women, men have more influence (male choice) over mating dynamics and the intensity of female-female competition increases. One result is that men invest more in mating effort and less in parenting (Geary, 2000; Guttentag & Secord, 1983).

*III. Sex hormones and endocrine functions*

1. As with other species, hormonal and endocrine mechanisms (e.g., testosterone) are predicted to moderate and perhaps mediate many sex differences in life history traits and aspects of phenotypic plasticity (Sinervo & Svensson, 1998). Hormones associated with developing the physical and social competencies associated with male-male competition likely result in the trade-offs of higher mortality rates and a shorter maximum life span. Female hormones may facilitate immune responses in women, but with the trade-off of higher risk of autoimmune disorders (Wizemann & Pardue, 2001).
2. Hormonal fluctuations across the menstrual cycle appear to influence women's mate choice preferences, the likelihood of cuckolding her mate, and patterns of relationship jealousy; they may also influence indicators of fertility associated with male choice (Bellis & Baker, 1990; Gangestad & Thornhill, 1998; Geary, DeSoto, Hoard, Sheldon, & Cooper, 2001; Scutt & Manning, 1996).

Other evidence of phenotypic plasticity in women's life history comes from the work of Wilson and Daly (1997), who found that age of first reproduction, number of children borne per woman, mortality risks, and local resource availability are all interrelated in modern-day Chicago. Women who grow up in contexts with high risk of violent death (related to male-male competition over limited resources) begin reproducing at an earlier age and have more children during their reproductive life span than do women who grow up in low-risk, high-resource ecologies (see also Chisholm, 1993). Similarly, in preindustrial Europe, women living in contexts with high infant and child mortality risks had more children during their reproductive life span than did women living in contexts with lower mortality risks (Korpelainen, 2000).

Wider social conditions also appear to influence women's reproductive pattern. In societies in which men's reproductive options are restricted by socially imposed monogamy, women's financial contributions to the family (e.g., a dowry) become a more prominent feature of male choice than in other societies (Flinn & Low, 1986; Geary, 1998). In these contexts, age of first marriage and reproduction may be delayed while women or her kin accrue the resources needed (e.g., for the dowry) to attract a high-status spouse (Gaulin & Boster, 1990). Hormones also influence women's reproductive and life history traits. For instance, hormonal fluctuations across the menstrual cycle are correlated with women's mate choice preferences, such that women may be more likely to cuckold their partner during the time of rising fertility risk, that is, around the time of ovulation (e.g., Bellis & Baker, 1990; Gangestad & Thornhill, 1998). Hormones may also contribute to the longer life span of women relative to men. Female hormones may contribute to enhanced immune responses and reduced risks for certain forms of premature death (e.g., heart disease; Witzmann & Pardue, 2001).

All these findings are in keeping with the earlier described patterns of phenotypic plasticity in other species. For instance, Daly and Wilson's (1997) intriguing findings are consistent with the cross-species pattern of earlier maturation being related to high adult mortality risks and phenotypic plasticity in age of first reproduction (e.g. Roff, 1992; Reznick & Endler, 1982). However, all of the human studies are based on phenotypic correlations and thus the patterns might reflect phenotypic plasticity, genetic correlations (e.g., between age of menarche and paternal investment), or, most likely, some combination.

### 3. *Sexual Selection and Men's Life History*

With the exception of paternal investment, the pattern of men's life history is the same as that found for other mammalian species in which males compete physically for access to females or for control of the resources females need to reproduce (see Table V; Allman *et al.*, 1998; Leigh, 1996; Wilson & Daly, 1985). Even paternal investment does not alter the general pattern, because men invest

less in parenting and more in mating than do women. Relative to females, the life history traits that men share with other mammalian males include an average and maximum life span that is shorter than females' (Allman *et al.*, 1998), a slower growth rate and longer growth spurt (Leigh, 1996; Tanner, 1990), higher mortality rates at all ages (Wizemann & Pardue, 2001), and greater behavioral risk taking and higher rates of competition-related violent death in adolescence and young adulthood (Daly & Wilson, 1988; Wilson & Daly, 1985). As with other species, all these life history traits are influenced by testosterone and other hormones and appear to involve a preparation for or engagement in male-male competition (e.g., Folstad & Karter, 1992; Dabbs & Dabbs, 2000; Wizemann & Pardue, 2001). Many of these same physical (e.g., height) and behavioral traits (e.g., risk taking) also influence female choice (Beck, Ward-Hull, & McClear, 1976; Kelly & Dunbar, 2001).

The slow growth and extended developmental period result in larger men than women (Tanner, 1990, 1992). Among other physical and physiological sex differences that become exaggerated during this time are running speed, physical strength, and physical activity level, as well as throwing distance, velocity, and accuracy (Eaton & Enns, 1986; Kolakowski & Malina, 1974; Thomas & French, 1985). These and related sex differences are often attributed to the division of labor in general and men's hunting in particular (Kolakowski & Malina, 1974; Tiger, 1969). However, the finding that men are consistently better on tasks that involve the ability to track thrown objects and to evade or block these objects (Watson & Kimura, 1991) may be the evolutionary result of male-male competition that involved the use of projectile (e.g., rocks) and blunt force weapons (see Keeley, 1996, for examples), with tracking and blocking being evolved defensive competencies needed to avoid projectiles (Geary, 1998).

As with women, individual differences in these physical and life history traits appear to be influenced by genetic and environmental factors (Gilger, Geary, & Eisele, 1991; Martorell, Rivera, Kaplowitz, & Pollitt, 1992). Due to slower growth, greater physical activity levels, and perhaps the immunosuppressive effects of testosterone, boys are more severely affected--physically and cognitively--by poor early conditions than are girls (Flinn, Quinlan, Decker, Turner, & England, 1996; Martorell *et al.*, 1992). One result is that the sex difference in physical size is smaller in poorly nourished populations (Gaulin & Boster, 1992). The form of male-male competition clearly shows phenotypic plasticity, as noted in Table V. In contexts with high mortality risks, often due to male-on-male violence, men reproduce sooner and often show lower levels of parental investment than do men in other contexts (Geary, 2000; Wilson & Daly, 1997). When physical male-on-male violence is suppressed and the attainment of culturally important resources (e.g., money) requires prolonged education and training, men have lower mortality risks and a longer life span, but they reproduce later and often have fewer children (Geary, 1998; Pérusse, 1993). To varying degrees, female choice is important in

all these contexts. In the latter contexts, for instance, women's preference for culturally successful men results in delayed marriage and reproduction for many men (Buss, 1996).

As with other species, the proximate influences on men's (and women's) life history traits almost certainly include sex hormones and other endocrine functions as well as social context. The hormonal correlates of male-male competition are highly sensitive to social and contextual cues (Geary & Flinn, 2002). Loss in male-male competition often results in heightened elevation of stress hormones, reduced testosterone levels, and perhaps compromised health (Dabbs & Dabbs, 2000). For men, early childhood stressors, such as extended family conflict or lower levels of paternal investment, are associated with atypical stress responses later in life and smaller adult size (Flinn *et al.*, 1996). These, in turn, can result in disadvantages with respect to both male-male competition and female choice. Still, many questions regarding men's life history and phenotypic plasticity in the expression of these traits remain unanswered. For instance, is the relation between adult mortality risks and early reproduction an expression of phenotypic plasticity, of genes that influence both early reproduction and tendency toward male-on-male violence, or of some combination? Do the immunosuppressive effects of stress hormones affect some men more than others, as appears to be the case with other species (Folstad & Karter, 1992)? Do these effects vary at different points in the life span?

### C. SEX DIFFERENCES IN DEVELOPMENTAL ACTIVITY

Unlike biologists and anthropologists, the research focus of developmental psychologists is largely on the developmental activity component of somatic effort shown in Figure 1. The details of developmental activity as related to somatic effort and the accumulation of reproductive potential are shown in Figure 6. In this view, parent-child relationships, the wider kin network in traditional societies, and

<b>Developmental Activity</b>					
<b>Growth and Maintenance</b>			<b>Reproductive Potential</b>		
Parent-Offspring Relationship	Kin Relationships	Self-Initiated Activities	Parent-Offspring Relationship	Peer Relations and Social Play	Solitary Play

Fig. 6. Components of developmental activity. Parent-offspring relations emerge from parents' reproductive efforts and the efforts of offspring to obtain additional parental resources, as related to the offspring's somatic effort and the accumulation of reproductive potential.

some self-initiated activities during childhood and adolescence, such as foraging in traditional societies, function to promote growth and maintenance during specific developmental periods (Bjorklund, 1997; Bjorklund & Pellegrini, 2002; Geary & Bjorklund, 2000). The function of other activities is, in theory, to accumulate reproductive potential, that is, to acquire the physical, social, behavioral, and cognitive competencies that enable successful reproduction in adulthood, whether the reproductive effort involves mating, parenting, or some combination. The function of parent-offspring relationships as related to social competition and reproductive effort (e.g., acquiring resources that facilitate competition with peers) in adulthood is described elsewhere (Geary & Flinn, 2001).

The focus here is on the developmental activity component of peer relationships and various forms of play. As stated previously, from a life history perspective one function of these activities is to refine the social, behavioral, and cognitive competencies that covaried with survival and especially--given comparatively low adult mortality rates--reproductive outcomes during the species' evolutionary history (Geary, 1998; Käär & Jokela, 1998; Kaplan *et al.*, 2000; Mayr, 1974). The basic skeletal structure of these competencies appears to be inherent, but fleshed out and adapted to local conditions as the juvenile engages in the associated activities, such as play hunting (Gelman, 1990; Gelman & Williams, 1998). The most fundamental of these competencies coalesce around the domains of folk psychology, folk biology, and folk physics (e.g., Atran, 1998; Leslie, 1987; Mandler, 1992), in keeping with the position that humans are fundamentally motivated to gain access to and control of the social (e.g., mates), biological (food), and physical (e.g., territory) resources that covary with survival and reproductive outcomes in the local social group and ecology (Geary, 1998; Geary & Huffman, 2002).

The general prediction is that children will evince a pattern of self-initiated activities that results in the practice and refinement of social, behavioral, and cognitive competencies that covaried with survival and reproductive outcomes during human evolution. The specific predictions relating to the current discussion are: (1) sex differences will emerge in the form of intrasexual relationships and these will be related to patterns of male-male and female-female competition; (2) girls will engage in more play parenting and family-oriented play, on the basis of the sex difference in parental investment; and (3) boys will engage in more activities associated with ecological dominance, specifically activities involved in hunting and territory maintenance. Full review and discussion of research related to these predictions is beyond the scope of this chapter (see Geary, 1998, 2002), but overviews are provided in the following sections.

### *1. Peer Relationships and Social Play*

Basic patterns of children's peer relationships and social play are considered in the following subsections, including social segregation and separate looks at prominent features of the social activities of boys and girls.

*a. Social Segregation.* If males and females differed in the competencies that covaried with survival and reproductive outcomes during human evolution, then children are predicted to segregate by sex and engage in activities that mirror this evolutionary history (Geary, 1998). In keeping with the first prediction, one of the most consistently found features of children's social behavior is the formation of same-sex play and social groups (Maccoby, 1998). Such groups are evident by the time children are 3-years-old and become increasingly frequent throughout childhood. For example, in a longitudinal study of children in the United States, 4- to 5-year-olds spent 3 h playing with same-sex peers for every 1 h they spent playing in mixed-sex groups; as 6-to 7-years-olds, the ratio of time spent in same-sex versus mixed-sex groups was 11:1 (Maccoby & Jacklin, 1987). The same pattern has been found for children in Canada, England, Hungary, Kenya, and Mexico (Strayer & Santos, 1996; Turner & Gervai, 1995; Whiting & Edwards, 1988). The degree of segregation varies across contexts and is most common in situations in which children are free to form their own social groups (Maccoby, 1988; Strayer & Santos, 1996).

The proximate mechanisms driving child-initiated segregation include the different play styles of girls and boys (described later) and differences in the strategies used to attempt to gain control of desired resources (e.g., toys) or to influence group activities. In situations where access to a desired object is limited, boys and girls use different social strategies (Charlesworth & Dzur, 1987). More often than not, boys gain access by playfully shoving and pushing other boys out of the way, whereas girls gain access by means of verbal persuasion (e.g., polite suggestions to share) and sometimes verbal command (e.g., "It's my turn now!"). Based on findings such as these, Maccoby (1988) argued that segregated social groups emerge primarily because children are generally unresponsive to the play and social-influence styles of the opposite sex. Boys, for instance, sometimes try to initiate rough-and-tumble play with girls but most (not all) girls withdraw from these initiations, whereas most other boys readily join the fray (Pellegrini & Smith, 1998). Similarly, girls often attempt to influence the behavior of boys through verbal requests and suggestions but boys, unlike other girls, are generally unresponsive to these requests (Charlesworth & LaFrenier, 1983). Segregation may also be related to the formation of the social categories of "boy" and "girl" and a tendency to prefer individuals in the same category. However, same-sex segregation occurs before many children consistently label themselves and other children as a boy or a girl, indicating that social categorization is not likely to be a sufficient explanation for this phenomenon (Maccoby, 1988).

The net result of segregation by sex is that boys and girls spend much of their childhood in distinct peer cultures (Harris, 1995; Maccoby, 1988), and differences in the social styles of boys and girls congeal in the context of these cultures.

*b. Boys' Peer Relationships.* Many features of boys' play, social relationships, and social motives support the position that one-on-one and coalitional male-male

competition were (and still are) prominent social dynamics during human evolution (Geary, 1998; Geary & Flinn, 2002). As with other species exhibiting male--male competition, boys' activities are more consistently directed toward the achievement of hierarchical dominance than are girls' activities, a sex difference found across culture, age, and social context (e.g., Feingold, 1994; Maccoby, 1988; Whiting & Edwards, 1988). Rough-and-tumble play is one of the earliest social manifestations of physical one-on-one dominance, or at least the practice of this. In situations where activities are not monitored by adults and not otherwise restricted (e.g., a play area that is too small), groups of boys engage in various forms of rough-and-tumble play---including playful physical assaults and wrestling---three to six times more frequently than do groups of same-age girls (DiPietro, 1981; Maccoby, 1988). In the United States the sex difference in playful physical assaults and other forms of rough-and-tumble play begin to emerge by about 3 years of age (Maccoby, 1988). The same general pattern is found in other industrial societies and in traditional societies in which it has been studied, although the magnitude of the sex difference varies from one culture to the next (Eibl-Eibesfeldt, 1989; Whiting & Edwards, 1973, 1988).

Frequency of boys' rough-and-tumble play peaks between the ages of 8-10 years (Pellegrini & Smith, 1998). At this time, boys spend about 10% of their free time engaged in this form of play. As boys move from childhood to adolescence, the line between play and actual physical aggression begins to blur, and a relation between these activities (e.g., bullying) and social dominance emerges. In one study of 10- to 12-year-old boys, physical aggression and bullying first increased during the early part of the school year, but then decreased as the year progressed--presumably as boys developed stable dominance hierarchies (Pellegrini & Bartini, 2001; see also Savin-Williams, 1987). As physical aggression decreased, affiliative behaviors increased. Unlike younger boys where physical aggression is often associated with unpopularity and social rejection (Newcomb, Bukowski, & Pattee, 1993), these activities in adolescent boys are associated with social dominance, as defined by peers and teachers, and with a higher frequency of dating and higher rated attractiveness by girls (Pellegrini & Bartini, 2001).

Affiliative behaviors following aggressive within-group dominance encounters are common in primate species and function to maintain group cohesion (de Waal, 2000). For humans, the pattern is consistent with the prediction that, for boys, play functions, in part, to practice the formation of competition-related coalitions, that is, to maintain a large enough social group to effectively compete against other groups of boys (Geary, 1998; Geary & Flinn, 2002). The most common venue for the practice of these competencies, such as coordinating group activities, is competitive group-level games. As an example, Lever (1978) found that 10- and 11-year-old boys participated in group-level competitive activities, such as football, three times as frequently as did girls. In addition, boys' spontaneous social play involved larger groups, on average, than did girls' social play and involved greater

role differentiation within these groups. Similar differences have been reported by others (Sandberg & Meyer-Bahlburg, 1994; Sutton-Smith, Rosenberg, & Morgan, 1963). By late adolescence boys' competencies regarding the cooperation and social support needed to function effectively as a competitive coalition, as in the context of team sports, is very sophisticated (Savin-Williams, 1987).

The sex difference in one-on-one and group-level competitive play is related, at least in part, to prenatal exposure to androgens (Collaer & Hines, 1995). For example, Berenbaum and Snyder (1995) reported that girls who were prenatally exposed to excess levels of androgens (i.e., congenital adrenal hyperplasia, CAH) engaged in more athletic competition than did their unaffected peers--about three out of four girls affected by CAH engaged in athletic competition more frequently than did the average unaffected girl. This difference, however, was not as large as the difference between unaffected boys and unaffected girls--more than nine out of ten unaffected boys reported engaging in athletic competition more frequently than the average unaffected girl. Hines and Kaufman (1994) found that girls affected by CAH engaged in more playful physical assaults, physical assaults on objects, wrestling, and rough-and-tumble play in general than did unaffected girls, but none of these differences were statistically significant. The lack of significance was possibly due to the testing arrangements used in this study. Here, most of the girls affected by CAH were observed as they played with one unaffected girl, a situation (two girls) that does not typically facilitate rough-and-tumble play.

*c. Girls' Peer Relationships.* In comparison to boys, the social relationships that develop among dyads of girls are more consistently communal, manifesting greater empathy, more concern for the well-being of the other girl, and a greater emphasis on intimacy and social/emotional support (e.g., Maccoby, 1988; Whiting & Edwards, 1988). In addition, girls' social groups tend to be smaller, often including dyads or triads, and are characterized by a motivational disposition centered on cooperation and equality among group members, as contrasted with boys' focus on social dominance (Ahlgren & Johnson, 1979; Knight & Chao, 1989; Rose & Asher, 1999). During the preschool years, the focus of girls' social activities is often sociodramatic play with a family-oriented theme (Pitcher & Schultz, 1983). As they grow older, the focus is more explicitly on the development and maintenance of a small network of friends, with these relationships focusing on interpersonal dynamics (e.g., relationships with other girls or boyfriends) and providing social and emotional support, typically as related to interpersonal conflict (Belle, 1987; Savin-Williams, 1987; Taylor *et al.*, 2000).

As described earlier, girls are also competitive, but unlike male--male competition, female-female competition is less physical and functions largely to manipulate and disrupt social relationships through shunning, gossiping, spreading lies, and so on (Crick *et al.*, 1997). As with rough-and-tumble play, relational

aggression and the associated sex difference emerge by age 3 and continue through childhood, adolescence, and adulthood (Crick *et al.*, 1999). Developmentally, relational aggression becomes increasingly sophisticated. A 3-year-old might try to control the behavior of another child by stating "If you don't play with me, I won't be your friend," whereas an older child will manipulate the social network, for example by spreading rumors (e.g., "She said that you...") of the girl she is attempting to control. The social sophistication of this form of aggression increases into adolescence and becomes increasingly focused on the disruption of the romantic relationships of other girls (Crick & Rose, 2000). Studies conducted outside of the United States typically find the same developmental pattern and sex difference, although the relevant cross-cultural research is meager in comparison to research on rough-and-tumble play (Crick *et al.*, 1999).

The costs associated with being relationally aggressive include higher rates of social rejection and depression (although some relationally aggressive girls are well liked by some other girls; Crick *et al.*, 1999). Relational aggression has benefits in disrupting the social networks of and creating distress in other girls and women---the presumed evolutionary function of this form of aggression. Geary (1998, 2002) argued that the function of women's social networks is to provide social support and stability as well as increased access to important resources, including men. These in turn are associated with better health for these women and, in some contexts, lower mortality and morbidity risks for their children (Flinn, 1999; Geary, 2000; Taylor *et al.*, 2000). In this view, girls and women should highly value the reciprocal and intimate relationships that define and maintain their social networks and should react more strongly than boys and men to the disruption of these relationships; competition for dominance within boys' and men's in-groups result in males being more tolerant of conflicted relationships (de Waal, 1993; Geary & Flinn, 2002).

Several analyses of the life events that trigger depressive symptoms in adolescent boys and girls support this position (Bond, Carlin, Thomas, Rubin, & Patton, 2001; Leadbeater, Blatt, & Quinlan, 1995). Both boys and girls experience symptoms of depression following personal failure, such as poor grades. However, a sex difference is found in reactivity to negative interpersonal events: Adolescent girls and women are much more likely to experience symptoms of depression following interpersonal conflict or loss of a significant relationship than are same-age boys and men. In addition, adolescent girls and women often experience symptoms of depression when negative life events affect individuals in their social networks, whereas boys and men typically do not. In fact, adolescent girls apparently are up to four times more likely than same-age boys to experience anxiety and depression as a result of disrupted interpersonal relationships, disruptions that are often the result of relational aggression (Bond *et al.*, 2001).

In sum, relational aggression is an effective method for disrupting the romantic and same-sex relationships of other girls and women and can result in significant

levels of distress, anxiety, and depression for the victims. The costs of relational aggression included the potential for social rejection, but the presumed benefits are increased control of and access to desired social relationships, including romantic relationships.

## 2. *Play Parenting and Family-Oriented Play*

For most species of primate, play parenting (e.g., caring for siblings) is frequently observed in young females that have not yet had their first offspring, and it is often associated with higher survival rates of the firstborn, and sometimes later born, offspring (Nicolson, 1987). Across five primate species, firstborn survival rates were from two to more than four times higher for mothers with early experience with infant care---obtained through play parenting---than for mothers with no such experience (Pryce, 1993), suggesting that play parenting is indeed a form of practice that refines parenting competencies. Maternal care is also influenced by prenatal exposure to sex hormones and the hormonal changes that occur during pregnancy and the birthing process, such that a combination of early play parenting and hormonal influences contribute to the adequacy of female caregiving in many primate species (Lee & Bowman, 1995; Pryce, 1995).

Humans are no exception. In addition to investing more in parenting than men (Geary, 2000), women engage in more play parenting and family-oriented play as children. The sex difference in play parenting is related, in part, to the fact that girls throughout the world are assigned child-care roles, especially for infants, much more frequently than are boys (Whiting & Edwards, 1988). Girls also seek out and engage in child-care, play parenting, and other domestic activities (e.g., playing house)---with younger children or child substitutes, such as dolls---much more frequently than do same-age boys (Pitcher & Schultz, 1983). During the early preschool years, these themes are commonly enacted during solitary play (e.g., playing house with a baby doll), but peers are incorporated into these themes as children become more socially experienced and competent. Beginning around 3-4 years of age, the social-symbolic play of boys tends to focus on issues of physical fighting and competition (e.g., "cowboys and Indians"), whereas that of girls is more commonly focused on family relationships (e.g., "mother and child"; Pitcher & Schultz, 1983).

As in other domains, the magnitude of this sex difference varies across age and context. Prior to about age 6, both girls and boys are generally responsive to infants, but after this age, and continuing into adulthood, girls are more responsive to infants and younger children than are boys (Berman, 1986; Edwards & Whiting, 1993). The emergence of this sex difference is related to a significant drop in the frequency with which older boys attend to and interact with infants and younger children (Berman, 1986; Sandberg & Meyer-Bahlburg, 1994). This sex difference has persisted over nearly 40 years of significant change in the social roles and opportunities of women in the United States (Sutton-Smith *et al.*, 1963), and it has

been found across other industrial societies and in traditional societies in which it has been studied (Eibl-Eibesfeldt, 1989; Whiting & Edwards, 1988).

The sex differences in interest in infants, children, and families, as well as in engagement in play parenting, are influenced by the prenatal hormonal environment and by hormonal changes occurring during puberty. Girls affected by CAH show less interest in infants and families and engage in play parenting, among other things, less frequently than their unaffected sisters (Berenbaum & Hines, 1992; Berenbaum & Snyder, 1995; Collaer & Hines, 1995; Leveroni & Berenbaum, 1998). Berenbaum and Hines (1992) compared 5- to 8-year-old girls affected with CAH with unaffected same-sex relatives and found that unaffected girls played with dolls and kitchen supplies 2 1/2 times longer than did girls affected by CAH. These girls, in turn, played with boys' toys (e.g., toy cars) nearly 2 1/2 times longer than did unaffected girls. The same pattern was found in a follow-up study 3-4 years later (Berenbaum & Snyder, 1995). Furthermore, when allowed to choose a toy to take home after the assessment was complete, unaffected girls most frequently chose a set of markers or a doll to take home, whereas girls affected by CAH most frequently chose a transportation toy (e.g., toy car) or a ball. Unaffected girls also show an increased interest in children following menarche (Goldberg, Blumberg, & Kriger, 1982), whereas the interests of girls affected by CAH remain more malelike (Berenbaum, 1999).

### 3. *Ecologically Related Play Patterns*

If men are inherently motivated to attempt to achieve ecological dominance, then sex differences should be found in activities that support this goal. Included among these activities are tool use, hunting, and exploration and control of the wider ecology (e.g., as in control of natural resources). Across traditional societies, men are indeed more likely to use objects as tools (e.g., metal work, weapon making), to hunt, and to travel in unfamiliar territory as related to hunting and warfare (Murdock, 1949). As noted earlier, these activities enable coalitions of men to define and maintain--typically in conflict with other coalitions--a territory for their group and to extract physical (e.g., control of water supply) and biological (e.g., food, medicine) resources from this territory. Although women's gathering contributes to the latter as well, it typically occurs within the confines of the territory maintained by men. In any case, sex differences in play and other developmental activities that would provide the practice needed to refine these competencies are predicted. The associated research base is not as extensive as the base on sex differences in social--developmental activities, but extant research is consistent with the prediction.

*a. Tool Use.* Skilled tool use in adulthood appears to be facilitated by object-oriented play during juvenility. Such play is uncommon in wild primates, except for a few tool-using species, including humans and chimpanzees (Byrne, 1995;

Goodall, 1986). Object-oriented play is often solitary and involves the nonfunctional manipulation of objects, such as throwing them, banging them, and so forth. The function of this play appears to be to learn about the different ways in which various objects can be used, which in turn appears to facilitate later tool use and later problem-solving skills as related to tool use. Chimpanzees that lack object-oriented play during juvenility are, as adults, less successful in problem-solving with objects (Byrne, 1995).

As with the chimpanzee, object-oriented play apparently helps children to learn about the physical properties of objects and the different ways in which these objects can be used and classified. For example, preschool children whose play was object oriented had higher scores on tests of spatial cognition (e.g., the ability to mentally represent and mentally manipulate geometric designs) and were better able to sort objects based on, for example, color and shape (Jennings, 1975). Boys and men are consistently found to be more object oriented than girls and women (Willingham & Cole, 1997). In addition, preschool boys learn to use tools more quickly and readily than preschool girls. Chen and Siegler (2000) found that 18-month-old boys were better than same-age girls at inferring how objects could be used as tools; were more skilled at using objects as tools (e.g., to retrieve a desired toy); and, learned to use objects as tools more quickly, that is, with less practice and less need for adult demonstration. As previously mentioned, girls affected with CAH show more male-typical object-oriented play than other girls, suggesting that exposure to prenatal androgens may influence this sex difference (Berenbaum & Hines, 1992).

*b. Ecological Exploration and Manipulation.* Beginning in middle childhood and increasing through adolescence, boys have larger play ranges than girls and explore and manipulate these ecologies (e.g., building things, such as forts) much more frequently than do girls (Matthews, 1992). These sex differences appear to contribute to the sex differences in certain spatial competencies, especially the ability to form a mental representation of the wider ecology, as contrasted with the ability to remember the location of specific objects in this ecology (see Silverman & Eals, 1992). The sex difference in the area of the play range appears to be related, in part, to greater parental restrictions on the ranges of girls than on those of boys. However, a sex difference in the size of the play range is found in the absence of any such restrictions, both in industrial societies and in those traditional societies in which it has been studied (Matthews, 1992; Munroe & Munroe, 1971). In studies of the exploratory play of children in suburban England, for instance, Matthews (1992) found that younger children---both boys and girls---tended to play within close proximity of one or both of their parents (see also Whiting & Edwards, 1988). In contrast, 8- to 11-year-old children were more likely to play away from home, and the area of the unrestricted play range of boys covered from one and a half to nearly three times the area of the unrestricted play range of same-age girls.

Whiting and Edwards (1988) reported a similar sex difference for older children in three separate groups in Kenya as well as for children in Peru and Guatemala. Nonetheless, the age at which this sex difference emerges appears to vary with the ecology of the group. For the Ache, who live in dense, tropical rain forest, the size of the range of boys and girls does not typically diverge until adolescence (Hill & Hurtado, 1996).

As with tool use, boys profit more from exploratory behavior than girls Matthews' (1987) study of the relation between exposure to a novel environment and the pattern of sex differences in the ability to spatially represent this environment illustrates the point. Here, 8- to 11-year-old boys and girls were taken on a 1-h tour of an unfamiliar area in suburban England. In one condition, the children were given a map of the entire area and were then taken on the tour, with the guide pointing out various environmental features. In the second--high memory demand--condition, children were given a map of half of the area and their tour was interrupted for 30 min at the halfway point, although the same environmental features were pointed out. At the end of the tour, the children were asked to draw a map of the entire area. The maps of boys and girls did not differ in the overall amount of information provided, but sex differences did emerge for other map features, especially with the high-memory-demand condition. Boys were better able than girls to mentally reconstruct the topography of an unfamiliar environment, retaining general orientation, clustering, and Euclidean (e.g., relative direction) relations among important environmental features.

The evidence is not definitive, but studies of CAH suggest hormonal influences on these sex differences. Girls and women with CAH are consistently found to outperform their female relatives on tests of spatial ability and report engaging in more spatial-related behaviors while growing up (Kimura, 1999; Resnick, Berenbaum, Gottesman, & Bouchard, 1986).

*c. Play Hunting.* With very few exceptions (e.g., Hewlett, 1992), hunting is almost exclusively a male activity in traditional societies (Murdock, 1949), and it is a skill that requires years of experience to master (Kaplan *et al.*, 2000). Play hunting has not been directly studied by developmental psychologists, but several patterns support the predicted sex differences. Boys attend to potentially dangerous and wild animals more often than girls do, and in traditional societies engage in play hunting more often than girls. Boys' symbolic play more often involves wild animals than domestic ones (Eibl-Eibesfeldt, 1989). Similarly, the drawings of !Ko (central Kalahari) boys depicted domestic and wild animals about three times more frequently than did girls' drawings. In many traditional societies, a sex difference in the focus of boys and girls daily food-gathering activities emerges in late childhood (Kaplan *et al.*, 2000). For example, until about 10 years of age, both Hadza (Tanzania) boys and girls forage. After this age, boys generally restrict their activities to hunting, despite the fact that their hunting returns--in

terms of calories---are much lower than would be the case if they continued to forage (Blurton Jones, Hawkes, & O'Connell, 1997). The long-term benefits can be significant, however, as skilled hunters often have higher status (related to male-male competition) and more reproductive opportunities than other men, as mentioned earlier.

#### 4. *Phenotypic Plasticity*

If one function of the developmental period is to enable inherent neural, cognitive, behavioral, and affective systems to be adapted through developmental activities to local conditions, then plasticity in life history traits should covary with the length of the species' developmental period. If so, then humans should show a higher degree of phenotypic plasticity than any other species, but presumably within the constraints of norms of reaction. As described earlier, many human life history traits do in fact covary with local conditions but these analyses have been limited to physical traits, such as age of maturation (Stearns & Koella, 1986). If the sex differences in social behavior and play patterns are the result of human life history evolution and the influence of sexual selection and other evolutionary pressures, then all the behaviors previously described should evince some degree of phenotypic plasticity. Unfortunately, relevant research is meager, but available studies support the prediction (Low, 1989; MacDonald, 1992).

To illustrate, the form and intensity of boys' rough-and-tumble play varies across cultures. In societies characterized by relatively high levels of physical male--male competition, the play fighting of boys tends to be rougher than the play fighting found in other societies. For instance, intergroup aggression is a pervasive feature of Yanomamö society (Venezuela and Brazil; Chagnon, 1988) and young Yanomamö boys often play fight with clubs or bows and arrows, practices that are typically discouraged in settings where physical male-male competition occurs infrequently. For the Sioux and Native American tribes that frequently engaged in intergroup hostilities, the activities of young boys were designed to encourage both one-on-one and coalition-based aggression and physical endurance (Hassrick, 1964; Loy & Hesketh, 1995). These activities were often sufficiently violent to draw blood, yet afterward the boys were friendly to each other. This pattern---intense but nonlethal in-group competition and mechanisms (e.g., positive affect during "horse play") to maintain the cohesion of the in-group in the service of intergroup competition---is a predicted feature of male--male competition in humans (Geary & Flinn, 2002).

These and other games enable the social, behavioral, and affective systems that support the universal tendency of boys to engage in rough-and-tumble play and coalitional competition to be adapted to local conditions (see Geary, 1998). The mechanisms that support such phenotypic adaptations are not well understood but probably involve a combination of parental and peer influences as well as genotype by environment interactions (Low, 1989; MacDonald, 1992).

### 5. Conclusion

The pattern of human developmental sex differences supports all three predictions described previously. First, many sex differences in peer relationships and play mirror adult forms of intrasexual competition, although the findings are more definitive for male-male than for female-female competition given the larger research base for the former (Maccoby, 1988; Crick *et al.*, 1999). More specifically, the basic patterns are consistent with an evolutionary history of one-on-one and coalitional male-male competitions, which very likely involved the use of blunt force and projectile weapons (for further discussion, see Geary, 1998), as related to the achievement of social dominance and resource control. Female-female competition is much less physical but is also related to resource control, although the resources are largely social and relational. Second, consistent with the sex difference in parental effort, girls engage in play parenting and other forms of family-oriented play much more frequently than do boys (Pitcher & Schultz, 1983). Third, boys engage in ecologically related play and other related developmental activities, such as exploration, much more frequently than do girls (Matthews, 1992). Many of these differences are influenced by prenatal exposure to sex hormones and to hormonal changes associated with puberty. Proximate hormonal influences on the expression of sex differences are, in fact, the norm across species, and they are commonly associated with the expression of traits that have been influenced by sexual selection (Geary, 1998).

Although not definitive, the results are also consistent with the view that one function of developmental activities is to practice and refine the competencies that covaried with survival and especially reproductive outcomes during human evolution. Reproductive outcomes are emphasized because of low adult mortality rates in traditional societies, such that much of the variance in evolutionary fitness is related to individual differences in mating success and parental success (i.e., keeping children alive) rather than survival per se (Blurton Jones *et al.*, 1997; Hill & Hurtado, 1996; Irons, 1979). Nearly all of the developmental activities described earlier are consistent with survival and reproductive activities in traditional societies and presumably during human evolution. Equally important, the associated competencies (e.g., coalitional competition) become increasingly sophisticated and adultlike during the developmental period and presumably as a result of developmental activities (e.g., Crick *et al.* 1999; Pellegrini & Bartini, 2001). The majority of these developmental activities are highly social or are related to social issues, as in the relation between hunting competencies, social status, and men's reproductive options (Kaplan *et al.*, 2000). The social nature of developmental activities combined with the more general covariations among length of the developmental period, brain size, and social complexity in primate species (e.g., Joffe, 1997), support the position that various forms of social competition (see Table III) have been driving forces in human evolution and have significantly influenced human life history (Alexander, 1989; Geary & Flinn, 2001).

The research reviewed here also supports the general prediction that the function of many developmental activities is the accumulation of reproductive potential and the specific hypothesis that sexual selection has been (and continues to be) an important influence on the evolution of sex differences in human life history traits and in developmental activity. In other words, the sex difference in the distribution of reproductive effort across mating and parenting is by definition sexual selection, and the associated sex differences in developmental activity enable the accumulation of competencies that will support sex differences in reproductive effort during adulthood.

## VI. Conclusion

Life history and sexual selection represent core theoretical principles in evolutionary biology and guide empirical research related to proximate influences and predicted evolutionary functions of developmental traits and patterns of social dynamics, respectively (Andersson, 1994; Darwin, 1871; Roff, 1992). The first goals of the current chapter were to introduce these principles to human developmental scientists and to illustrate their utility for predicting and explaining developmental patterns and sex differences in nonhuman species. The next and more important goal was to construct a theoretical framework for conceptualizing the potential relations between sexual selection in humans and human life history traits, including children's developmental activities. The construction of this framework was guided by the assumptions that social competition, including sexual selection, has been a driving force in human brain, cognitive, behavioral, and social evolution (Alexander, 1989; Geary & Flinn, 2001) and that developmental activities reflect an evolved motivational disposition to practice and thus refine the associated competencies. More precisely, the function of many developmental activities is presumed to be the accumulation of reproductive potential that is then expended in adulthood in the form of reproductive effort: mating, parenting or some combination (Alexander, 1987).

As an example, consider that humans share with many other species the same basic life history traits that have been found to covary with male-male competition and an accompanying sex difference in parental effort. Included among these traits are sex differences in life span, maturational dynamics, adult size, and premature death due to male-on-male violence, among other traits (Allman *et al.*, 1998; Leigh, 1996; Wilkins, 1996; Wilson & Daly, 1985). The pattern is clearly consistent with the position that male-male competition--likely exaggerated by female choice--has influenced the evolution of many features of human life history, including components of physical development, reproduction, and a few behavioral traits (i.e., male-on-male aggression; Roff, 1992). At the same time, standard life history analyses do not fully capture the potential influence of social-behavioral

components of male-male competition and other features of sexual selection on life history evolution, although a few initial analyses have been conducted (e.g., Sawaguchi, 1997). Nor do standard life history analyses capture the importance of developmental activities as related to sexual selection and life history, with very few exceptions (e.g., Collis & Borgia, 1992). When social-behavioral and developmental activities are considered in relation to the importance of coalitional male-male competition and human ecological dominance in traditional societies and presumably during human evolution (Alexander, 1987, 1989; Geary & Flinn, 2001; Wrangham, 1999), many aspects of human life history and associated sex differences fall into place.

Sex differences in rough-and-tumble play and participation in sports and other coalitional activities are well documented empirically (e.g., DiPietro, 1981; Lever, 1978; Maccoby, 1988), with the occasional consideration of these patterns as potentially related to male-male competition (Pellegrini & Smith, 1998). However, the consistency of these developmental sex differences with coalitional male-male competition and with one-on-one competition as related to the formation of within-coalition dominance hierarchies has not been fully appreciated. The position here is that these developmental activities are evolved components of human life history that reflect a motivational disposition for boys to engage in activities that prepare them for the forms of one-on-one and coalitional competition that defined male-male competition during human evolution (Geary, 1998). The social nature of male-male competition and associated developmental activities also support Alexander's (1987, 1989) hypothesis that social competition was a driving force during human evolution.

Other features of boys' developmental activities, such as object play and play hunting, are in keeping with Kaplan and colleagues' hunting hypothesis--specifically, that hunting/foraging demands were important influences on the evolution of human life history and associated sex differences (Kaplan *et al.*, 2000). The position here is that these activities are indeed important, and related to the evolution of human ecological dominance. At the same time, these activities (e.g., hunting) are aspects of a much broader suite of social, behavioral, and cognitive competencies related to social competition, within (e.g., mating choice) and between groups (Geary & Flinn, 2001). Stated differently, many of these developmental activities enable the accumulation of social, behavioral, and cognitive competencies needed for later reproductive efforts, at least for reproductive efforts in traditional societies and presumably during human evolution.

The relation between life history and other components of sexual selection, specifically male choice and female-female competition, are not well understood. For humans, male choice and female-female competition are, nonetheless, integral aspects of sexual selection and, as with male-male competition and female choice, have likely influenced the evolution of human life history traits and developmental activity. As an example, pioneering research by Crick and colleagues on relational aggression provides solid empirical evidence that girls and women

do indeed compete with one another (Crick *et al.*, 1997, 1999; Crick & Rose, 2000), findings readily interpreted in terms of sexual selection and female-female competition (Geary, 1998,2002). As with boys' rough-and-tumble play and coalitional games, girls' relational aggression emerges during the preschool years and becomes increasingly sophisticated, socially and cognitively (e.g., in terms of theory of mind), with maturation and practice (Crick *et al.*, 1999). The function of these social activities is to influence and attempt to control social behavior of other girls and women (sometimes boys and men) and with adolescence becomes increasingly focused on romantic relationships, that is, disrupting the romantic relationships of other girls and women. The latter is consistent with the prediction that female-female competition should, in part, be related to paternal investment, that is, developing a spousal relationship and thus access to the man's social and material resources (Geary, 2000; Trivers, 1972).

As with boys, many other features of girls' self-initiated activities are interpretable from an evolutionary perspective, although not sexual selection *per se*. The most obvious of these are play parenting and family-oriented play, which, of course, follow from the sex difference in parental effort. In any case, developmental activities that focus on peer relationships and play parenting both enable the accumulation of competencies related to reproduction in adulthood, female-female competition and parenting, respectively.

In sum, basic components of human development, such as length of the developmental period and life span, as well as the details of developmental activities and accompanying sex differences, are readily interpretable from the combined perspectives of life history and sexual selection. Proximate factors, such as gender categorization (Eagly, 1987), are potentially important influences on the expression of many sex differences. Indeed, phenotypic plasticity in life history traits and forms of sexual selection are predicted and have been illustrated in a few cases (Low, 1989; Stearns & Koella, 1986). In other words, many of the proximate influences on sex differences might be studied in terms of the broader framework of phenotypic plasticity as related to life history and sexual selection. In any case, a fully informed, human developmental science must incorporate life history traits and the various components of sexual selection.

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