The Endocrinology of the Human Adaptive Complex
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CHAPTER FIVE

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Introduction

The *human adaptive complex* is a coadapted complex of traits including (1) the life history of development, aging, and longevity; (2) diet and dietary physiology; (3) the energetics of reproduction; (4) social relationships among men and women; (5) intergenerational resource transfers; and (6) cooperation among related and unrelated individuals (Kaplan, 1997; Kaplan et al., 2000; Kaplan et al., 2001; Kaplan and Robson, 2002; Kaplan et al., 2003; Robson and Kaplan, 2003; Kaplan and Gurven, 2005; Gurven and Kaplan, 2006; Gurven and Walker, 2006; Kaplan, Gurven, and Lancaster, 2007). It describes a very specialized niche characterized by (1) the highest-quality, most nutrient-dense, largest-package-size food resources from both plants and animals; (2) learning-intensive, sometimes technology-intensive, and often cooperative food acquisition techniques; (3) a large brain to learn and store a great deal of context-dependent environmental information and to develop creative food acquisition techniques; (4) a long period of juvenile dependence to support brain development and learning; (5) low juvenile and even lower adult mortality rates, generating a long, productive life span and population age structure with a high ratio of adult producers to juvenile dependents; (6) a three-generational system of downward resource flows from grandparents to parents to children; (7) biparental investment, with men specializing in energetic support and women combining energetic support with direct care of children; (8) marriage and long-term reproductive unions; and (9) cooperative arrangements among kin and unrelated individuals to reduce variance in food availability through sharing and to more effectively acquire resources in group pursuits.

The publications cited above show that the majority of the foods consumed by contemporary hunter-gatherers worldwide are calorically dense hunted and extracted (taken from an embedded or protected matrix—underground, in shells, and so on) resources, accounting for 60% and 35% of calories, respectively. Extractive foraging and hunting proficiency generally does not peak until the midthirties, because they are learning and technique intensive. Hunting, in particular, demands great skills and knowledge that takes years to learn, with the amount of meat acquired per unit time more than doubling from age 20 to age 40 even though strength peaks in the early twenties. This learning-intensive foraging niche generates large calorie deficits until age 20 and great calorie surpluses later in life. This life history profile of hunter-gatherer productivity is only economically viable with a long expected adult life span.

This chapter is divided into two parts. The first section reviews components of the human adaptive complex and the evidence on which our understanding is based. The second section discusses directions for new research, with a focus on the uniquely human relationships between men and women and on their implications for the life history of the endocrine system.

Part I

Life Histories of Wild Chimpanzees and Human Foragers

To appreciate the implications of the human adaptive complex for the life histories of foragers and horticulturalists, it is useful to compare humans with the chimpanzee, another large-bodied, long-lived mammal and our closest living relative in phylogenetic terms. Table 5.1 presents major differences in five critical parameters of life history: survivorship to age of first reproduction, life expectancy at the beginning of the reproductive period, absolute and relative length of the postreproductive period, spacing between births of surviving offspring, and growth during the juvenile period (Lancaster et al., 2000). Human and chimpanzee life history parameters based on data from extant groups of hunter-gatherers and wild chimpanzees indicate that forager children experience higher survival to age 15 (60% versus 35%) and higher growth rates during the first 5 years of life (2.6 kg/yr versus 1.6 kg/yr). Chimpanzees, however, grow faster in both absolute and proportional weight gain between the ages of 5 and 10. The early high weight gain in humans may be the result

Table 5.1 Life history characteristics and diet of human foragers and chimpanzees.

Life History Characteristics	Human Foragers		Chimpanzees
Maximum life span	~120		~60
Probability of survival to age 15	0.6		0.35
Expected age of death at 15 (years)	54.1		29.7
Mean age first reproduction (years)	19.7		14.3
Mean age last reproduction (years)	39		27.7*
Interbirth interval (months)**	41.3		66.7
Mean weight at age 5 (kg)	15.7		10
Mean weight at age 10 (kg)	24.9		22.5
Composition of Diet (%)			
Collected	9		94
Extracted	31		4
Hunted	60		2
Contributions by Sex (%)	Men	Women	
Adult calories	68	32	Sexes independent
Adult protein	88	12	
Caloric support for offspring	97	3	
Protein support for offspring	100	0	

*Age of last reproduction for chimpanzee females was estimated as two years prior to the mean adult life expectancy.

**Mean interbirth interval following a surviving infant.

Sources: Kaplan et al., 2000; Lancaster et al., 2000.

of the earlier weaning age (2.5 years versus 5 years), followed by provisioning of highly processed and nutritious foods. Fast growth and weight gain during infancy and the early juvenile period may also represent an adaptation to support the energetic demands of brain growth development, since a significant portion of this weight gain is in the form of fat.

The chimpanzee juvenile period is shorter than that for humans, with age at first birth of chimpanzee females about 5 years earlier than among forager women. This is followed by a dramatically shorter adult life span for chimpanzees. At age 15, chimpanzee life expectancy is an additional 15 years, whereas foragers can expect to live an additional 38 years, having survived to age 15. Importantly, women spend more than a third of adult life in a postreproductive phase, whereas few chimpanzee females spend any time as postreproductive. The differences in overall survival probabilities and life span of the two species are striking: less than 10% of chimpanzees ever born survive to age 40, and virtually none survive past 50, whereas 45% of foragers do, and more than 15% of foragers born survive to age 70!

Finally, despite the fact that human juvenile and adolescent periods take longer, and that human infants are larger than chimpanzees at birth, forager women are characterized by higher fertility. The mean interbirth interval between offspring when the first survives to the birth of the second is 1.6 times longer among wild chimpanzees than among modern forager populations.

To summarize, human foragers show a juvenile period 1.4 times longer and a mean adult life span 2.5 times longer than chimpanzees. They experience higher survival at all ages postweaning but slower growth rates during midchildhood. Despite a long juvenile period, slower growth, and a long postreproductive life span, forager women achieve higher fertility than do chimpanzees.

Consumption and Productivity through the Life Course

Table 5.1 also demonstrates the overlap in component categories of the diets of foraging societies and chimpanzee communities as well as the wide differences in relative proportions (Lancaster et al., 2000). For example, hunted meat makes up about 2% of chimpanzee but 60% of forager diets. Chimpanzees rely on collected foods for 94% of their nutrition, especially ripe fruits. Such foods are nutritious and are neither hard to acquire nor learning intensive, at least relative to human resource pursuits. Humans depend on extracted or hunted foods for 91% of their diet. The data suggest that humans specialize in rare but nutrient-dense resources (meat, roots, nuts), whereas chimpanzees specialize in ripe fruit and fibrous plant parts. These fundamental differences in diet are reflected in gut morphology and food passage times in which chimpanzees experience rapid passage of bulky, fibrous meals processed in the large intestine, whereas humans process nutritionally dense, lower-volume meals amenable to slow digestion in the small intestine (Milton and Demment, 1988).

Figure 5.1 presents the survivorship and net food production through the life course of humans and chimpanzees (Kaplan and Lancaster, 2003). Humans consume more than they produce for the first third of their life course. In contrast, chimpanzees are self-supporting by the age of 5. Thus, human juveniles, unlike chimpanzee juveniles, have an evolutionary history of dependency on adults to provide their daily energy needs. Even more striking is the steady increase in productivity over consumption among humans into their thirties and early forties. Forager males begin to produce more than they consume in their late teens, but their peak productivity builds slowly from their early twenties until their mid to late thirties and then is sustained for 20 or more years at a level of approximately 6,500 kcal per day. In contrast, forager women vary greatly from group to group in energy production, depending on the demands of intensive child care (Hurtado and Hill, 1990). In some groups, they consume more than they produce until menopause, when they are freed from child care demands; in other groups, such as the Ache, they remain nutritionally dependent on men throughout their lives. The provisioning of reproductive women and children has a powerful effect on the production of children by humans by reducing the energy cost and health risk of lactation to the mother and by lifting the burden of self-feeding from the juvenile, thus permitting a shortened interbirth interval without an increase in juvenile mortality (Hawkes et al., 1998).

The human adaptation is both broad and flexible, in one sense, and very narrow and specialized, in another. It is broad in the sense that, as foragers, humans have existed successfully in virtually all of the earth's

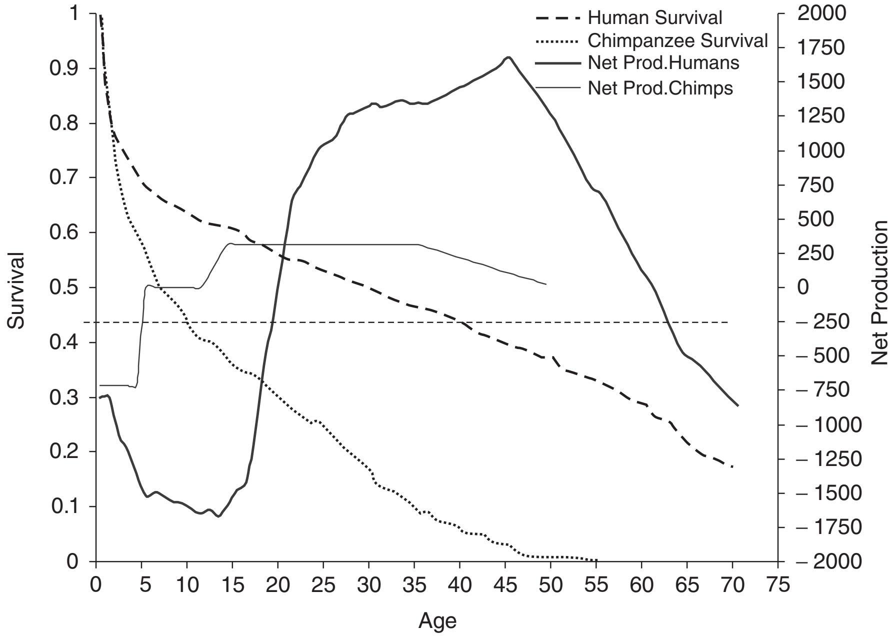

Figure 5.1 Survival and net food production: human foragers and chimpanzees. From Kaplan and Lancaster, 2003, 181.

major habitats. It is narrow and specialized in that it is based on a diet composed of nutrient-dense, difficult-to-acquire foods and a life history with a long, slow development, a heavy commitment to learning and intelligence, and an age profile of production shifted toward older ages. In order to achieve this diet, humans are very unproductive as children, have very costly brains, are extremely productive as adults, and engage in extensive food sharing both within and among age and sex classes.

The Sexual Division of Labor and the Acquisition of Skilled Performances

A feeding niche specializing in large, valuable food packages, and particularly hunting, promotes cooperation between men and women and high levels of male parental investment, because it favors sex-specific specialization in embodied capital investments and generates a complementarity between male and female inputs. The economic and reproductive cooperation between men and women facilitates provisioning of juveniles that both underwrites their embodied capital investments and acts to lower mortality during the juvenile and early adult periods. Cooperation between males and females also allows women to allocate more time to child care and improves their nutritional status, increasing both survival and reproductive rates. The nutritional dependence of multiple young of different ages favors sequential mating with the same individual, since it reduces conflicts between men and women over the allocation of food. Finally, large packages also appear to promote interfamilial food sharing. Food sharing assists recovery in times of illness and reduces the risk of food shortfalls due to both the vagaries of foraging luck and the variance in family size due to stochastic mortality and fertility. These buffers against mortality also favor a longer juvenile period and higher investment in other mechanisms to increase life span.

Unlike most other mammals, men in foraging societies provide the majority of the energy necessary to support reproduction. After subtracting their own consumption from total production, women supply an average of 3% of the calories to offspring, with men providing the remaining 97%, among the 10 foraging societies for which quantitative data on adult food production are available (Kaplan et al., 2000). Hunting, as opposed to gathering of animal protein in small packets, is largely incompatible with the evolved commitment among primate females to intensive mothering, carrying of infants, and lactation on demand in the service of high infant survival rates. First, hunting is often risky, involving rapid travel and encounters with dangerous prey. Second, it is often most efficiently practiced over relatively long periods of time, rather than in short stretches, due to search and travel costs. Third, it is extremely skill intensive, with improvements in return rate occurring over two decades of daily hunting. The first two qualities make hunting a high-cost activity for pregnant and lactating females. The third quality, in interaction with the first and second, generates life course effects such that gathering is a better option for females *even when they are not lactating,* and hunting is a better option for males (Gurven and Kaplan, 2006). Since women spend about 75% of their time during their reproductive years either nursing or more than three months' pregnant, it would not pay them to hunt because they never get enough practice to develop the skills to make it worthwhile, even when they are not nursing or pregnant or are postreproductive.

In our view the sex-based specialization in investment in skills over the life course (the sexual division of labor), together with the long period of parental investment leading to multiple child dependents, is directly responsible for high male parental investment, the universality of the marriage institution, and the extensive economic and reproductive cooperation among husbands and wives. This original specialization in different skills and in the procurement of different resources generated a complementarity between human men and women that is rare among mammals. The specialization generated two forms of complementarity. Hunted foods complemented gathered foods because protein, fat, and carbohydrates complement one another with respect to their nutritional functions (Hill, 1988). A second form of complementarity came from the fact that males tend to concentrate on large, shareable packages of food, such as meat, which shifts the optimal mix of activities for women, increasing their time spent in child care and lowering their efficiency demands in food production.

The end result of the human division of labor can be reduced to a few basic principles that reflect its core functions: men are allocated tasks that require strength, endurance, concentration, and risk taking. This places men in the role of both protectors and hunters, focusing their productive efforts on big game at the top of the food pyramid. Women are collectors, concentrating lower on the food pyramid to gather medium-quality food products such as the reproductive and storage organs of plants. This work is much lower in risk and thus compatible with lactation and the care of small children. The sexual division of labor goes far beyond hunting and gathering. It is typical of traditional societies as well. Brown (J. Brown, 1970) found that, in surveying the Human Relations Area Files, tasks assigned to women have very specific properties in line with the classic division of labor. In surveying the practice of crafts and other specializations in traditional societies, Brown found that only a limited number are not practiced by women: metallurgy; long-distance travel and trade; handling large, dangerous domestic animals; and warfare. Women's tasks such as gardening, market trade, and the crafts of pottery and cloth production have a set of practical characteristics: (1) they do not require rapt concentration, (2) they can be easily interrupted, (3) they do not require long-distance travel from home, and (4) they are not dangerous. In other words, they are all forms of productive labor that are compatible with the care of small children.

Human females evidence physiological and behavioral adaptations that are consistent with an evolutionary history involving extensive male parental investment. They both decrease metabolic rates and store fat during pregnancy, suggesting that they can lower work effort and are being provisioned (Sellen, 2006). During lactation, women in foraging societies decrease work effort and focus on high-quality care such as lactation and carrying (Hurtado et al., 1985; Lancaster et al., 2000; Gurven and Kaplan, 2006). In contrast, nonhuman primate females do not store appreciable fat, and they increase work effort during pregnancy and lactation; as a result, they have increased risk of mortality (Altmann, 1980; Cheney et al., 2004). Human specialization could not have evolved if women had not depended on men throughout human history for most of their food provision.

Part II

Sexual Division of Labor and Complementarity: Directions for Future Research

Given that the division of labor and long-term mateships have been such a critical feature of human reproductive strategies, it is likely that endocrine regulation of behavior, psychology, and physiology over the life course is designed to support the complementary roles of men and women. Such regulation should be sensitive to the costs and benefits of defection and desertion as numbers of dependent children change over time. It should also be responsive to the energetic demands of children and the complementary roles that men and women play in meeting those demands. The remainder of this chapter will discuss four areas of new research entailed by those considerations: (1) children's contribution to marital stability, (2) women's sexual preferences during conceptive ovulations in natural fertility populations, (3) male physical and psychological characteristics in relation to the division of labor, and (4) the process of acquisition of sexually dimorphic embodied capital.

PARENTAL INVESTMENT AND MATESHIP STABILITY

Marriage is probably the most complex cooperative relationship in which humans engage. It involves the production and processing of resources for familial consumption, distribution of those resources, the provision of child care, production and maintenance of belongings and residential amenities, and sexual rights and responsibilities. The ability to coordinate on the allocation and execution of those responsibilities (that is, the ability to "get along") is fundamental to successful marriage and appears to play a role in mate choice (Buss, 2003). In traditional societies, as well as contemporary, it is not uncommon to hear remarks about success and failure in coordinating and getting along as comments about why marriages succeed and fail.

A problem that people face in mate choice is that long-term, multiple dependency of offspring of differing ages—unlike reproduction in litters or in succession, with feeding independence established at weaning—makes mate switching much more costly. Once one has reproduced with a given partner, a change in partners can entail reduced investment in those previous children. Moreover, most mate choice occurs before economic abilities are proven. For example, at a marriage age of around 20, Ache and Tsimane men are only 25% and 50%, respectively, as proficient at hunting as they will be at their peak in their mid- to late thirties (Kaplan et al., 2001; Gurven, Kaplan, and Gutierrez, 2006). This issue remains true for most marriages even today. Excluding marriages based on inherited wealth, most others are formed and reproduction is begun before the full productive and reproductive potentials of the partners are clear.

From the perspective of both men and women, there are great gains from choosing a good partner, and there are great risks of economic and sexual defection. For the most part, it is a long-term choice with direct consequences for fitness. It is further complicated by the fact that partners contribute to fitness not only through behavior but also through genetic inputs, which can lead both to further complementarities or to conflicts of interest. Marriages redirect social interaction and cooperation not just within the pair-bond but across members of respective extended families.

Social capital, which can be defined as stored information by others about a person's characteristics, social status, and social support, is likely to play an important role in mate choice. Capital affecting perceptions about fairness, industriousness, loyalty, promiscuity, and economic abilities is likely to influence mate choice decisions by both men and women. Some of the same factors affecting the choice of production and sharing partners may also affect the choice of marriage partners (see Kaplan, Gurven, and Lancaster, 2007, for a discussion).

Extensive cooperation among human men and women would only make sense if the reproductive performance of spouses were linked. Women approach zero fecundability some 5 years before menopause (Holman and Wood, 2001). Forager men do have the option to continue reproducing with younger women but generally do not do so. For example, 83% of all last births to Ache women also represent a last birth for the fathers of these children (Gurven, Kaplan, and Gutierrez, 2006). An obvious reason for this is that the last child born to a couple still represents an additional 18 years of parental provisioning and investment. In traditional sedentary or herding societies, some men with resources do have the option of polygyny and can add new, younger wives as they age and so extend their own reproductive years. Nevertheless, the fact is that most marriages in time past and in the world today are either monogamous or serially monogamous; and even when polygyny is a cultural ideal, few men can attain it. Murdock's cross-cultural sample of 849 societies lists polygyny for 83.5% of traditional societies, but in 55.7% of these, polygyny is occasional (<20%), and only 27.8% are labeled as polygyny being common (>20%) (Lancaster and Kaplan, 1992).

We also know that the presence of children stabilizes marriage in societies ranging from traditional (Hill and Hurtado, 1996; Winking, 2006) to modern industrialized societies (Morgan, 1996; Anderson, Kaplan, and Lancaster, 2007). Betzig (1989) in a study of the causes of conjugal dissolution taken from authoritative accounts on 160 societies in the Standard Cross-Cultural Sample found that the two leading causes of divorce were infidelity and infertility, closely ranked at 88 and 75, respectively, with cruelty or maltreatment ranking third at 54. The first two speak directly to the issue of children as pivotal in marriage: the one in terms of the genetic relationship of children to their parents and the other to their very existence. Betzig proposes that the practice of trial mateships so common in both tribal societies and under modern conditions most often solidifies into full or common-law marriage with the production of children. It is interesting to note that the two largest ever studies of sexual behavior done in the United States and England in response to the HIV epidemic gave no information about the presence of children on marital fidelity in spite of the fact that their charge was to model sexual networks and the spread of disease (Johnson et al., 1994; Laumann et al., 1994). The authors do note that in a lifetime most sexual partnerships are accumulated before and after marriage and that the sexual revolution accounts for a historic increase in partners under those statuses. However, they made no attempt to distinguish between the sexual behaviors of marital partners *with* as opposed to *without* children.

The fact that humans are unique in raising multiple, nutritionally dependent offspring of differing ages also reduces the payoffs to defection and increases the benefits for men and women to link their economic and reproductive lives over the long run. Men and women who divorce and remarry during the time they are raising offspring will face conflicts of interest with new spouses over the division of resources (Anderson, Kaplan, and Lancaster, 1999). If they marry someone with children from a previous marriage, they may disagree with their new spouses over the allocation of food and care to their joint children, relative to children from previous marriages. These potential conflicts increase the benefits of spouses staying together and having all or most of their children together.

We know very little about the psychological and physiological processes underlying the formation of long-term pair-bonds and the role that children play in cementing those bonds. Prior to the birth of children, both men and women should be sensitive to cues about their partner's quality and ability to successfully accomplish their sex-specific role and their willingness to cooperate over the long run. During this period of evaluation, we might expect people to be more willing to consider alternative partners.

Winking and colleagues (Winking et al., 2007) found such an effect among Tsimane forager-horticulturists. Tsimane men were much more likely to have extramarital affairs in the first year or two of their marriages. Moreover, the likelihood of affairs diminishes radically with each additional child born to the couple. In spite of the fact that the reproductive value of men's wives decreases as they age, men are less likely to divert resources from their families and engage in affairs as both members of the couple age and have children. These results, especially if they are supported by further cross-cultural evidence in traditional societies, provide strong evidence against the mating effort or show-off hypothesis of men's work proposed by Hawkes and colleagues (Blurton Jones et al., 2000; Hawkes and Bliege Bird, 2002) and in favor of the view that the reproductive lives of men and women are linked through their complementary roles.

The endocrine supports of this system have yet to be investigated. Men appear to be responsive to the costs and benefits associated with both mating and parental effort, as they change over the life course. While there are very general changes in endocrine activity as men age, the particular life circumstances of men, such as entry into and out of bonded mateships and the birth of children, may also be reflected in and supported by endocrine responses (see Gray and Campbell, this volume). The relationship between the cognitive processing of costs and benefits, the motivation to engage in sexual activity in and out of mateships, and the feelings of parental concern have yet to be investigated in detail. We hypothesize that men's endocrine activity will play an important role in mediating those relationships.

A similar set of life history concerns should also govern women's behavior. For women, the presence of dependent children should be of particular importance, perhaps more so than whether or not they are mated. The mating strategies of women with and without dependent children should be very different, especially with respect to the multiple dependency of young of differing ages and condition. It raises the question of what the psychology of mate preference is for women who are mothers of young children in which the costs and benefits of seeking "good" genes in preference to male paternal investment are very different from those of childless women, regardless of whether or not they are mated. For that matter, throughout human evolutionary history, most sexually mature women who were available in the mating market already had children from previous relationships. Only young girls during the subfecund postadolescence period would be likely to have mate choice unfettered by the needs of dependents.

Over evolutionary and historical time, women more than men were likely to be single parents due to spousal death, divorce, or desertion (Vinovskis, 1990; Shackelford, Weekes-Shackelford, and Schmitt, 2005; Weekes-Shackelford, Easton, and Stone, 2007). Among the Ache, for example, death in childbirth was a rare event; the maternal death rate was 1 per 150 births, and the probability of death was higher for males from age 10 throughout adulthood (Hill and Hurtado, 1996). Such women should evidence a strong psychological preference for stable men with good parenting and provisioning skills, which would include the physical prowess to perform the demanding and high-risk tasks traditionally assumed by men, such as hunting large game, working at hard manual labor, risk taking, and protecting women and children from outside threat. These preferences cloud the stated division between being a good father and having good genes, since in times past being a good father and husband required good genes in terms of health and prowess.

Again, we suspect that there will be endocrine supports of this sensitivity to age and number of dependent children in the physiology of women. We also hypothesize that the quantity and quality of male support for children will also affect women's commitment to marriage and interest in alternative male suitors and that sensitivity to both dependency needs and male inputs will be mediated, at least partly, through endocrine controls. In the next section, we explore women's sexual preferences during conceptive ovulations in natural fertility populations in more detail.

WOMEN'S MATE CHOICE PREFERENCES DURING CONCEPTIVE OVULATIONS IN NATURAL FERTILITY POPULATIONS

In the past 15 years, evolutionary psychologists have produced a convincing body of articulated research on the evolution of human female mate choice (Gangestad, 2006; and Roney, this volume). The major findings of these studies are that women's sexual preferences vary according to where they are in their menstrual cycle. These preferences were found to fall in two phases, the nonovulatory parts of the cycle and a seven-day window leading up to and including ovulation. Because the research was on menstrual cycle effects, women who were on the pill, pregnant, or lactating were excluded from the sample. During the ovulatory window, women show strong preference for men with higher levels of testosterone, more symmetrical bodies and faces (Thornhill and Gangestad, 1999), more masculine faces (Penton-Voak et al., 1999; Johnston et al., 2001), a complementary major histocompatibility complex (Wedekind et al., 1995; Garver-Apgar et al., 2006), and personal histories of health (Gangestad and Thornhill, 2004). However, high levels of testosterone are associated not only with genetic quality but also with promiscuity. Men preferred during the nonovulatory window have lower levels of testosterone and are not as symmetrical or masculine but are more likely to indicate the ability to support a family. These results suggest that women have two kinds of sexualities linked to their menstrual cycle. During the ovulatory window, women prefer men with indicators of good genes, but during the nonovulatory parts of the cycle, they prefer men who are more likely to give paternal investment as measured by lower testosterone levels and access to resources. However, research on women in natural fertility populations representative of times past and most of the world today would greatly improve our understanding of the evolutionary forces and the endocrine architecture governing women's mating decisions during fertile menstrual cycles.

As established earlier, a major effect of the division of labor and the collaboration of human parents in the provisioning and care of their offspring is a parental condition unique to women: the dependency of multiple young of different ages (Lancaster, 1991, 1997; Draper, 1992). Figure 5.1 reveals the full impact of having multiple nutritionally dependent young with differing needs over many years. During infancy a mother provides both milk and care, but her older children between the ages of 5 and 15 are in a nutritional deficit of 1,500 calories on average. Unlike other primate offspring, human children need not self-feed at weaning. Figure 5.2 shows the major reduction in birth spacing for humans compared to the great apes. The mean interbirth interval between offspring when the first one survives to the birth of the second is 1.62 times longer among wild chimpanzees than among modern forager populations, thus reducing the interbirth interval to about 3 to 3.5 years for foragers and horticulturalists (Galdikas and Wood, 1990; Lancaster et al., 2000) and probably for natural fertility populations in general (Sellen, 2006). Consequently, because weaning long precedes nutritional independence for humans, the line between maternal investment by lactation for a toddler and the gestation of a subsequent child is less finely drawn.

Besides the dependency of multiple young of differing ages, women in natural fertility populations also have a characteristic hormonal profile during their reproductive span. Beginning with menarche at about age 16 and continuing to menopause around age 50, women spend most of this time either pregnant or lactating and not in menstrual cycling. In fact,

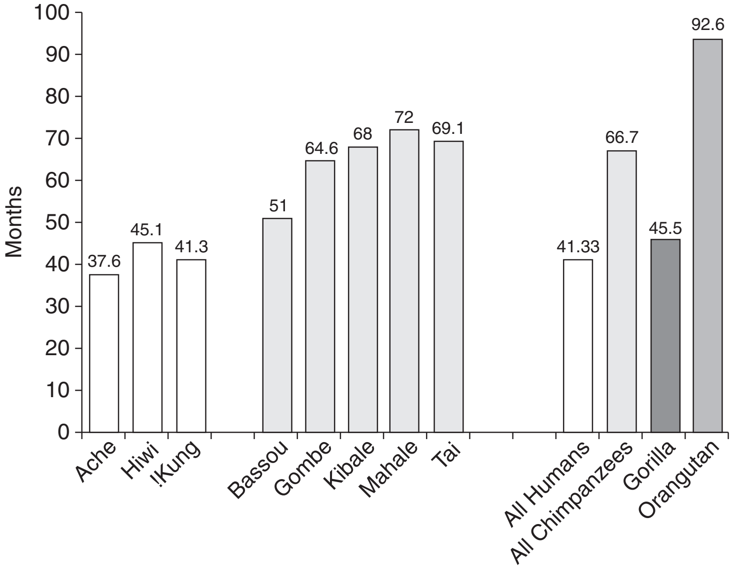

Figure 5.2 Birth spacing: human foragers and chimpanzees. After Lancaster et al., 2000.

menstrual cycling is a rare event; and even when these cycles occur, the majority are nonovulatory because most are during the first few years after menarche during the adolescent subfecundity period when ovulation is highly irregular or after age 45 when there is little likelihood of ovulation (Strassmann, 1997). Compared to the 350 to 450 cycles that women living in modern, low-fertility, contracepting societies can expect, women in natural fertility populations have 100 to 130 menstrual cycles in a lifetime, and perhaps only half of these will be ovulatory (Short, 1987; Eaton et al., 1994; Strassmann, 1997). In fact, such women will only ovulate repeatedly when they are sterile. Reproductive biologist R. V. Short was first to identify this pattern of excessive cycling today and to link repeated exposure to unopposed estrogens to the high rate of reproductive cancers in modern women. This insight has since been supported by research among a number of non-Western populations (Eaton et al., 1994; Strassmann, 1999).

Short also was very interested in the role of lactation as a natural contraceptive responsible for optimal birth spacing during most of human history and in the world today (Short, 1987, 1994). In natural fertility populations, (1) ovulatory menstrual cycles are very rare events, (2) the natural condition of women during their reproductive years is pregnancy or lactation, (3) lactation suppresses ovulation and controls birth spacing at the same time, and (4) most conceptions in natural fertility conditions occur during lactation (Short, 1987, 1994; Gray et al., 1990; Lewis et al., 1991; Kennedy and Visness, 1992). Well-nourished Australian and Scottish women who breast-fed exclusively for 6 months and on demand in the following months experienced on average 10 months of lactational amenorrhea, followed by 11 months of anovulatory menstrual cycles (Lewis et al., 1991). Similar results have been published in a meta-analysis of eight countries by Kennedy (Kennedy and Visness, 1992). Lactation, then, is a good contraceptive during the first year but not later, and most often the resumption of ovulation is forewarned by a menstrual cycle. However, the duration of lactation under natural fertility is much longer than 1 year, and the resumption of fecundity is not predicated on weaning (Lunn et al., 1984; Worthman et al., 1993; Tracer, 1996; Vitzthum et al., 2000; Ellison and Valeggia, 2003; Valeggia and Ellison, 2004). Sellen (Sellen and Smay, 2001) reviewed a sample of 113 ethnographic and demographic reports on the duration of breastfeeding published between 1873 and 1998. He found that duration of breastfeeding was 29.0 ± 10 months, with a median of 29.5 and a mode of 30.0. This, in combination with typical interbirth intervals of 3 years, supports Short's contention that most children are conceived while their mothers are breast-feeding a previous infant. The exception would be a firstborn child or a replacement baby whose older sibling died during its first 2 years of life.

These studies indicate that weaning in natural fertility populations is initiated by the recognition of a new conception and that conception is not dependent on weaning. In fact, researchers often report that infants are breast-fed until the second trimester of their successors' gestation—time enough for the implantation and viability of the next pregnancy to be assured (Tracer, 1996; Valeggia and Ellison, 2004; Nepomnaschy, 2007). Such a pattern of continued lactation during the first trimester of gestation of a subsequent child is highly adaptive for humans. The first trimester of gestation is the lowest in terms of energy demands on the mother, but it is also the highest in terms of pregnancy loss. Hormone assays indicate that mean early pregnancy loss nears 75% for women of reproductive age, and most of these have chromosomal or other defects (Holman and Wood, 2001). Selection would not favor sacrificing the interests of the suckling in the interests of a not-yet-conceived sibling until a successful pregnancy is firmly established.

The implication of this research on lactation and the resumption of ovulation in natural fertility societies is that the majority of children are conceived by mothers who are lactating and ovulating at the same time. In other words, conception occurs under a much richer hormonal environment than is usually considered in which levels of estrogen and progesterone are high enough for ovulation and implantation and levels of prolactin and oxytocin are high enough to sustain lactation. The main effect of prolactin during the postpartum period is to maintain milk production. Its levels surge following each sucking episode and remain chronically elevated as long as suckling continues. It inhibits pusatile secretion of gonadotropin-releasing hormone (GnRH), which, in turn, suppresses ovarian steroid production. According to Short, prolactin orders up the next meal, and oxytocin serves the current meal (Short, 1994). Oxytocin's classic role is to stimulate smooth muscle contraction in such vital reproductive processes as child birth, uterine contraction after birth, milk letdown, and orgasm. Another of its functions is to suppress cortisol and so reduce stress and foster a general sense of calm (Uvnäs-Moburg, 1998, 2003). It is the contentment hormone of nursing mothers. Oxytocin in concert with dopamine supports emotional attachment and bonding and conditions a preference for social partners whether a baby, mate, or pet (Uvnäs-Moburg, 2003; and Sanchez et al., this volume).

This research on lactation and conception in natural fertility populations brings to the front an obvious question. Since most pregnancies have been and are to mothers, and most often mothers of infants, research on female sexual preference in relation to the menstrual cycle needs to be done on the excluded categories: women on the pill, pregnant, and lactating. There is no published research on mating preferences of women who have been nursing for over a year, and yet these would be the typical condition of most conceptions in natural fertility populations. A research agenda that is more inclusive is in order. Given the importance of maintaining continued male parental investment for existing offspring, we hypothesize that variation in mate choice between the ovulatory and nonovulatory portions of the menstrual cycle identified in Western populations among nulliparous women and parous women who are not lactating would be greatly attenuated in natural fertility populations.

THE IMPACT OF THE SEXUAL DIVISION OF LABOR ON MALE SIZE AND MUSCULARITY

The tasks in the sexual division of labor that fell to human males have one thing in common: they cannot be done carrying an infant or being accompanied by a toddler. They demand the physical prowess of hunting large game, handling dangerous domestic animals, working at hard manual labor, risk taking in general, and protecting women and children from outside threat. In other words, men must be risk takers both as producers and as protectors in order to play their complementary role in the division of labor. Dabbs and Dabbs (2000) link these roles to the hormone testosterone, which facilitates male performance as "heroes, lovers, and rogues." What they do not do is to link these behaviors to being effective fathers. They and others see these male behaviors as the products of sexual selection (antithetical to fatherhood when defined only in terms of caregiving) and not male behaviors that need to complement what women can do in the raising of families.

Sexual dimorphism in muscularity and body size is an ancient feature in the anthropoid primates and is usually understood as sexually selected adaptations for intrasexual competition over access to females. However, according to Plavcan and van Schaik (1997), although monogamous anthropoids show low degrees of weight dimorphism, as would be predicted by the action of sexual selection, polygynous anthropoids show high variation in weight dimorphism that is not associated with measures of mating system or operational sex ratio. We know that human body size has become progressively smaller in the past 50,000 years—probably linked with the rise of technology that has accompanied human evolution and progressively distanced the human body from the harshest demands of its environment (Ruff, 2000, 2006). Tall human populations have a higher degree of stature dimorphism than do short ones, so the more recent prehistoric reduction in stature and size has probably also been associated with a reduction in sexual dimorphism in the tallest populations. Attempts to link population differences in the degree of sexual dimorphism in body size to mating systems in modern humans have thus far failed. Wolfe and Gray (1982) compared size dimorphism to the number of polygynous marriages and also the level of male parental investment in traditional societies, but no cross-population correlations could be found.

There is reason to believe that sexual dimorphism in humans may be due to factors other than sexual selection. One feature of human sexual dimorphism that we can link directly to the division of labor is stored body fat in the hips, thighs, and buttocks of women that is accessed during lactation (Rebuffé-Scrive et al., 1985; Lancaster, 1986; P. Brown, 1991; Sohlstrom and Forsum, 1995). Sex differences in body fat are more pronounced in humans than in stature or body size. Humans show only mild sexual dimorphism in variables like stature: males are only 5–9% taller than females and 11–20% larger in body mass (P. Brown, 1991; Cachel, 2006). Although males and females may carry proportionally similar pounds of fat, the sites of deposition are very different. Males deposit most of their fat around the midline. In contrast, women have fatter skinfold thicknesses at four sites on the trunk and five sites on the arms and legs, with the thighs being 45% fatter than males (P. Brown, 1991). The sites are readily accessed for energy via the hormones of lactation (Rebuffé-Scrive et al., 1985). Unlike the vast majority of nonhuman primate females, who must support lactation through their feeding effort, human females frequently reduce work effort during pregnancy and lactation (Altmann, 1980; Hurtado et al., 1992; Lancaster et al., 2000). They can rely on men for energetic support, as well as other kinswomen who are not lactating. These extra sources of energetic support, coupled with the critical energetic demands of human postnatal brain growth, may be why human women store body fat, presumably at the expense of physiological efficiency for foraging (for example, in terms of thermal regulation and the costs of carrying nonproductive mass).

Similarly, the greater muscularity and body mass of men need not be a selected adaptation for male-male violence. Comparing the rates of violence in chimpanzees and humans gives support to the idea that male-male physical competition over females within the social group is vastly less important in humans. Wrangham and his associates compared the rates of lethal violence between chimpanzees and human subsistence societies and found them similar (Wrangham, Wilson, and Muller, 2006). In sharp contrast, chimpanzees had rates of within-group nonlethal physical aggression between two and three orders of magnitude higher than humans. Although preliminary data, these results indicate a major reduction in male-male violence within human groups and supports Boehm's hypothesis on the evolution of human egalitarianism (Boehm, 1999).

It may be that selection on the hormonal regulation of human male growth, in terms of both stature and mass, is more the result of productive efficiency in acquiring nutrients to support reproduction and dependent children than of direct male competition. The effects of longitude and rainfall on male body size and form, well known to physical anthropologists (Bergman's rule that body size increases with latitude and Allen's rule that limbs are shorter in relation to trunk length in colder climates), provide some partial support for this view. Among the Ache, hunting efficiency peaks at the average male body height, with shorter and taller men having lower hourly return rates (Hill et al., n.d.). The full impact of the workload required to support multiple young of differing ages is modeled in Figure 5.3, illustrating the cumulative numbers of dependent infants, children, juveniles, and adolescents for Ache and Ju/'hoansi mothers (Gurven and Walker, 2006). The load peaks between the ages of 35 and 40 years but remains substantial well into the mother's fifties, especially in the higher-fertility Ache. Leonard (2003) compares the total energy expenditures and physical activity levels of adult men and women in 11 non-Western groups. For both men and women, rural subsistence groups have the highest expenditure levels. Men of rural subsistence groups have average energy expenditure levels of 12.5 MJ/day, and women, 10.0. When physical activity is compared, men have values of 2.02 PALs (a measure of physical activity levels), compared to 1.83 for women. Furthermore, the declines in physical activity and energy expenditure associated with modernization are more pronounced in men than women. Testosterone is necessary to sustain the physical capacity in musculature, lung, and heart function for such high levels of male labor into the late fifties. Ellison and his associates have found that between the ages of 45 and 60 there is little difference between human populations in male testosterone (I) levels. Figure 5.4 illustrates that the proverbial drop in T levels with aging is found only in groups that start at a very high level, such as males in the United States, and that subsistence populations show little age-related decline compared to U.S. and European men (Ellison et al., 2002; Campbell, Gray, and and Ellison, 2007).

In summary, sexual dimorphism in men and women appears to have direct connections to the sexual division of labor. Human males show

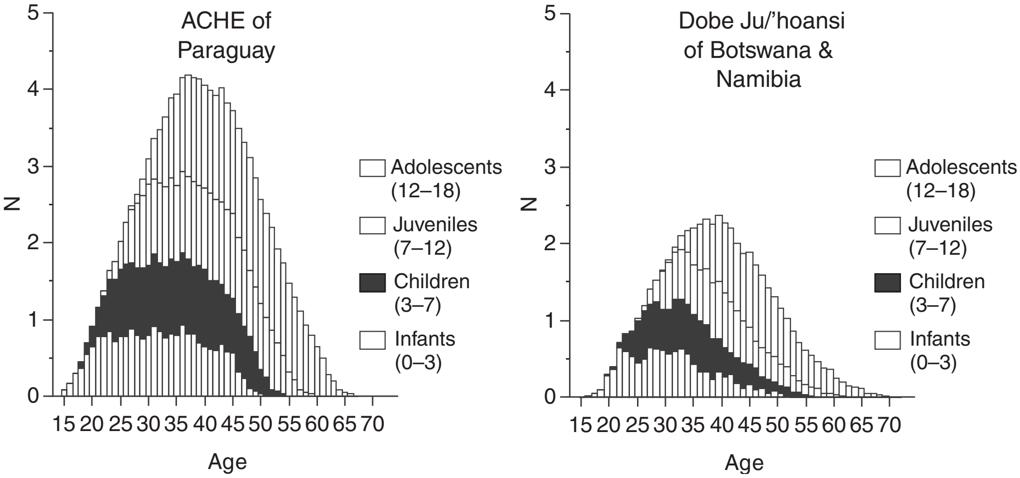

Figure 5.3 Number of dependents at different maternal ages for two forager groups: Ache and Ju/'hoansi *(inset)*. After Gurven and Walker, 2006.

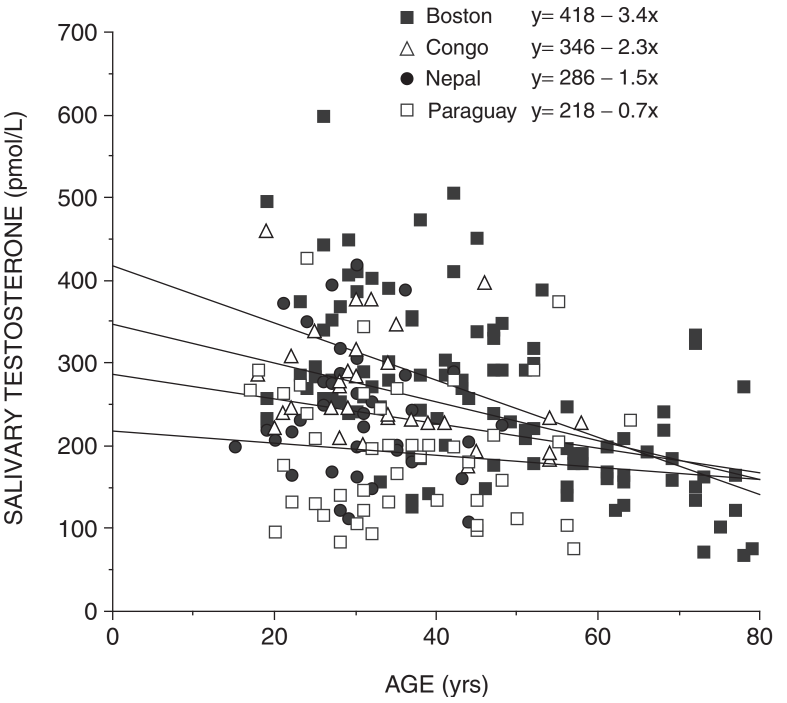

Figure 5.4 Salivary testosterone levels and male aging in the United States and three subsistence societies. Courtesy of P. Ellison.

adaptations for sustained and heavy work effort that facilitates women's care of children and children's learning, whereas women's sexually dimorphic characteristics are based on a lowered work effort during the reproductive years and specialized fat storage depots that support the growth of the human brain.

THE ONTOGENY OF COMPLEMENTARITY IN THE SEXUAL DIVISION OF LABOR

The division of labor allows the two sexes to divide up the productive work so that each can master a single set of complementary skills. Even during infancy, humans display sex-differentiated behavior, and by middle childhood these divergences have become clearly pronounced (Geary, 1998). Aversion to physical proximity with the opposite sex rapidly increases during middle childhood, going from a tolerance of one foot at age 5 to seven feet by age 13. Puberty has the opposite effect. This social segregation is most pronounced in situations where children form their own social groups and are not monitored by adults (Geary, 1998). Preferences for specific activities also exist so that girls may prefer pretend play and boys rough-and-tumble play, which leads to spontaneous segregation by sex (Bjorklund and Pellegrini, 2002). Just as important is the strong preference during middle childhood to associate with same-sex peers, and time spent in social play peaks at this age (Pellegrini and Smith, 1998). The pattern described here suggests that juveniles are preparing for adult behaviors that are not directly related to finding a mate or reproduction. The physiological and behavioral preparations to find and attract mates do not begin in earnest until puberty (Lancaster, 1986). In fact, they would be major distractions to the acquisition and practice of adult foraging skills. A. Campbell (2006) has developed a model in which the physiological event of adrenarche plays an important role in launching a number of years of sex-specific learning. Adrenarche marks the start of middle childhood and is characterized by slowed growth and adrenal production of the steroid dehydroepiandrosterone sulfate (DHEAS) in both sexes. DHEAS levels climb steeply during middle childhood, from about 2 μmol/L to nearly 8 μmol/L by age 14. DHEAS is converted to both testosterone and estradiol by peripheral tissues and is an important source of these hormones before gonadal production at puberty begins. What is particularly interesting is that the level of DHEAS in the two sexes is identical, and it is not until after puberty that males begin to maintain higher levels than females for the rest of their adult lives.

Middle childhood, initiated by adrenarche, is uniquely related to human life history adaptations by serving as a time for juveniles to engage in activities related to sex-specific skills necessary for entry into the adult human ecological and social niche formed by the division of labor. The brain has nearly attained its adult size, suggesting that during middle childhood time and energy are invested in brain maturation or programming rather than in growth. Bock and Johnson (2004) in a study of village children's activities in the Okavango Delta in Botswana found that children play at productive tasks such as grinding maize or catching fish; but as they gain competency in a task, they spend less time playing at it. For example, girls will pretend to grind maize into meal, but as they become more proficient, they spend less time pretending and more time doing. The evolution of the life history phase of middle childhood establishes the time in life when the sex-specific physical, cognitive, and social skills necessary to the adult productive world are established in a developmental context free of the demands of self-feeding and the distractions of reproductive hormones and mate seeking characteristic of adolescence.

Conclusion

Each facet of the human adaptive complex and its component parts is directly related to, and dependent on, the sexual division of labor between of men and women and intergenerational transfers across the life cycle. Unlike other species, the very entrance of *Homo sapiens* into its adaptive niche is based on the specialization of the two sexes in procuring food from two different levels of the food chain, a separate allocation of risk taking and care of young, the feeding of juveniles, and food sharing that widens the diet of both sexes and reduces variability in the food supply. Consonant with the investment in the acquisition of specialized and complementary skill sets by the two sexes is a long life course characterized by a long period of dependence in the first part of life and an even longer adulthood characterized by high production and transfers to children and grandchildren.

It should not be surprising, then, that we should find sex-specific adaptations in physiology and biology that reflect this mutual interdependence and stabilize such critical relationships. In this chapter, we have focused on four aspects of these adaptations: the stabilizing effect of offspring on (1) parental relationships and on (2) mate choice preferences; (3) complementarity in sexual dimorphism; and (4) the evolution of middle childhood, a uniquely human stage of development in which sex-specific skills are acquired free of the burden of growth and self-feeding and the distractions of pubertal hormones and adolescent mate seeking.

The relationships among skill investments, the long human life span, and intergenerational transfers have been the focus of several other papers by the authors and their collaborators (Kaplan, 1997; Kaplan and Lancaster, 2000; Kaplan et al., 2000. Lancaster et al., 2000; Kaplan and Robson, 2002; Robson and Kaplan, 2003; Gurven and Kaplan, 2006). We expect a similar sensitivity to life stage in the hormonal regulation of physiology and behavior and that the optimal mix of investments in survival, maintenance, and reproductive effort will reflect selection to reach the grandparental phase of the human life cycle. This could be the subject of another chapter.

Human evolutionary ecology identifies differences between human groups as largely environmentally induced variation in the expression of basically similar genotypes. This view sees facultative responses to environmental differences as the essential human adaptation to socioecological variation and change. Much of the discussion of this chapter has focused on the original human adaptive complex. However, we know there have been major socioecological changes since humans claimed some 50,000 years ago the top of the food chain as their own by means of a restructuring of the human life course and the relationship between the sexes (Lancaster and Kaplan, 1992). Paramount among these are (1) the development of extrasomatic wealth and the monopolization thereof that led first to variance in male quality and then to social stratification, (2) the growth of technology that reduces the value of sexual dimorphism in the division of labor by making male and female labor and skill sets substitutable, and (3) a reduction in fertility and family size so that active reproduction and child care compose increasingly smaller portions of the total human life span. Certainly these trends are not universal, but they are increasingly felt in world societies.

In spite of these major shifts in human experience, critical features of human reproductive partnerships such as marriage, sexual commitment, and the dedication of adults to rear offspring continue. In the Western world, monogamy has lost many of its variants such as concubinage and minor secondary families (Betzig, 1986, 1992, 1993, 1995; Betzig and Weber, 1993). Parental investment strategies have also shifted toward greater focus on the endowment of embodied capital through education and training rather than inheritance (Lancaster, 1997; Kaplan and Lancaster, 2000; Lancaster et al., 2000). The embodiment of capital appears to be much more labor-intensive than is immediately obvious. Although Western societies have focused on universal education provided at all levels, school attendance does not ensure education. Parental involvement is now recognized as a key feature in child educational development, and parental time and commitment are not readily shared between families (Kaplan, Lancaster, and Anderson, 1998; Anderson, Kaplan, and Lancaster, 1999, 2001, 2007; Anderson, 2000). While the socioecological context of the original evolution of the human adaptive complex has radically altered, the life history and reproductive patterns of the division of labor (marriage partnerships and parental investment) are still in place, along with the endocrinology and biology that support them.

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