This essay considers human brain evolution in terms of a larger set of co-evolved traits, to which we refer as the human adaptive complex (HAC). The embodied capital theory of human life history evolution explains the evolution of human brain size, development, and function as components of a co-adapted complex of traits, including (a) the life history of development, aging and longevity, (b) diet and dietary physiology, (c) energetics of reproduction, and (d) social relationships among men and women, (e) inter-generational resource transfers, and (f) cooperation among related and unrelated individuals (Kaplan 1997; Kaplan et al. 2000, 2001, 2003; 2006; Kaplan and Robson 2002; Kaplan and Gurven 2005; Gurven and Walker 2006; Gurven and Kaplan 2006; Gurven et al. 2006, Robson and Kaplan 2003).

According to the theory, the HAC is a very specialized niche, characterized by 1) the highest-quality, most nutrient-dense, largest package size, food resources; 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 lifespan 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) bi-parental investment with men specializing in energetic support and women combining energetic support with direct care of children; 8) marriage and long term reproductive unions; 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.

In the publications cited above, we show that the majority of the foods consumed by contemporary hunter-gatherers worldwide are calorically-dense hunted and extracted (taken from a protected substrated – under ground, in shells, etc) resources, respectively accounting for 60% and 35% of calories, respectively. Extractive foraging and hunting proficiency generally does not peak until the mid-thirties, 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 20s. 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 lifespan. Among hunter-gatherers without access to western medicine, people can expect to live about 40 more years if they survive age 15, and an additional two decades if they survive to age 45. Chimpanzees, our closest living relative, can only expect to live to age 27 if they survive to age 15. Parents and grandparents finance the juvenile learning phase through food transfers.

Those data, and cross-species analyses of primate brain size and life history (e.g. Kaplan et al. 2003; Kaplan et al in press) provide substantial support for learning-based, dietary (ecological) theories of primate brain expansion, and for the co-evolution of age of first reproduction, longevity and brain size. There are, however, alternative social models of brain expansion. The social brain hypothesis (e.g. Byrne 1995, e.g. Dunbar 1998) is generally
formulated as the evolution of *Machiavellian intelligence* in response to a social arms-race of political maneuvering and information manipulation in large groups. Recently, a signaling version of the social hypothesis has been proposed in which selection for intelligence derives from its ability to signal mutational load in mating competition (Miller, this volume).

In this paper, we develop embodied capital theory to include social capital. In doing so, our goal is to incorporate both social and ecological forces in brain evolution in a unified theory of the HAC.

**Cooperation and the human adaptive complex**

Human food acquisition is inherently social in a number of ways. First, the mix of hunting and gathering in which people engage in order to maximize the rate of nutrient gain per unit effort results in a division of labor by sex (and, to some extent, by age). The human commitment to carrying, rather than caching, children and to providing high quality childcare (a trait shared throughout the primate order) is incompatible with hunting, as it is practiced by humans, because it involves long distance walking and often dangerous pursuits. As a result, in all foraging groups, women allocate the majority of their time to gathering and childcare and men to hunting (although the exact mix depends on ecology). Associated with this division of labor is the practice of marriage and family formation. All human groups recognize marriage, as a bond which regulates sexual activity (especially of women), in which a man and a woman form a cooperative bond in raising children. This bond is generally characterized by intensive food sharing within the family, and a division of labor in the organization of other household tasks and the care of children. Moreover, in foraging groups, the reproductive careers of men and women are highly linked. While divorce is common in many foraging groups, most couples tend to have the majority of their children together, and men often have their last child when their wives reach menopause. The relationship between men and women in foraging societies is arguably the most intense and multi-faceted cooperative relationship in which they engage.

Second, social learning plays a critical role in the intergenerational transmission of knowledge and practices. Moreover, social learning probably increases the rate at which human children, adolescents and adults learn how to hunt and gather efficiently (Blurton Jones and Marlowe, 2002). Forager children and adolescents have years of experience listening to others tell stories and anecdotes about different foraging activities before ever seriously engaging in these activities themselves. In nonhuman primates, the frequency of social transmission of information strongly predicts wide-ranging variation in primate brain size, and most of this information pertains to foraging (Reader and Laland 2002).

A third characteristic is that human diets are inherently risky and food sharing is a fundamental component of the HAC. At the individual level, foraging luck is often highly variable. Hunting, in particular, can produce highly variable returns, especially in the case of large game. Food sharing among families is practiced by foragers, in order to even out the daily food supply and buffer against the risk associated with large, mobile packages of food. A social brain also becomes increasingly important in the context of strategic sharing of game (Stanford 1999). For example, efficient sharing requires the monitoring of meat and other contributions made by other group members.

Fourth, human foraging, especially hunting, is often more effectively done in cooperative groups. Many species can be prevented from escaping predation by groups of cooperating hunters. In cooperative foraging activities, individual roles are often well specified, and the coordination is intentional and consciously understood by all members of the cooperative party.
When all of this is put together, the complexity and intensity of human cooperative relationships, especially among nonkin, such as spouses and friends, is unparalleled. Cooperation is risky and fragile, because the possibility of defection always looms in the background. As a result, choice in partners and in the contexts in which to cooperate can have profound effects on peoples lives and therefore puts a large premium on intelligence.

**Social capital and the competitive market for cooperators**

Here, we introduce the concept of *social capital*, borrowed from sociology and economics, to evolutionary discourse, and then apply it to HAC. While social capital has been traditionally thought of as the web of connections that one attains through family and friends (Coleman 1988, Putnam 2000), Lin (1999) provides an individually-based definition of social capital as, “*investment in social relations with expected returns.*” We offer a somewhat modified definition, *information or perceptions embodied in other individuals with expected fitness returns through its effects on social interactions.*

In the case of nonhuman primates social capital is mainly in the form of information about dominance relations, and sexual/reproductive states or qualities. For example, the social capital for dominant individuals is information stored in the brains of subordinates, based on a history of previous interactions. Dominants can expect a return on this capital to the extent that this information affects the behavior of subordinates. As a result, dominants can often obtain priority access to a feeding site or sexual partner with a simple facial or bodily gesture.

**The Human case: Social capital and access to resources**

Our proposal is that in traditional human groups social capital investment is of tremendous significance and cognitively demanding, exerting considerable selective force on human psychology and intelligence. Social capital, however, plays a different role in people’s lives than in nonhuman primates, because of the special features of the HAC described above.

There is increasing evidence that food is not shared equally to all band members in most hunting and gathering societies, except under specific circumstances (Gurven 2004). People have preferred partners, in which reciprocal exchange is greatest. The most common social arrangement appears to be one of variably-sized food distribution networks, depending on the food resource and its means of obtainment. In many groups, there is evidence of significant producer control over sharing and limited scope of partners. For example, among Hiwi foragers, hunters tend to exercise control over how much and to whom they share meat, restricting those who receive shares to some 15-20% of potential recipients in large groups (Gurven et al. 2000). Thus, there is a potential market for cooperative partners. The ability to engage in profitable partnerships may require a great deal of social intelligence, and the ability to understand how one’s actions will affect future access to food and food exchange.

This logic may explain why humans commonly cooperate in experimental games and punish defectors (Henrich et al. 2001). The tendency to cooperate on the first move allows people to experience greater gains from cooperation and to demonstrate their quality as potential cooperators in future interactions. People have a moral approach to these problems because a more Machiavellian approach, which would take advantage of all opportunities for defection in one-shot games, is outcompeted by a moral psychology when there is uncertainty about the possibility of being detected as a defector and the costs of being labeled as a cheater have great long-term consequences. Potentially, runaway selection on the ability to detect subtle signs of a Machiavellian strategy in the context of a food acquisition strategy that depends on cooperation
and sharing may have been of great importance in the evolution of social intelligence and moral reasoning.

Human psychological traits and social norms of sharing are likely reflect the relative strengths of two opposing forces: gains from cooperation and possibilities for free-riding (Tooby, Cosmides, and Price 2006). Those opposing forces may have led to the evolution of some general moral sentiments, supported both by the emotional/motivational psychology of individuals and common cultural norms. This reasoning predicts that natural selection has shaped our psychology to possess the following traits: 1) perceptual sensitivity to potential gains from cooperation; 2) motivation to take advantage of those gains; 3) perceptual sensitivity to opportunities for free-riding; 4) motivation to avoid being free-rode upon; 5) motivation to take advantage of opportunities for free-riding; 6) perceptual sensitivity to the short and long-term personal costs and benefits of social norms regarding cooperative behavior (from the perspectives of both self and others); 7) motivation to negotiate social norms so that personal benefits from cooperation and free-riding are maximized; 8) motivation to obey and enforce social norms so that punishment is avoided and those who disobey norms or fail to enforce them are punished.

Social Capital, Mating and Marriage

Human marriage is probably the most complex cooperative relationship in which we engage. It involves the production and processing of resources for familial consumption, distribution of those resources, the provision of childcare, 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. In traditional societies, like our own, it is not uncommon to hear remarks about success and failure in coordinating and getting along as comments about why marriages succeeded and failed.

A problem that people face in mate choice is that long term dependency and multiple dependency make mate-switching more costly for humans. 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 marriage age of around 20, Ache and Tsimane men are only 25% and 50%, respectively, as proficient hunters as they will be at their peak in their mid to late thirties.

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. And, for the most part, it is a long term choice with direct consequences for fitness. It is further complicated by the fact that not only do partners contribute to fitness through behavior, but also through genetic inputs, which can lead to both 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 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.

Such considerations leave ample scope for display behavior. Thus, while, over the long run, the primary motivation for economic production may be the raising of a family, symbolic forms of production and sharing may be important investments in social capital. Some proportion
of food sharing behavior is likely to be symbolic investments in social capital affecting future cooperative interactions. Importantly, as emphasized by others (Bird 1999, Hawkes 1990, Smith 2004), displays of hunting competence and generosity may play an important role in mating success. In fact, many foraging and forager-horticulturalist societies, such as the 'Kung and the Tsimane, practice brideservice, in which young men hunt to feed their future father-in-law’s family prior to having full marital rights.

Moreover, since, for reasons discussed above, intelligence and cognitive ability are likely to be important in food production, social access to shared food, and efficient childcare, we might expect young men and women to invest in social capital through displays of social and ecological intelligence. We might also expect people to be very discriminating in their appreciation of those displays. In addition, as discussed by Miller, to the extent that such displays are honest advertisements of genetic fitness and mutational load, there would be another incentive to engage in and discriminate among displays.

CONCLUSION

Our proposal is that ecological and social intelligence, coupled with specific psychological characteristics, are fundamental components of the human adaptive complex. This psychology, the complex analytical brain, and the extended life history co-evolved in the hominid line, all because of the dietary shift towards large, high quality food packages and division of labor in food production and childcare. It is this feeding adaptation that generates gains from cooperation. In this sense, both social and foraging intelligence are ecologically determined.

Cooperative strategies, however, also entail gains from, and risks of, defections. This places a premium on decisions about when and with whom to cooperate. Behaviors that facilitate being selected as a cooperative partner may have played a great role in individual and family food consumption patterns. Given that marriage is a fragile and complex human social relationship, we should expect that it has played an important role in shaping both our intelligence and our psychological characteristics.

With respect to timing, several alternative scenarios may be distinguished. One possibility is that the ability to engage in abstract logical reasoning evolved in response to the cognitive demands of tool-based extractive foraging and knowledge-based hunting (Lieberman 1990). Those internal symbolic abilities established a cognitive infrastructural pre-adaptation for symbolically based communication. Alternatively, the gains from cooperation may have set the stage for the evolution of symbolically-based communication systems that, in turn, served as a cognitive pre-adaptation for the evolution of abstract logical reasoning and its application to the food quest. Verbal language, via gossip and coordination communication, may also have played a large role in this adaptive complex (Alvard and Nolin 2002). A third possibility is a gradual, ratcheting co-evolutionary process, as described for the co-adaptation of life history, parental investment, and brain size. In addition, some of the cognitive substrates for solving economic and social problems may be shared. For example, inferences about animal behavior, such as their likely escape strategy if the hunter’s presence is detected, are critical for hunting success. Animal ‘mind-reading’ and human mind-reading may involve similar cognitive abilities, including the ability to discriminate among types of minds (deer, child, adult friend, adult enemy, etc.). To the extent that such substrates are shared, selection would act on the total effects of increased abilities, summed over all routes through which those abilities affect fitness. Distinguishing among such possible sequences is another difficult challenge facing human evolutionary
scientists. The abilities to scenario-build in solving both foraging and social problems, and to engage in high-level abstract logical reason appear to have evolved in one lineage only. Perhaps, our species is an outlier, precisely because the human adaptive complex demands both ecological and social intelligence.
References


