

Chapter 10

PHYSICAL ATTRACTIVENESS IN ADAPTATIONIST PERSPECTIVE

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The literature on human attractiveness spans the sciences, social sciences, and humanities, and dates back at least to the time of Plato. Consequently, scholars across the disciplines have proposed and investigated a variety of ideas about what makes some people more or less attractive than others (e.g., Etcoff, 1999). Addressing this vast literature from an adaptationist perspective is well beyond the scope of this chapter. This chapter limits itself to (1) outlining an adaptationist perspective on physical attractiveness, (2) presenting the basic questions that this perspective leads us to ask, (3) reviewing some important empirical advances in the answering of these questions, and (4) highlighting research avenues calling for increased attention. I argue that human physical attractiveness assessment is generated by adaptations functioning to evaluate evolutionarily relevant cues to human social value across multiple domains of interaction (e.g., kin, mating, cooperation) and that evolutionary human life history theory and data from small-scale foraging societies are instrumental in generating predictions about these domains of social value and the cues associated with them. Multiple, converging lines of evidence are useful to test whether a given phenotypic trait is an adaptation (e.g., Symons, 1989; Tooby & Cosmides, 1990, 1992). In the case of complex adaptations (e.g., immune systems, social exchange reasoning, or attractiveness-assessment psychologies), the most compelling case is made when there is evidence that: (1) the species in question recurrently faced a particular adaptive problem during recent evolutionary history, (2) the structure in question has a complex functional design that is so improbably well-suited to solving that adaptive problem that we are forced to reject pure chance as an alternative hypothesis, and (3) the organism in question shares with all normal conspecifics that design or a facultative developmental program that builds that design.

Attractiveness Assessments as Measures of Social Value

We are powerfully attracted by some features (e.g., breasts, biceps, buttocks, lips, teeth) but less so by others (e.g., elbows, pinky fingers). We are repulsed by slightly different versions of things we are attracted to (e.g., wrinkled as opposed to smooth skin). Why do we find some features attractive and others not? The answer lies in what our preferences and revulsions cause us to do. Preference mechanisms motivate us to engage in behaviors that tended to increase fitness under the environmental conditions in which they were selected: Eating ripe fruit supplied our bodies with vital calories and nutrients; copulating with sexually mature conspecifics of the opposite sex increased our chances of reproducing. Conversely, revulsions discourage us from engaging in behaviors that were detrimental to survival and/or reproduction: Avoiding fetid swamps reduced our chances of contracting insect- or water-borne disease; being wary of snakes reduced our chances of being bitten by them. In short, preferences evolved because they increased the probability of an individual interacting with a stimulus in ways that tended to increase the distribution of the suite of alleles linked with that preference (Buss, 1992; Symons, 1979; Thornhill, 2003).

Attractiveness was a factor in many choices our ancestors had to make in daily life: what to eat, where to camp, with whom to ally themselves or mate. Each task involved a different adaptive problem and stimulus. In choosing a camp, for example, an individual would prefer a clear, level area with protective cover and good views in all directions, located near drinking water and plant and animal resources, and relatively free of pests (e.g., Appleton, 1975, 1984; Kaplan, 1992; Orians, 1980; Orians & Heerwagen, 1992). When choosing an ally, an individual would prefer good health, vigor, intelligence, generosity, reliability, and loyalty. Different suites of preference mechanisms are expected to have evolved in response to different adaptive problems and the stimuli associated with them. Because the cues associated with the relevant fitness-promoting aspects of ancestral environments varied from task to task, each preference suite is expected to target a different set of cues (although there may be some overlap between suites; see later discussion). Within each suite, selection is

expected to have produced different assessment and preference mechanisms in response to each cue (e.g., Buss, 1992, Symons, 1979, 1995; Thornhill, 2003; Tooby & Cosmides, 1992; Sugiyama, 1996, 2004a). Thus, there is no general definition of attractiveness that applies to all stimuli. Consider sexual attraction: If we chose mates using the criteria for choosing food, we would find tubers, grubs, and buffalo as sexually arousing as healthy, fit, sexually mature members of our own species, and we would rapidly approach extinction.

Individuals may be attracted to objects that exhibit cues that were associated with a fitness-enhancing object under ancestral conditions but lack the fitness-enhancing properties themselves (Symons, 1987; Tooby & Cosmides, 1990). For example, our nonhuman primate and hominid ancestors lived in a world in which sweetness was a statistically reliable cue of nutritious, energy-packed foods (e.g., fruit, honey); consequently, our ancestors evolved a preference for sweetness, which motivated them to consume these healthy foods. Our preference psychology continues to attract us to sweet foods, but this often prompts a trip to the pastry shop instead of the fruit stand, a decidedly fitness-decreasing behavior (Eaton et al., 1988; Nesse & Williams, 1994).

Individuals may also be attracted to cues that have not been under selection *per se*. For example, finches have species-typical mate preferences for the color of bands put on their legs by researchers. Female zebra finches exhibit mate preferences for males with red rather than blue leg bands, while double-bar finches prefer light blue over red bands (Burley et al., 1982; Burley, 1986). At least some of these preferences appear to be a byproduct of species-recognition mechanisms, since both double-bar and zebra finches prefer colors similar to their own species' plumage. Humans are certain to exhibit similar nonfunctional preferences, and complete understanding of human attractiveness will need to distinguish these preferences. However, because we lack principled guidelines for predicting such nonfunctional preferences, this chapter focuses primarily on hypothesized functional preferences whose features can potentially be predicted.

A leading alternate explanation of human attractiveness assessments is that our "capacity for culture" or a general-purpose learning psychology allows society, culture,

or the media to tell us which sex to desire and/or what features are attractive (for discussion see Pinker, 2002; Tooby & Cosmides, 1992). On this view, who and what are attractive varies arbitrarily across cultures, individuals assess the physical attractiveness of both sexes based on local cultural dictates, and they tend to prefer the sex that society tells them to. If this view were correct, standards of attractiveness would vary randomly across the cultural and geographic landscapes of human experience. They do not (e.g., Buss, 1987; Cunningham et al., 2002; Langlois & Roggman, 1990; Rubenstein et al., 2002; Jones & Hill, 1993; Sugiyama, 2004a; Symons, 1979, 1995).

There is considerable cross-cultural agreement on which faces are more attractive (e.g., Cunningham et al., 2002; Dion, 2002; Langlois & Roggman, 1990; Langlois et al., 1991; Thornhill & Gangestad, 1993; Rubenstein et al., 2002; Zebrowitz, 1997). Galton (1879) noted that composite faces constructed by superimposing several individual photographs were more attractive than the faces from which they were made. Symons (1979) proposed that attractiveness-assessment mechanisms take as input the faces observed, then average those faces to produce templates of female and male facial attractiveness. All else equal, deviations from these templates decrease attractiveness. He reasoned that “the local populations’ central tendency often approximates the naturally selected optimal design; hence selection is expected to have favored the ability to detect and prefer the central tendency” (Symons, 1995, p. 97). To test this hypothesis, Langlois and Roggman (1990) created computer-generated composites of up to 32 faces: Composites were rated more attractive than almost any of the individual faces from which they were made, and the more faces used in the composite, the more attractive the face was found (see also Rhodes et al., 1999; Rhodes & Tremewan, 1996; Jones & Hill, 1993 [Aché]; Rhodes et al., 2002 [Japanese]; Pollard, 1995; Rubenstein et al., 1997). Local population average is only one dimension of facial attractiveness. Subsequent research shows that facial attractiveness-assessment mechanisms may produce attraction to predictable deviations from the central tendency (e.g., Alley & Cunningham, 1991; Johnston & Franklin, 1993; Perrett et al., 1994; Symons, 1995), and Symons has modified his hypothesis accordingly (1995). It is nevertheless clear that “averageness” is a cross-

culturally recurrent feature affecting some of the variance in facial attractiveness assessment.

Perceptions of facial attractiveness emerge early in life in ways not easily explained by cultural learning theories. In a series of studies with children ranging in age from newborn to 25 months, infants noticed and preferred faces similar to those judged attractive by adults. Subjects were simultaneously presented with two faces; time spent gazing at each was recorded as a measure of attraction. Beginning at a few days old, infants look longer at faces that adults rated attractive than at those adults rated unattractive (Kramer et al., 1995; Rubenstein et al., 1999; Samuels & Ewy, 1985; Slater et al., 1998), regardless of whether the faces were Asian, African American, or Caucasian (Langlois et al., 1987; Langlois et al., 1991). Babies also more frequently avoided and showed distress in response to an experimental confederate wearing an unattractive mask, but boys more often approached the confederate when she wore an attractive mask (Langlois et al., 1990).

Human Life History and the Domains of Social Value

Humans are an intensely social species, and our conspecifics are valuable to us for purposes other than mating (e.g., Sugiyama & Chacon, 2000; Sugiyama & Scalise Sugiyama, 2003; Tooby & Cosmides, 1996). Human evolutionary life history provides the key to understanding different domains of human social value (i.e., the value of individuals as potential interactants) and the physical cues correlated with them. Human survival and reproduction are dependent on solving adaptive problems associated with social interactions in four partially overlapping realms: reproductive, kin, cooperative, and coalitional relationships. Some individuals are more valuable to ego than others (e.g., as kin, mates, allies). Individuals who were attracted to individuals exhibiting relevant cues of high social value would have been more successful than those who were less discriminating. Human attractiveness-assessment psychology is therefore expected to index the social value of a potential partner using criteria correlated with the relevant category (e.g., descendant, mate, ally), depending on context. In other words, cute, sexy, handsome, and dominant are not exactly the same, and each appears to reflect a different aspect of social value (e.g., Cunningham et al., 1997; Keating,

2002; Zebrowitz & Rhodes, 2002). The question of how different attractiveness adaptations relate to each other and to different aspects of social value will be central to the next generation of adaptationist investigations of attractiveness. Anomalous findings and individual differences in attractiveness assessments may well resolve under this approach.

Scholars disagree about when and why key features of modern human life history came about (e.g., Hawkes et al., 1998; Kaplan et al., 2000; Flinn et al., 2005), but certain facts are clear: Humans have delayed reproduction; long life span; biparental investment; intergenerational care and provisioning of weaned juveniles and adults; coalitional child rearing, aggression, and foraging; and intense investment in skill and knowledge acquisition (e.g., Flinn et al., 2005; Hawkes et al., 2000; Hill & Kaplan, 1999; Hrdy, 1999; Kaplan et al., 2000; Tooby & DeVore, 1987). Human mating is flexible, exhibiting both long- and short-term mateships, serial monogamy, and a mild degree of polygyny (e.g., Beckerman & Valentine, 2002; Buss & Schmitt, 1993; Daly & Wilson, 1987; Fisher 1992; Lancaster & Kaplan, 1994; van den Berghe, 1979). Extra-pair copulations also occur (e.g., Buss, 2000; Fisher 1992; Chagnon, 1997; Thornhill & Gangestad, 2003). In small-scale societies, adult mortality is such that individuals frequently have multiple mates over their lifetime, and many children do not reside with both biological parents (e.g., Chagnon, 1997; Hill & Hurtado, 1996; Howell, 1979; Sugiyama, in press). Adults discriminate in their allocation of parental investment in juveniles depending on paternal certainty, phenotypic state of the juvenile, and local environmental parameters (e.g., Blurton Jones et al., 1997; Hewlett, 1992; Hrdy, 1999; Gelles & Lancaster, 1987; Marlowe, 1999a, b, 2001). Lethal and sublethal violence between individuals and coalitions are also recurrent features of human existence across societies (e.g., Chagnon, 1988, 1997; Daly & Wilson, 1988; Descola, 1998; Ember & Ember, 1997; Hill & Hurtado, 1996; Keeley, 1996; Martin & Frayer, 1997;). Evolution of each of these features of human life history presented our ancestors with numerous adaptive problems.

Life history theory examines how natural selection produced age-related allocation of resources between somatic (growth and maintenance) and reproductive (mating and parenting) effort (e.g., Charnov, 1993; Charnov & Schaffer, 1973; Hill &

Hurtado, 1996; MacArthur & Wilson, 1967; Schaffer, 1974; Williams, 1966). Within a species' typical life history pattern, selection produces suites of reproductive, decision-making, and other motivational adaptations that generate adaptively "strategic" (usually unconscious) trade-offs in life effort in response to evolutionarily relevant environmental variables (e.g., Chisholm, 1993; Clutton-Brock, 1991; Daly & Wilson, 1984; Hill & Hurtado, 1996; Stearns, 1992; Trivers, 1972, 1974). Determining how individuals use local environmental cues to adjust their allocation of life resources is a main goal of understanding variation within a species' general life history parameters (e.g., Belsky, 1997; Betzig et al., 1988; Blurton Jones et al., 1994; Draper & Harpending, 1982; Hill & Hurtado, 1996; Sugiyama, in press). Attractiveness-assessment mechanisms are a crucial component of the psychology involved in the processing of socioenvironmental cues relevant to the adaptive problems inherent in the life history traits listed earlier.

Mate Value

Reproductive effort includes identifying and acquiring mates. People differ in mate value, defined as the degree to which an individual would promote the reproductive success of another individual by mating with him or her. For example, copulation with an 8-year-old is ineffectual for reproduction; copulation with carriers of contagious disease is dangerous; copulation with individuals bearing severe genetic anomalies could result in costly pregnancies that produce nonviable offspring. Human mate value includes not only current fertility and fecundity but also reproductive value—the probable number of future offspring a person of a certain age and sex will produce. Over time, selection would spread genes that organized developmental properties motivating individuals to be attracted to conspecifics exhibiting cues of high mate value because these preferences likely led to more successful reproduction than alternative designs that may have arisen.

Components of human mate value appear to include phenotypic qualities such as health, fertility, fecundity, age, intelligence, status, parenting skill, kindness, and willingness and ability to invest in offspring (Buss, 1989; Gangestad & Simpson, 2000; Symons, 1979, 1992, 1995; Thornhill & Gangestad, 1999). Some variance in phenotypic

qualities is heritable; therefore, some aspects of phenotypic quality may reflect underlying genotypic quality. Our mate-selection psychology must assess a potential mate for cues associated with each of these components, weigh their relative importance under current conditions, and then integrate these inputs to arrive at a comprehensive estimation of mate value (Buss, 1994; Miller, 2000; Symons, 1995; Sugiyama, 2004a). Some cues to mate value are physically observable, and the sum of these assessments contributes to our perception of potential mates' "physical attractiveness." Some features associated with high male mate value differ from those associated with high female mate value; criteria of male and female attractiveness are expected to differ when this is the case (e.g., Buss, 1987; Daly & Wilson, 1987; Symons, 1979, 1995).

Because individuals differ in the degree to which they possess the qualities associated with high mate value, some individuals make better mates than others. The result is competition for access to mates, especially high-quality mates. Darwin referred to the selective force created by this competition as sexual selection and identified two types. <I>Intrasexual selection</I> is the process whereby traits are selected that enable individuals to compete with members of the same sex for sexual access to the opposite sex (e.g., antlers, horns, tusks). <I>Intersexual selection</I> is the process whereby individuals with a given trait are preferred by the opposite sex as mating partners, with the result that said trait is spread, elaborated, or maintained in the population even if it has no survival value (e.g., Daly & Wilson, 1987; Darwin, 1872; Fisher, 1958; Miller, 2000; Ridley, 1993; Symons, 1979).

Costly signaling theory (also known as the handicap principle) posits that traits associated with good genes or the provision of material benefits can evolve into elaborate displays. On this view, elaborate displays can evolve as "honest" signals about underlying phenotypic and genotypic qualities of their bearers (Zahavi & Zahavi, 1997). When a trait signals information about its bearer that is useful for the bearer to transmit and for the recipient to receive, false signals might also be selected for, undermining the signal value of the trait to both sender and receiver. However, if the cost of sending the signal is such that only some individuals can afford to fully develop it and that cost is linked to the underlying phenotypic or genotypic quality being signaled,

recipients can be assured of the signal's "honesty." Elaborate anatomical features, such as the peacock's tail, could evolve this way: Only high-quality males can produce the finest displays, so hens can reliably use male display in their mate choices, and the cost of the display to the cock is offset by his increased mating opportunities. Handicap signals are not restricted to mating: They can evolve whenever the conditions of costly signaling are met.

Because mating competition can be costly, it is often to an individual's advantage to assess the relative mate value of potential rivals before competing with them. Ancestral males capable of doing this could save time and energy by forgoing, avoiding, or subverting competition with those rivals they were unlikely to outcompete. Conversely, ancestral males could increase their mating access by focusing energies on driving off, dominating, outshining, undermining, or stealing mates from rivals against whom they had a reasonable chance of success. Similar benefits would accrue to females able to assess their competition and respond accordingly (e.g., Buss, 1994, 2000; Hess & Hagen, 2002; Pawlowski & Dunbar, 1999). This assessment amounts to an evaluation of the attractiveness of the same sex—not for the purpose of mating but to assess an individual's relative mate value (Pawlowski & Dunbar, 1999). Men are expected to use cues associated with male mate value to assess the fitness of their rivals, and women are expected to use cues associated with female mate value to assess the fitness of their rivals. Male and female assessments of a given individual's sexual attractiveness will, therefore, often concur, regardless of that individual's sex. ^It follows that assessment and preference psychology are integrated but separable components of attractiveness psychology. In assessments of male sexual attractiveness, for example, women might experience feelings of desire (if the male were judged attractive), repugnance (if the male were judged unattractive), or indifference. In contrast, we might expect men to experience feelings such as submissiveness (if the male were judged attractive and dominant) or self-confidence and dominance (if the male were judged unattractive). Men and women have different adaptive objectives when evaluating the sexual attractiveness of a given male. Men must decide whether they should provoke, avoid a confrontation with, or cooperate with another male, and have, therefore, been under selection to evaluate the prowess of

other males vis-à-vis their own. Women must decide whether they should copulate with, ally themselves with, or avoid a given male, and have, therefore, been under selection to evaluate males in terms of the fitness costs and benefits they present as mates and fathers. When it comes to evaluating female attractiveness, the tables are turned. Men must decide whether they should copulate with, cooperate with, or avoid a given female, and have, therefore, been under selection to evaluate females in terms of their fertility and sexual accessibility. Women must decide whether they should provoke, avoid a confrontation with, or befriend another female, and have, therefore, been under selection to evaluate the attractiveness and dominance of other females vis-à-vis their own.

Areas where we would expect to find sex differences in attractiveness assessment include the relative importance placed on different physical attractiveness cues. Overall, men place more value on good looks in a long-term mate than do women because female mate value is very closely linked to physiological condition (e.g., Buss, 1989; Buss & Schmitt, 1993; Symons, 1979, and see later discussion). Men may focus more on cues associated with potential rivals' physical formidability and dominance—size, strength, speed, physical agility, or their correlates—in assessing their own and their competitors' relative sexual attractiveness to women because these attributes could spell death or loss of a mate at the hands of a rival (e.g., Chagnon, 1988, 1997; Daly & Wilson, 1988). A host of data from psychological studies (e.g., Buss et al., 1992; Dijkstra & Buunk, 2001), homicide patterns (e.g., Daly & Wilson, 1988), and intratribal conflict (e.g., Chagnon, 1979, 1988, 1997) support the view that various aspects of mating competition are often causes of violence. For women, male mate value includes both: traits associated with genetic quality, health, and physical formidability, and traits associated with ability and willingness to invest in a woman and her offspring (e.g., Buss, 1987; Symons, 1979). Assessments based on these two criteria may diverge. Good looks appear to be relatively less important for women than for men in long-term mates because most women may have to trade off genetic quality and health for investment. However, these trade-offs are context-dependent: Women place more importance on physical characteristics in short-term and extra-pair sex partners (Buss & Schmitt, 1993; Greiling & Buss, 2000) and during the fertile phase of

their ovulatory cycles. Women show increased preference for “masculine” male faces in prospective short-term mates (angular, deep brow; square jaw) but for less “masculine” male faces (softer, rounder) in a long-term mate (Penton-Voak et al., 1999; Perret et al., 1998; see later discussion).

Female Mate Value

Female mate value is linked to age, health, fertility, fecundity, and parity (e.g., Buss, 1992; Symons, 1979, 1995). In natural fertility foraging societies, women first give birth at about 17 to 20 years of age (Hill & Hurtado, 1996; Kelly 1995; Kaplan et al., 2000). A woman’s reproductive value—the probable number of future offspring a woman will have—is highest just before she begins fertile ovulatory cycles because she has all her reproductive years in front of her, yet the probability that she will die prior to reproduction is lowest. Fertility—the probability that copulation will result in pregnancy—varies across the reproductive life span. Peak age-specific female fertility in industrialized nations is around 22 years, but the best data from foraging populations indicate a peak age-specific fertility rate varying from about 22 years among the !Kung of Botswana and the Yanomamö of Venezuela to about 28 years among the Aché of Paraguay. Diet, work effort, stress, and social variables affect hormonal indices of female fertility and fecundity (ability to conceive when intercourse occurs during reproductive cycling), suggesting that within the reproductive life span, female reproduction varies with the socioecological contexts in which a woman finds herself (e.g., Ellison, 2001b, 2003 Hill & Hurtado, 1996).

The minimum investment necessary for women’s successful reproduction is high. It includes accumulation of bodily reserves and maintenance of a positive energy balance, gestation, placentation, and the mortality risk associated with bearing a large-headed offspring via a relatively narrow pelvis (e.g., Bentley et al. 1998; Ellison, 2001a; Valeggia & Ellison 2003a; Trevathan, 1987). Nursing, too, is energetically costly (Dewey, 1997). During this time, reproductive function is suppressed as a function of each woman’s relative energy balance (e.g., Ellison, 2001a, b; Jasienska et al., 1998; Valeggia & Ellison, 2001, 2003b). Kelly (1995) lists the average weaning age for each of 30 hunter-gatherer groups: The mean average weaning age for these groups is

30.9 months. The interbirth interval for women in a mostly overlapping group of 11 foraging societies is 3.47 years, and the average total fertility rate is between five and six children. On average, forager women appear to get pregnant relatively soon after weaning the previous child (Kelly 1995).

Women, including forager women, may live well past their reproductive years, although maternal and grand-maternal investment of material and social support in descendants may continue after they reach adulthood (e.g., Hawkes et al., 1998, 2000; Hill & Hurtado, 1996; Hill & Kaplan, 1999; Hrdy, 1999). As a woman ages after menarche, she has progressively lower reproductive value, until fertility ceases altogether. Among Aché women, the average age of last birth is 42. By age 46, the yearly probability of birth is 0 (Hill & Hurtado, 1996). Kelly (1995) lists data on mean age at last birth for women in 10 foraging societies; the average mean is 34.9 years.

The human female reproductive environment of evolutionary adaptedness (EEA) was such that for most of the time between menarche and menopause a woman was not fecund. Based on Yanomamö data, Symons (1995) calculated that an ancestral woman could possibly conceive on just 78 of 8,030 days during her average reproductive life span. Kelly's (1995) data on foragers yield a similar conclusion. With average age at first birth of 17 and last birth by age 42 (for Aché), an average female forager's potential fertile life span is about 25 years, during which she is likely to have five children (Ellison, 2001b). She would have been pregnant or lactating for 5,985 days—almost two-thirds of her reproductive lifetime. With 3 fertile days per month, she could possibly be fecund on just 314 days in her 9125-day fertile lifetime, assuming she suffered no ill health, food constraints, failures of social support, or other stressors. For men, women's reproductive capacity itself is an extremely valuable fitness resource, access to which constitutes a primary constraint on men's relative reproductive success.

Because female reproductive value declines with age postmenarche, cues associated with advancing age are expected to be negatively correlated with female sexual attractiveness (e.g., Buss, 1989; Symons, 1979, 1995). Similarly, with each birth, the average forager woman loses another sixth of her reproductive value, on average. Thus, cues associated with parity are expected to be negatively correlated with female sexual attractiveness. Because some cues to fecundity are observable, selection is also

expected to have produced adaptations to use statistically reliable cues to fecundity-related hormonal status in assessments of female mate attractiveness. Symons (1979, 1995) therefore argues that selection for preferences for cues of high reproductive value resulted in males being attracted to cues of nubility (i.e., female has begun ovulatory cycling but has not yet given birth), as indicated by cues to age, fertility, and parity. Because women do not advertise estrus, attraction to cues of nubility would dramatically increase a male's chances of reproducing, and a man who maintains exclusive mating access to a woman over her reproductive lifetime could on average sire five or six children with her. Finally, women with positive energy balance and good health are likely to be more fertile than those with negative energy balance and poor health; thus, men are expected to have evolved preference mechanisms that find cues of good health and nutrition attractive, and women are expected to use the same cues in assessments of their reproductive rivals. Even though selection may have produced attraction to cues of nubility, attraction to cues of nubility alone might compromise long-term mateships and would have the effect of concentrating male reproductive effort on fathering only the first of a woman's average six offspring. Other cues that a woman is resuming ovulatory cycling postpartum, such as lightening of the skin (Symons, 1995) or having a child approaching weaning age, should predict some of the variance in real-world female sexual attractiveness. Males face investment trade-offs between mate quantity and quality, and between mating and paternal investment. The costs and benefits associated with each will be affected by local paternal effects on offspring fitness and the relative costs and opportunities of obtaining multiple mates. The latter will be affected by a particular male's mate value, the degree of effective polygyny or operational sex ratio, and the relative value of long-term versus short-term mating for women.

Male Mate Value

Women who mate with men with traits associated with high genetic quality are more likely to have high-quality offspring (i.e., via "good genes" sexual selection). Women's attractiveness-assessment psychology is thus predicted to include mechanisms for evaluating cues associated with male genotypic quality. One cue to

genotypic quality is phenotypic condition, part of which is heritable. In addition to genetic quality, male mate value includes provision of material resources to mates, their offspring, and other adults (Gurven et al., 2000; Hewlett, 1992; Kaplan et al., 2000; Marlowe, 1999a, b, 2001; Sugiyama and Chacon 2000, in press). Across societies, women appear to assess and prefer men as long-term mates who evince cues of willingness and ability to invest in a woman and her offspring, such as kindness, intelligence, industriousness, and ability to acquire resources (e.g., Buss, 1989). Female mate choice for these traits is important in humans because of the long period of juvenile dependence and high cost of child rearing. Among the Aché, juveniles with father living suffer a third lower mortality than those whose father has died (Hill & Hurtado, 1996), although the relative contribution of males to their offsprings' fitness varies across social and ecological contexts (e.g., Hewlett, 1992; Marlowe, 1999a, b).

Human males grow for a longer period, mature more slowly, and reproduce later than females (e.g., Bogin, 1999; Ellison, 2001b; Hill & Hurtado, 1996). They also exhibit higher variance in reproductive success across individuals than do females (e.g., Daly & Wilson, 1987; Chagnon, 1997; Hill & Hurtado, 1996). Because paternity is less certain than maternity, men's age at first reproduction is more difficult to track directly, but males in foraging societies typically do begin reproducing later than females, somewhere in their early 20s. Male fertility among the Aché, !Kung, and Yanomamö indicate a rise in fertility beginning in the late teens and peaking in the mid-30s to early 40s. Mean age at last birth for 23 Aché men who lived to at least 60 years old was 48 years: Although about half of the men stopped reproducing as early as women did, the other half continued reproduction for longer periods, including six men who continued reproduction past their mid-50s. Further, male foraging success peaks relatively late in life, around age 40 (Walker et al., 2002). Because male mate value is not so closely linked to youth, female choice is not expected to focus as much on male youth per se, but rather on cues of genotypic and phenotypic quality and productive ability (Buss, 1989; Symons 1979). Selection is expected to have favored female assessment for phenotypic cues of male fertility. However, because one fertile male can potentially inseminate multiple females, preference for cues to fertility per se is perhaps less intense in women than in men.

Women can benefit from pursuing a mix of long- and short-term mating strategies in an effort to reduce trade-offs inherent in each (e.g., Buss & Schmitt, 1993; Thornhill & Gangestad, 2003). From a female perspective, poor health and/or genetic quality are liabilities in any prospective mating partner. However, women are expected to find physical traits linked to underlying genetic qualities relatively more important in short-term than in long-term mates. Long-term mateships entail child rearing; thus, prospective long-term partners must be evaluated for their parenting abilities as well as their physical attributes. Thus, size, strength, pugnacity, and physical dominance may be traded for ability and willingness to invest in the woman and her offspring. For women, parenting skills are less important in a short-term mate for obvious reasons. One ultimate benefit of a short-term mateship to a woman is an opportunity to provide better genes to her offspring than she can acquire through a long-term partner, and many of the traits associated with aggressive formidability—for example, size, strength, endurance—are proximate cues of good genes (e.g., Buss & Schmitt, 1993; Thornhill & Gangestad, 2003). In addition, some physical traits under the influence of testosterone are associated with differences in male mate value that may influence the male's propensity to pursue short- or long-term mating strategies. Females may use these traits as cues to probable male mating behavior. Women may be expected to use these same criteria in their assessments of the relative social value of their fathers, brothers, and other male kin to others, but to weight the criteria differently.

Descendant Value

Juveniles differ in their social value to their parents and grandparents in their probable value as reproductively successful descendants. Parental investment (PI) theory focuses on how individuals allocate resources among existing offspring, current versus future offspring, and quantity versus quality of offspring (e.g., Trivers, 1972, 1974, 1985). In parentally investing species, we expect adaptations that generate parental allocation of resources to juveniles as if in response to three basic criteria: (1) the probability that the juvenile is the adult's progeny, (2) the probability that the juvenile will be able to translate investment into future reproductive success, and (3) the

probable fitness outcomes of alternate potential uses of available resources (Trivers, 1972, 1974).

The probability that an individual is an adult's progeny is partially assessed via adaptations functioning to rapidly learn specific phenotypic (e.g., olfactory, visual, auditory) cues based on early postnatal exposure (Porter, 1991), and there is recent evidence that males may use facial resemblance to themselves to adduce probable paternity. Platek et al. (2002, 2003) found that, when presented with different facial morphs created using each subjects' image and those of children, males were more likely to preferentially choose their own child/face morphs over those created using other subjects' faces as recipients of aid in hypothetical investment scenarios. Functional magnetic resonance imaging indicated that men's and women's neural activation patterns did not differ when viewing non-self-morphs, but did differ when viewing self-morphs, suggesting sex differences in neural processing of facial resemblance cues. In a similar study using color photographs, DeBruine (2004) found that both men and women used facial resemblance in investment decisions, while Apicella and Marlowe (2004) found that men self-reported greater investment in their children when they thought their children bore more resemblance to themselves.

The probability that a juvenile will translate investment into successful reproduction is in part related to his or her genotypic and phenotypic condition and contingent on socioecological context (e.g., Hrdy, 1999). Adaptations are expected that assess these features. Physical cues that were evolutionarily correlated with good health and high genetic quality provide physically observable correlates of a juvenile's probable ability to translate investment into reproduction and are expected to be found attractive in offspring. Physical cues of low genotypic or phenotypic quality are associated with reduction in parental care, suggesting these traits are unattractive to parents. For instance, physical deformity is a recurrent proximate cause for infanticide cross-culturally (Daly & Wilson, 1984); poor physical tone, lethargy, or lack of pedomorphic characteristics in infants may increase risk of abuse (McCabe, 1984, 1988) or maternal neglect when resources are scarce (e.g., Hrdy, 1999); and vocal qualities associated with premature birth are aversive to adults (Mann, 1992). Conversely, physical cues associated with infancy such as large eyes, small noses, and

rounded head are attractive to parents and others (Alley, 1983; Sternglanz et al., 1977; Zebrowitz, 1997), and parents of attractive infants are more attentive and affectionate toward them (Hildebrandt & Fitzgerald, 1983; Langlois et al., 1995).

Kin Value

Anthropologists have long recognized that in prestate, nonstratified societies (like those that characterized most of human evolution), social relationships fundamentally organized by kinship and kinship-like institutions (Chagnon, 1997). All known human cultures, past and present, include three basic kinds of social relationships based on kinship-like institutions: marriage, descent, and kinship classification systems. All kinship classification systems are based on three basic principles: sex, descent, and generation. These systems fall into seven basic types, depending on how precisely the kin terms divide kinship classification along these basic dimensions.

These common features of social organization reflect the value of kinship cross-culturally, and kin selection theory helps explain this value, even though classificatory kinship and biological kinship do not completely overlap. Individuals can increase the alleles they bear not only via their own reproduction but also via aid to those with whom they share those alleles by virtue of recent common descent (Hamilton, 1964; Maynard Smith, 1964; Williams & Williams, 1957). Kin selection theory shows how this kin-based altruism may be selected for: when the cost to the altruist of providing the aid is less than the benefit to the recipient devalued by the probable degree to which they are related (Hamilton, 1964). From ego's perspective, others vary in probable kin value. They differ in (1) their probable degree of relatedness to ego, (2) the probability that they will translate any investment by ego into future reproductive success, and (3) the probable fitness outcomes ego might reap from alternate uses of any available investment. Some individuals have higher kin value, and to the degree that they exhibit reliable cues to this value, they are expected to be more attractive than others. Adaptations for recognizing kin in humans include ones that appear to assess the likelihood of close biological relatedness based on relative proximity during critical stages of the life course (Lieberman et al., 2003; Shepher, 1971; Westermarck, 1826; Wolf & Huang, 1980). As with offspring, the probability that kin can translate investment

into successful reproduction is affected by their phenotypic and genotypic quality, including the related variables of health, age, fertility, fecundity, and sex, all of which are associated with physically observable cues.

Cooperative and Coalitional Value

Although he overstated the case, Levi-Strauss (1969) saw marriage in traditional societies as an alliance or exchange primarily between men (the consanguineal male relatives of the bride and groom). Certainly, who mates with whom is of interest not only to the principals. With its concomitant social, economic, and reproductive rights, duties, and obligations, the universal institution of marriage reflects the fundamental interests of individuals in the mateships of their offspring, siblings, and close relatives. Mateships build and bind alliances, sons- and daughters-in-law play integral social and economic roles, and reproductive unions serve as vehicles for a descent group's reproductive future. Accordingly, family members regularly assess potential daughters- and sons-in-law with respect to their coalitional, productive, and reproductive assets, and the ethnographic literature reveals that many marriages, especially first marriages, are arranged (e.g., Chagnon, 1997; Fraser, 1985).

Another basic feature of human life history is the high degree of investment in juveniles provided by individuals other than the biological mother, including biological and social fathers, aunts, uncles, and grandparents. Hrdy (2002) argues that humans are essentially cooperative breeders, with multiple females and males cooperating in the raising of offspring. If this is the case, humans may cultivate relationships with others based on their suitability as alloparents. Relevant cues in making this choice may overlap with cues of long-term mate value but will diverge in some areas. Sex of alloparent is less important than sex of mate. Fertility and fecundity might oppositely affect relative mate and alloparent value: A postmenopausal woman has low reproductive value but could provide valuable benefits (e.g., resources, knowledge) as an alloparent (Hawkes et al., 1998, 2000). Moreover, she would not face a trade-off between investment in allochildren and her own current reproduction. Similarly, prereproductive females often provide alloparental care for younger siblings. But the

opportunity costs of doing so increase as they have children of their own, thus decreasing their alloparental value to their parents.

Based on data from foraging societies, other ancestral cooperative activities include foraging (e.g., Alvard, 2004; Hill, 2002; Sosis, 2000), information transmission (e.g., Mithen, 1990; Scalise Sugiyama, 2001; Sugiyama & Scalise Sugiyama, 2003;), and aid during health crises (Gurven et al., 2000; Sugiyama, 2004b; Sugiyama & Scalise Sugiyama, 2003). Health, physical abilities, generosity, cooperativeness, and intelligence provide at least some cues to an individual's value in the realms of foraging, coalitional aggression, health aid, and child rearing.

Finally, even individuals with whom ego does not directly cooperate can have social value when they yield positive externalities such as increasing ego's food supply, attracting potential mates to ego's proximity, deterring attacks, serving as sources of information, or helping ego's allies (e.g., Etkoff, 1999; Sugiyama & Scalise Sugiyama, 2003; Tooby & Cosmides, 1996). Conversely, individuals may have unintended negative effects on us. Unhealthy individuals may increase disease exposure. In small-scale societies, impulsively aggressive individuals may incite conflict, and the mentally ill might act unpredictably in ways that harm others' interests (e.g., Chagnon, 1988; 1997; Sugiyama, unpublished ethnographic data).

Coalitional Value

As noted above, humans engage in a considerable amount of conflict, some of which results in homicide. And in a world of close-range, nonmechanized weaponry, individual strength, size, speed, and agility are highly advantageous. The word for headman often translates as "big" or "big man," and tribal leaders are often bigger than average (e.g., Brown, 1991). Leadership, organizational abilities, strategic acumen, and motivational skill are also valued in coalitional politics (e.g., Chagnon, 1997; Patton, 2000; Sugiyama & Scalise Sugiyama, 2003) and may be assessed through observation or reputation. In addition, the value of a coalitional partner is based in part on his or her reliability, loyalty, strategic intelligence, and willingness and ability to back up coalitional interests with force (e.g., Chagnon, 1997; Patton, 2000).

Some of these abilities may be assessed through physical and behavioral cues, and adaptations for assessing the attractiveness of males as mates and allies are expected to target them. For example, reliability and ability to help defend coalitional interests will be affected by an individual's health: All else equal, individuals in frail health will be less reliable and less able defenders. Further, immune-compromised individuals may increase disease transmission among coalition members. Because physical prowess furthers success in foraging, fighting, and deterrence of violence, cues of physical prowess are likely to be important in assessments of male attractiveness by males. For men, physical prowess and aggressive formidability are linked to survival, social status, and, consequently, their social value to other males. Thus, males are expected to display these qualities to other males and to be adept at predicting the outcomes of physical conflicts based on assessment of the traits correlated with these qualities (e.g., dominance, tenacity, pugnacity, pain tolerance, agility, strength, endurance). All else equal, men should find males who exhibit these cues attractive coalition partners. Because successful coalition building and maintenance also require certain social and mental skills, traits associated with these qualities are expected to be found attractive in potential coalition partners as well. Male coalitional assessment psychology must, therefore, be able to weigh the degree to which a given male possesses these abilities and their relative importance to the coalition in question. A coalition of brawny, athletic warriors lacking planning ability could benefit from adding to its ranks a man who is physically deficient but strategically brilliant. My ethnographic observations indicate that shamans are often important political players even after they can no longer go on raids (see also Chagnon, 1997).

Organization of Attractiveness-Assessment Mechanisms

Mates and kin are often cooperative and coalitional allies; thus, some cues of mate, offspring, kin, and coalitional value may overlap. Others may not; for example, an individual may desire kindness in a mate but ruthlessness in a war ally. We must, therefore, understand how adaptations generating our perceptions of attractiveness are

organized and why we see cross-cultural and individual variability in assessments of attractiveness.

A critical variable in the deployment of many adaptations is the phenotypic state of the assessor. For mating, parenting, and alliance formation, this state includes developmental stage, sex, health, nutritional, reproductive, and mating status. Other variables these adaptations must assess include:

1. How many coresident kin do I have (e.g., Chagnon, 1975, 1979, 1997; Hill & Hurtado, 1996; Sugiyama, in press)?
2. How many people value me, how much do they value me, and for what (Sugiyama, 1996; Sugiyama & Chacon 2000; Sugiyama & Scalise Sugiyama, 2003; Tooby & Cosmides, 1996)?
3. Are my father and/or mother alive (e.g., Hagen et al., 2001, Hill & Hurtado, 1996; Sugiyama, in press)?
4. How aggressively formidable am I compared to others? (e.g., Chagnon, 1988, 1997; Patton 2000).
5. How attractive am I to others as a mate (e.g., Buss, 2000; Gangestad & Simpson 2000)?
6. How attractive am I as friend or ally (Gurven, 2000; Sugiyama, 1996; Sugiyama & Chacon 2000; Sugiyama & Scalise Sugiyama, 2003; Tooby & Cosmides, 1996)?

Even though the underlying functional design of attractiveness-assessment adaptations are expected to be universal, we should expect to see strategic variation in their behavioral expressions at the population, group, and individual levels. Certain cues are expected to be weighted differently in arriving at an assessment of overall physical attractiveness. Variance in these weightings will be based on: (1) which features are statistically more likely to be associated with a particular aspect of the social value in question; (2) local environmental features (e.g., famine, health risk) that reliably change the relative value of attractiveness cues; (3) ecologically variable cues most highly cross-correlated with each other in the local environment; and (4) the phenotypic condition of the assessor. Overall judgment may reflect a compromise between the outputs of each of these components. Additionally, outputs of different

assessment components may conflict with or enhance others in the production of a final perception of attractiveness (e.g., Møller & Pomiankowski, 1993; Grammar et al., 2002; Manning et al., 1999; Symons, 1995; Sugiyama, 2004a).

Each assessment mechanism can vastly reduce the computational complexity of its task by processing only a minute set of the information available in its environment. Nevertheless, each mechanism must be deployed under the appropriate conditions, and doing this requires information intake and analysis. This analysis implies a hierarchically organized but parallel processing system of feedback loops that inform the system based on cues received and instantiated (for a lens model, see Miller & Todd, 1998). It might look (in verbal terms) something like this:

1. Is this an animate object (e.g., is it unitary? does it exhibit self-propelled motion)? If yes, go on; if no, inhibit systems associated with analysis of animate objects.
2. Is this a person? If yes, go on; if no, inhibit systems associated with person perception.
3. What sex is this person? If male, inhibit female assessment systems.
4. Is this person a potential threat?

And the questions would continue down the chains of assessment. This sketch should not be taken too literally. For one, the computer program metaphor is simply that—a metaphor, not a theory of neurobiological instantiation of these functional processes. And the verbal description of mate value criteria simply describes the higher-order conclusion based on specific traits assessed. For instance, the stimulus cue of an hourglass-shaped torso or a certain gait may leap through the system to “woman” such that some chains of analysis—“self-propelled,” “short arms, long legs,” “big ovoid head”—are bypassed entirely if the cue feedback is sufficiently unambiguous to reach levels critical for activation of the conclusion. The criterion “sufficiently unambiguous” itself evolved via selection and will be different for different domains and for different contextual cues in the local environment (which themselves are analyzed by parallel mental operations). Parallel processing—that is, the simultaneous performance of multiple information-processing tasks, the solution to each of which is codeterminate and requisite to reaching a final judgment—is continuously and routinely performed by

perceptual adaptations (Pinker, 1997). This view of attractiveness-assessment cognition markedly differs from the view that attractiveness-assessment mechanisms will produce cross-culturally uniform standards, with some criteria always weighted more than others (e.g., Yu & Shephard, 1998; Tovée & Cornelsson, 1999; Singh, 1993a; but see Marlowe & Wetsman, 2001; Sugiyama, 2004a).

Assessment of Cues to Human Social Value: Health, Phenotypic, and Genotypic Quality

Phenotypic condition refers to an individual's ability to efficiently acquire resources and convert them into fitness. Across all domains of social value, all else equal, an individual's value is higher if he or she is more likely than not to survive and maintain health—that is, if he or she exhibits good phenotypic condition. Health risk is a ubiquitous adaptive problem in current and prehistoric societies (e.g., Steckel et al., 2002; Sugiyama, 2004b). Hill & Hurtado (1996) note that illness and disease are the leading cause of death among the Yanomamö (74%) and !Kung (80%) and caused about a quarter of all precontact Aché deaths. Some of these deaths were due to introduced diseases, but many were not. For the precontact forest-living Aché, accidents were the second leading cause of death, followed by degenerative and congenital diseases. Although male and female mortality rates differ somewhat, in general, age-specific mortality rates show a U-shaped function across the life span, with high mortality during infancy dropping steeply until around age 15 and then creeping upward until they tail rapidly upward between about 60 and 65 years of age. While humans have relatively lower extrinsic mortality compared with chimpanzees, almost half of Aché foragers nevertheless die before their 50th birthday.

Potential death is not the only fitness cost of health risk. Poor nutrition, sickness, and injury reduce fertility, growth, and fitness, and can significantly interfere with ability to provide for self, offspring, and allies (e.g., Sugiyama, 2004a; Sugiyama & Chacon, 2000). Endemic intestinal parasites are commonly found among modern foraging peoples, and diarrheal disease remains a leading cause of juvenile mortality worldwide. Among Shiwiar forager-horticulturalists of Ecuador, lacerations are common across the

life span (Sugiyama, 2004b, c). Among the Yora of Peru, topical bacterial infection accounted for the majority of days on which individuals were disabled and could not forage or garden (Sugiyama & Chacon, 2000). Bites or infestation from ectoparasitic insects (e.g., mosquitoes, no-see-ums, ticks, chiggers) are ubiquitous among the Shiwiar, and many of them leave observable scars (Sugiyama, 2004b). Bot flies and sand fleas parasitize human hosts. If left untreated, open wounds from sand flea larvae can result in infection, making walking difficult and in extreme cases leading to death (Chagnon, 1997; Hagen et al., 2001). On a worldwide scale, ectoparasitic insects are major disease vectors causing high morbidity and mortality. Malaria, spread by anopheles mosquitoes, is a prominent culprit. In some areas, selection pressure from *Malaria falciperum* is so intense it maintains sickle cell trait, even though in the homozygous condition sickle cell anemia is fatal (Nesse & Williams, 1994). Parasite resistance is a critical feature in the evolution of mate choice, and sexual reproduction itself may have evolved in an arms race against rapidly coevolving pathogens (e.g., Hamilton & Zuk, 1982; Tooby, 1982).

Individuals vary in susceptibility to accidents and disease due to (1) differences in immune function, (2) chemical and behavioral factors associated with an individual's attractiveness and exposure to insects that are disease vectors, and (3) personality factors associated with risk taking, coordination, and so on (e.g., Kelly, 2001; Knols et al., 1995; Lindsay et al., 1993; Mukabana et al., 2002; Sugiyama, 2004b). At least some of this variance is heritable. Moreover, individuals who are less susceptible to disease are less effective sources of transmission and thus should be preferable as group members and cooperative allies. Cues associated with the related factors of health, phenotypic, and genotypic quality are, therefore, expected to be attractive across all social value domains, even though relative preference for their cues might vary somewhat across them and across environmental condition (e.g., Low, 1990; Symons, 1979, 1995; Trivers, 1972). Gangestad and Buss (1993) analyzed cross-cultural data collected from thousands of individuals and found that, even controlling for income and distance from the equator (where pathogen prevalence is generally higher), the relative value of physical attractiveness in potential mates was greater in areas with higher pathogen prevalence.

Skin Quality

Given the close link among insect bites, disease, infection, and skin lesions and/or scars, it is no wonder that clear skin is assumed to be associated with attractiveness (Symons, 1995). Skin quality provides not only a cue to age (Symons, 1979, 1995) but also a partial record of an individual's current and lifetime health (e.g., Sugiyama, 2004b). In small-scale ancestral societies where the range of skin color variation is constrained compared to modern Western societies, relative skin tone can signal health. For example, hepatitis, iron deficiency, and parasitic infection can produce a yellowish or washed-out skin cast. Individuals with clear, unblemished skin tend to be relatively less exposed to or affected by parasites or the diseases they transmit (Sugiyama, 2004b). Clear skin also indicates absence of skin-damaging disease (e.g., measles, pox, leishmaniasis) and/or "good genes" for immune function indicated by an individual's ability to heal without infection (e.g., Singh & Bronstad, 1997). Finally, in women, dermatoses are correlated with elevated sex hormone and ovarian disorder (Schiavone et al., 1983; Steinberger et al., 1981; in Grammar et al., 2002).

Although the evolutionary prediction that smooth skin should be found attractive (because it is linked with youth, fertility, and reproductive value in females) has been made repeatedly (e.g., Symons, 1979, 1995), direct studies of skin texture/quality and attractiveness are few, perhaps because it is intuitively clear that wrinkled skin (a cue of older age), open sores, oozing pustules, and disfiguring scars are unattractive (e.g., Symons, 1995; Etcoff, 1999). In a study of facial symmetry (see later discussion), symmetrical faces constructed by putting together one side of a face and its mirror image were not found as attractive as their unsymmetrical originals (Swaddle & Cuthill (1995). However, Perrett et al. (2000) showed that this was an artifact of the fact that the mirror images increased skin blemishes. When they controlled for skin blemishes, the symmetrical faces were rated more attractive. Jones et al. (2004) found that subjects' ratings of skin health were positively correlated with ratings of male facial attractiveness. Grammar (2000) presented subjects with faces whose shapes were standardized and found that skin texture significantly influenced attractiveness ratings, although Langlois et al. (1994) noted methodological confounds in the study.

Grammar et al. (2002) had men rate the attractiveness of front, back, and facial digital photographs of 92 nude Caucasian women, standardized for size and orientation, on a seven-point scale. The photographs were measured for 36 physical traits predicted to be associated with attractiveness. As predicted, skin homogeneity was positively correlated with rated facial, front view, and total attractiveness. Although the correlations did not reach conventional levels of statistical significance, multidimensional measures on so complex a trait as attractiveness are such that any one trait may account for only a small portion of the variance in attractiveness (Grammar et al., 2002). Skin texture might be such a trait, or it could be that the relative value of skin texture in health appraisal (and, therefore, attractiveness) in a population with few ectoparasitic infections is relatively low. I would predict that natural levels of variation in skin quality among natural fertility, forager or horticulturalist peoples (i.e., peoples regularly exposed to parasitic, pathological, and outdoor causes of skin damage) would account for a higher proportion of the variance in attractiveness assessments than among Western subjects rating images of Western models.

Hair Quality

Grammar et al. (2002) found that hair length was significantly correlated with female attractiveness. Hair grows at the rate of about one-half inch per month, until it falls out upon reaching 2 to 3 feet in length. Starvation causes loss of hair, nutritional deficiencies in vitamins and minerals cause damaged hair, and malnourishment causes observable changes in hair color (e.g., dark hair takes on a reddish tone). Hair, therefore, provides an observable record of an individual's recent health and nutrition (serving as an indicator of diet and health over a 2- to 3-year period) and reflects heritable genotypic quality (Etcoff, 1999). Shiny, strong hair provides a cue to recent good health, developmental condition, and genotypic quality. Tellingly, long hair is often preferred across cultures, and long, lustrous hair is often associated with beauty (Etcoff, 1999). Hinsz et al. (2001) collected hair samples and contributor information from over 200 women ages 13 to 73 and found that younger, higher reproductive value women tended to have longer hair than older women, as predicted if higher reproductive value women were more likely to use their hair as an advertisement of that fact. And

hair samples that beauticians rated as higher quality came from women who self-reported to be in better health, although age of donor probably contributes significantly to that result. It is interesting that hair grows fastest among women around the ages of peak fertility (Etcoff, 1999), with the result that evidence of environmental damage has less time to accumulate before new hair grows in, and evidence of health or dietary problems reflects a shorter period of time.

Oral Health

Diet is closely linked to health and fitness, and an individual's nutrition can be compromised by masticatory inefficiency, poor dentition, or dental disease (e.g., Symons, 1995; Walker et al., 1998). Caries rates and periodontal disease can be affected by small differences in diet, developmental stress, and heritable genotypic variation (e.g., Hillson 1996; Walker et al., 1998). Even though dental development is relatively well buffered against environmental disturbances, linear enamel hypoplasia (horizontal grooves in the enamel caused by developmental stress during enamel formation) provides visible evidence of developmental stress (Hillson 1996; Skinner & Goodman 1992). Left untreated, painful caries can reduce feeding efficiency. Left untreated long enough, they can result in dental abscess, infection and inflammation of bone tissue, and even death. Strong, even, white teeth thus provide a constellation of cues to health, developmental history, masticatory efficiency, and genotypic quality, and are thus predicted to be attractive (e.g., Symons, 1995). While most academics rarely confront individuals with untreated dental disease, in my experience conducting dental surveys among indigenous Amazonian groups, the breath of individuals with abscessed teeth or multiple carious lesions is far more aversive than that of others in the same population, even when no toothbrushes, toothpaste, or modern dentistry are available. Common halitosis stems from bacterial growth on the back of the tongue. While this growth probably doesn't have much direct negative effect on fitness, it might provide a cue to an individual's overall resistance to bacterial infection. Olfactory cues can, therefore, provide cues to oral health and hygiene and, less directly, to developmental integrity and genetic quality. However, despite the fact that dental hygiene is a

multimillion-dollar industry, I found no direct tests of these predictions in the evolutionary literature.

Movement Patterns

Grammar et al. (2002) explain that movement patterns depend on motor control of biomechanical structures. Bone, muscle, and neuronal motor control are affected by heritable, developmental, and current physiological state, and there are biomechanical energetic optima of movements (Grammar et al., 2002). Individuals vary on these traits, such that individuals can be reliably identified by gait (Stevenage et al., 1999; in Grammar et al., 2002). Symons (1979) predicted that sprightly gait would be attractive in females because it was correlated with youth and nubility. Attaching lights to critical parts of the body allows movement to be studied without being confounded with other visual cues. These techniques have shown that relative youth can be predicted from gait (Montpare et al., 1988). Similarly, biomechanical features of health or other aspects of genetic or phenotypic quality should be assessable by movement. For instance, symmetry affects biomechanical efficiency (Manning & Pickup, 1998), and symmetry appears to be a correlate of genotypic and phenotypic quality (e.g., Thornill & Gangestad, 1993; see later discussion). Animal studies have shown that movement differs between sick and healthy individuals. In particular, ability to move consistently through repeated motions (e.g., walking) may provide information about phenotypic condition, including health (Grammar et al., 2002). And motion is used in assessments of attractiveness for members of the opposite sex (Grammar et al., 2002). In particular, when digitally masked or pixilated images of men and women dancing were shown to subjects, they were found more attractive and erotic the larger and more sweeping their movement. Women who made slow, more fluid movements were found more attractive. In addition to information about sex, age, and identity (which subjects are able to predict from movement alone), Grammar et al. (2002) suggest that these motions also convey information about underlying genetic quality and resistance to developmental disturbances.

Fluctuating Asymmetry and Developmental Stability

Externally visible features of many animals' bodies are designed to be bilaterally symmetrical. However, environmental stress can disrupt developmental pathways. On average, random developmental disturbances are expected to affect development on both sides of the body equally, but mutational load or homozygosity may increase small random variations from symmetry during development, known as <I>fluctuating asymmetry</I> (FA; Mather, 1953; Palmer & Stobbeck, 1986; Van Valen, 1962; Watson & Thornhill, 1994). FA thus provides a potential observable indicator of developmental instability: Individuals with lower FA appear to have either higher genetic quality, less exposure to developmental disturbances, or both. As an indicator of genotypic quality and ability to withstand developmental stress, pathogens, and genetic anomalies via more efficient use of developmental resources or enhanced immune function, FA has been hypothesized as one cue to genotypic and phenotypic quality. Because maintaining symmetrical development in the face of developmental disturbances is costly, FA may be an "honest" signal of genotypic and phenotypic quality related to a number of aspects of fitness. This signal quality is thought to be accentuated in males by display of physical features under developmental control of testosterone. Testosterone has negative effects on immune function, so only males with high genetic quality and immune function can have both high testosterone and high degrees of symmetry. Selection for preference for low FA opposite-sex individuals is therefore predicted (e.g., Gangestad & Thornhill, 1999; Møller & Swaddle, 1997; Palmer & Stobbeck, 1986; Thornhill & Gangestad, 1993; Thornhill & Møller, 1997; Watson & Thornhill, 1994).

Research on a variety of species shows that FA is negatively correlated with fitness-related measures of growth, survival, fecundity, intrasexual competitiveness, and mating success (Lagesen & Folstad, 1998; Møller, 1990, 1992a, 1992b, 2002; Thornhill, 1992a, 1992b). FA appears to be heritable, such that offspring are likely to exhibit these advantages to some extent, although the degree of heritability is debated (Fuller & Houle, 2003; Gangestad & Thornhill, 1999; Van Dongen, 2000). In men and women, symmetry appears to be associated with correlates of genotypic and phenotypic quality, including physical, cognitive, and mental health. More symmetrical men are more muscular (Gangestad & Thornhill, 1997b), are larger (Manning, 1995), have a lower

resting metabolic rate (Manning et al., 1997), and have a greater degree of testosterone-related facial cues of dominance and reproductive health (Gangestad & Thornhill, 2003) than do less symmetric males. Body weight, musculature, and testosterone levels may be condition-dependent: Higher genetic quality males are best able to develop and maintain large size, musculature, and high testosterone (Gangestad & Thornhill, 1997a, b, 2003)—costly signals of “masculine” traits that pay off in intrasexual competition and intersexual attraction. Women reported finding these masculine traits particularly desirable in short-term mates and extra-pair sex partners (Buss & Schmitt, 1993; Greiling & Buss, 2000). They also appear to be more attracted to and more likely to have sex with men exhibiting these “masculine” traits during the fertile phase of their ovulatory cycle, as was predicted if female short-term mating is strategically deployed to increase the genetic quality of their offspring (Bellis & Baker, 1990; Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Johnston et al., 2001; Thornhill & Gangestad, 2003).

FA is also negatively correlated with aspects of female health. Manning (1995) show an association between body weight and FA in women. In a large study of 26-year-old men and women, Milne et al. (2003) found female FA was significantly associated with body mass index (BMI) and overall reported number of medical conditions. Although FA was not significantly associated with blood pressure, cholesterol, or cardiorespiratory fitness, the authors suggest this could simply be the result of relatively low levels of environmental stressors in Westernized societies, leading to more homogeneity in FA (Milne et al., 2003). Among Hadza foragers, FA is higher than in U.S. college students, suggesting the Hadza do experience more developmental stress (Gray & Marlowe, 2002).

Given these associations between FA and poorer phenotypic condition, Gangestad et al. (1994) predicted that symmetrical individuals would be perceived as more attractive than less symmetrical individuals. To the extent that individuals in better phenotypic condition should have, higher kin, coalitional, and offspring value, we should expect low FA to be more attractive across these domains of social value. Given that male FA is inversely related to cues of masculinity mediated by testosterone—for example, dominance, aggressiveness, large size, and musculature—we should expect

males to find low FA and its correlates particularly attractive in their close male allies (as opposed to their enemies), at least as long as the benefit the ally provides is greater than the cost he imposes as a mating competitor. Sexual and coalitionary rivals are also likely to be assessed in part based on FA, but we would expect a negative emotional response to low FA and higher testosterone individuals that would increase in proportion to their formidability as sexual or coalitionary competitors (i.e., the greater the threat, the more intense the negative emotional response).

Relative symmetry is associated with facial attractiveness, as well as mating behavior and opportunities. FA is negatively correlated with facial attractiveness ratings of both males and females (Baker, 1997; Gangestad et al., 1994; Thornhill & Gangestad, 1993, 1994, 1999a). The clearest demonstrations of the link between attractiveness and symmetry use natural stimuli, rather than composites (e.g., Cunningham, et al., 1991) or mirrored chimeras (e.g., Kowner, 1996; Langlois et al., 1994), because the latter manipulations confound FA with either averageness or skin texture and may create unnatural-looking faces by exaggerating or reducing some features, particularly those that show directional asymmetry (DA; or nonrandom asymmetry not indicative of developmental disturbance; Farkas & Cheung, 1981; Little et al., 2002; Symons, 1995). Image manipulations of symmetry have led to contradictory results. Symmetrical faces created by taking half a facial image (split on the vertical midline) and joining it with its mirror image are not more attractive than the original, although averaging these first two chimera images does yield increased attractiveness (Langlois et al., 1994; Kowner, 1996; Rhodes et al., 1999; Sauels et al., 1994; Swaddle & Cuthill). Most studies on natural variation in facial symmetry show a positive relationship between symmetry and attractiveness (Grammer & Thornhill, 1994; Langlois et al., 1994; Mealey et al., 1999; Rhodes et al., 1998, 1999; Rikowski & Grammer, 1999; Scheib et al., 1999; but see Jones & Hill, 1993).

If low FA is associated with the ability to withstand developmental disturbance, such that symmetry is correlated with other cues of phenotypic condition, then low FA individuals may be found attractive because of those other cues, in addition to symmetry per se. If so, the link between symmetry and attractiveness would not be direct. Sheib et al. (1999) found that, when presented with male half-faces (split

along the vertical midline), women's attractiveness ratings of half-face images were associated with symmetry of the full face, just as strongly as the women's ratings of the full faces. More symmetrical men had longer lower jaws and more prominent cheekbones, features that appear to reflect developmental influence of testosterone (see later discussion). Jones et al. (2001) also found that the relationship between attractiveness and facial symmetry is not direct, but mediated by the association of symmetry and apparent health (see also Shackelford et al., 2000). The direct effect of facial symmetry on attractiveness was small.

Body symmetry is also associated with facial symmetry and ratings of attractiveness, health, and fitness, supporting the idea that FA is related to underlying features of phenotypic condition. Thornhill and Gangestad (1994) measured seven nonfacial body traits of 122 undergraduates and found a positive correlation between age at first copulation and degree of asymmetry. They also found negative correlation between FA and self-reported number of lifetime sex partners, even when age, height, ethnicity, marital status, physical attractiveness, and physical anomalies were controlled. FA was important in evaluations of both male and female attractiveness. Gangestad measured FA of men from a small village on Dominica using 10 different body traits. Both male and female college students rated facial photographs of the more symmetrical men more attractive (Thornhill & Gangestad, 2002). Waynforth (1995) found FA related to higher morbidity and lower fecundity and marginally associated with higher age at first reproduction and fewer lifetime sex partners among Mayan men in Belize. Hume et al. (2001) studied the relationship among facial attractiveness ratings, FA (based on 22 traits), BMI, health, and age among almost 100 male and 100 female subjects, whose attractiveness was then rated by a large number of other men and women. For both males and females, there was a negative association between attractiveness and FA. For females, BMI and past health problems were the best predictors of female attractiveness; for males, it was the socioeconomic status of the environment in which they were raised.

Men with low FA report earlier age of first intercourse, higher numbers of sex partners, higher number of extra-pair copulation partners, and shorter time elapsed until sex with a new partner (Gangestad & Thornhill, 1997a; Thornhill & Gangestad, 1994,

2003). This pattern appears to be the product of individual differences in male mating strategy depending on males' relative attractiveness (and thus opportunities based on female mate choices) and hormone-mediated sociosexual strategies that covary with FA. This may exacerbate the trade-off women face between choice for good genes and for likely investment. As predicted, female attraction to low-FA males increases with woman's current fecundity and in short-term (or extra-pair) mating contexts (as does preference for male physical attractiveness and its correlates generally; see, e.g., Buss & Schmitt, 1993; Greiling & Buss, 2000). Degree of male symmetry predicts a significant amount of their partners' copulatory orgasms (Thornhill et al., 1995), which may bias paternity toward symmetrical males via increased sperm retention (Baker & Bellis, 1995), and women experience more frequent orgasm with extra-pair mates (Thornhill & Gangestad, 2003). In the study of FA and attractiveness among Dominica men, women showed greater preference for symmetrical male faces as a function of the woman's probability of conception based on the phase of her ovulatory cycle. Finally, body scent may be associated with phenotypic condition, and when women were presented with T-shirts worn by different men, women not using hormonal contraceptives preferred the body scent of more symmetrical men, but only during the fertile times in their cycle. Hormonally contracepting women showed no shift (Gangestad & Thornhill, 1998b; Rikowski & Grammar, 1999). These studies indicate that all future research on female mate preferences must distinguish not only between short- and long-term female mating preferences but also between preferences during the fertile and nonfertile phases of the ovulatory cycle.

Hormonal and Sexually Dimorphic Cues to Health, Phenotypic, and Genotypic Quality

Some cues to social value differ between the sexes. Sexually dimorphic features develop partially under the influence of testosterone and estrogens. Sexual dimorphism in body size, strength, and physical weaponry typically evolves because of higher levels of intrasexual competition in one sex than in the other. Sexual dimorphism in ornamentation is usually the result of intersexual selection or mate choice. Sexually dimorphic traits therefore provide a variety of possible cues to the relative social value

of both men and women, although the cues associated with each sex are expected to differ in certain predictable ways. Different morphological traits may be associated with relatively higher or lower social value in a given domain in different environments and be more or less important depending on local context. The underlying psychology generating attractiveness assessments for each assessed feature of body morphology is thus expected to generate differing assessments of attractiveness based on local environmental features. This discussion focuses on cues of social value related to the face, height, body mass, and bodily proportions.

Because mammalian female reproductive potential is usually less than that of males, intrasexual competition is typically higher among males, and males are correspondingly larger. If females preferentially mate with larger (or better-armed) males, the selective benefit of larger size is increased. In primates, dimorphism corresponds roughly with a species' mating pattern: Single-male/multifemale groups tend to have higher dimorphism than those living in "monogamous" pairs. In between are those, like humans, who live in multimale/multifemale groups and show mild size dimorphism in height, weight, and upper body musculature. A closer predictor of dimorphism is the species' operational sex ratio, or the ratio of reproductively active males to females expected in a given group at a given time (Mitani et al. 1996).

In primates with multimale/multifemale groups, such as common chimpanzees and baboons, males may form coalitions to prevent solitary males or other coalitions from gaining sexual access to group females. For humans, having larger, stronger, more physically adept and aggressively formidable allies can be beneficial in these circumstances. However, an individual's coalition members are also his sexual rivals in the contest to mate with female group members: More formidable coalitional allies mean more formidable potential intrasexual competitors. For males, then, there are trade-offs between preferred size of allies and preferred size of competitors.

For females, one adaptive problem presented by sexual dimorphism is that males may use their size and strength advantage coercively. One solution to this problem is for females to obtain physical protection from other males (Buss & Schmitt, 1993). All else equal, females who preferred larger, stronger, more dominant males as sires for their offspring would tend to have sons who inherited these qualities. Females

who preferred males exhibiting ability and willingness to invest in their offspring would tend to rear more offspring to maturity.

Formal modeling of these trade-offs is necessary to predict evolutionarily stable mixes of strategies within specific constraints. However, among Jivaroan-speaking indigenous Amazonians, living groups tend to include one or a few <I>juunt</I> (i.e., big men), whose coalitional ties to other groups form the basis for larger, intergroup coalitions and around whom aggregate a coalition of (usually) younger, smaller, less dominant, affinally or consanguineally related males (e.g., Descola, 1998; Patton, 2000). Younger men may jockey for status among themselves, but as they approach <I>juunt</I> age and status, they may increasingly conflict with established big men. Chagnon (1975, 1979, 1997) clearly shows that among the Yanomamö, when status or mating conflict increases to the point that the stability of intragroup coalitions is too frequently perturbed, the group fissions. As group size increases, group formidability increases, but so do internal conflicts.

Throughout the juvenile period, individuals face a trade-off between investment in immune function and growth. Adult size is partially heritable, but nutrition, pathogen exposure, and immune function affect how much energy is available for growth (e.g., Bogin, 1999; Gunnell et al., 2000; Read & Allen, 2000; Revera et al., 1995; Roberts et al., 2000; Sivertonin, 2003). All else equal, in subsistence societies, larger individuals have higher phenotypic quality: They are more likely to survive and are better able to resist pathogens and to convert available ecological resources into somatic resources (e.g., Beririragi, 1985; Hill & Hurtado, 1996; Hoppa, 1993). Further, human growth is determinate: Growth ends when reproduction begins because the energetic costs of doing both simultaneously are too high (Hill & Hurtado, 1996). For women, the fitness benefit of additional growth includes the accumulation of somatic resources for later reproductive effort, increasing probability of survival (Jousilahti et al., 2000), lower offspring mortality (Sear et al. 2004), and lower maternal and infant mortality (taller women tend to have wider pelvises, easier births, and higher infant birthweights; see Kirchengast et al., 1998; Martorell et al., 1981; Rosenberg, 1992). The potential benefits of earlier reproduction include lower

prereproductive mortality risk and a longer time span in which to reproduce (Hill & Kaplan, 1999; Hill & Hurtado, 1996).

Height

Men tend to have partners who are shorter than themselves and vice versa (Gillis & Avis, 1980). In modern populations, there is generally a positive association between male height and health (Kuh & Ben Shlomo, 1997; Kuh & Wadsworth, 1993; Macintyre & West, 1991; Silventoinen et al., 1999) and reproductive success (RS) (Nettle, 2002a; Mueller & Mazur, 2001; Pawlowski et al., 2000). As noted earlier, relative height provides some information about phenotypic quality. However, extreme shortness and tallness may be associated with health problems in both sexes (e.g., Mueller & Mazur, 2001; Nettle, 2002a). Height is associated with the rated attractiveness of men (e.g., Feingold, 1982; Gillis & Avos, 1980; Hensley, 1994), with American women rating short men undesirable for either long- or short-term mates. Tall, strong, athletic men are strongly desired as marriage partners (Buss & Schmitt, 1993), and taller-than-average men are preferred to men of short or average stature as dates and mating partners (Ellis, 1992). In analyses of personal ads, 80% of women who stated height preferences wanted men 6 feet tall or taller (Cameron et al., 1977). Ads placed by taller men receive more responses (Lynn & Shurgot, 1984; Pawlowski & Koziel, 2002). Women even seem to take height into consideration in sperm donors (Scheib et al., 1997).

Preference for tall men does not appear to be limited to intersexual choice. Coalitionary leadership and height seem to be associated in both small-scale and state societies. In U.S. presidential elections, the taller candidate is more likely to win, with the margin of victory positively correlated with height (McCann, 2001). Senators and CEOs appear to be taller than the average American man (Etcoff, 1999; Keyes, 1980). Further, there appears to be a positive association between height and socioeconomic success (Bielicki & Szklarska, 1999; Frieze et al., 1990, 1991; Hensley & Cooper, 1987; Jackson, 1992). In an experimental study, 72% of recruiters for sales positions preferred the taller of two job applicants, but only one recruiter preferred the shorter candidate (the remainder had no preference; Kurtz, 1969). Among a large sample of

British men, taller-than-average men had higher numbers of live-in partners and lower chance of either being childless or having had no significant mating relationship (Nettle, 2002a). However, Nettle found no significant association between total number of offspring and height, although the men had not yet completed fertility: They were not yet of the age where they were likely to have had all children from a second marriage, and they had ready access to contraceptives.

If male size is positively associated with aggressive formidability, yet involves energetic or other trade-offs, then a reliable, efficient solution to these trade-offs would include a context-sensitive height-assessment adaptation functioning such that intensity of male height preference increases with increasing levels of intragroup conflict and intergroup coalitional conflict. Intensity of preference for taller males is also expected to vary with resource stress: Because taller males are those who could better afford the costs of growing larger, relative height provides a costly signal of phenotypic quality, amplified under resource and pathogen stress.

In their study of the intercorrelation of 36 female physical traits, Grammar et al. (2002) found a significant correlation between a woman's height and her attractiveness, which in factor analysis loaded highly with traits associated with their factor of nubility. Conversely, Hensley (1994) found no evidence that men use height in assessments of females. Sear et al. (2004) investigated the relationship between height and RS in a natural fertility population of Gambian women, providing evidence that ancestral males could have benefited from mate choice for locally taller women under some conditions. They found the expected trade-off between growth and age of sexual maturity, with taller women having later age at first birth. But the physiological benefits of increased growth paid off during their reproductive life span in higher RS: Offspring of taller women exhibited lower mortality.

Conversely, using data from Britain's National Child Development Study (a longitudinal study of socioeconomic and health among all children born in Britain during one week in 1958) to investigate the relationship between female height and lifetime RS, Nettle (2002b) found a weak but highly significant inverted U-shaped relationship between relative female height (at age 23) and RS at age 42, controlling for own or husband's socioeconomic status. Highest RS was for women between .7 and 1.7

standard deviations below the mean. Women of mean height had the highest number of marriages or long-term mates and were least likely never to have had a long-term mating relationship. Nettle also found the expected trade-off between growth and age of sexual maturity, with taller women beginning to reproduce later. However, age of the British sample corresponds with widespread availability of hormonal contraceptives, and the mean fertility was low for all heights observed, so later first reproduction of taller women cannot account for their lower RS. As predicted, given the life history trade-offs involved, female height preferences appear to change with (mild) socioecological risk. Pettijohn and Jungeberg (2004) found a significant positive correlation between yearly indicators of economic stress (predicted to covary with perceived ecological risk) and the height of <I>Playboy</I> Playmates chosen <I>Playboy</I> magazine Playmate of the Year.

Weight, Body Fat, and BMI

Body fat provides a potential cue to female mate value because fertility, pregnancy, and lactation are supported by substantial fat stores (Frisch, 1990; Frisch & McArthur, 1974;). Fat reserves may buffer decrease in female reproductive function related to arduous work regimes (Janienska & Ellison, 1998) and seasonal negative protein-energy balance (Bentley et al., 1998), as well as the mortality risk and reproductive decline associated with illness/injury and poor health (e.g., Anderson et al., 1992; Brown & Konner, 1987; Sugiyama & Chacon, 2000, Sugiyama, 2004b). Workload, resource availability, and health risks are ecologically variable, so if psychological adaptations evolved to use body weight in assessments of attractiveness, they are expected to embody features that adjust preferred level of female body fat to these and other relevant features of the local environment during development and to update assessments with changes in these variables across the life span (Sugiyama, 1996, 2004a). Cold-adapted populations tend to have higher subcutaneous body fat, so factors such as climate are likely to affect local body fat preferences as well.

Among the Aché, there is a positive linear relationship between female body weight and fertility at 30 years of age (Hill & Hurtado, 1996) similar to the pattern of height and fertility for Gambian women. Variance in Aché women's age-specific weight

is higher than variance in male weight. And, in contrast to the increase in weight associated with age in contracepting, industrialized societies, Aché women show a common mammalian pattern in which they achieve peak weight just before reproductive maturity (age at first birth), followed by a decline in weight over the reproductive life span. In foraging populations, then, high weight is not a reliable cue of middle age, old age, or parity; rather, it can covary with nubility. Females among Shiwiar forager-horticulturalists of Ecuador show a similar pattern (Sugiyama, 1996).

Cross-culturally, preferred female body fat level increases with risk of local food shortages (Anderson et al., 1992). Studies show that preference for plumper women is common in non-Western societies with subsistence-based economies and/or higher risk of food shortages (Anderson et al., 1992; Brown & Konner, 1987; Ford & Beach, 1951; Sobal & Stunkard, 1989). All claims about attractiveness-assessment adaptations related to body weight must take this ecological variability—as well as age-related changes in body weight—into account. When North American subjects rate the attractiveness of standardized female line drawings depicting low, normal, and high (but not obese) body weight, normal-weight figures are regularly preferred by North American White and Hispanic subjects (Singh, 1993a, 1993b, 1994a). Among 12 line drawing stimulus figures ranging from anorexic to obese, British, Kenyan, and Ugandan subjects rated normal-weight figures most attractive (Furnham & Radley, 1989), but Kenyans and Ugandans rated high-weight figures significantly more attractive than did British subjects or Kenyans living in Britain (Furnham & Baguma, 1994; Furnham & Alibhai, 1983). My Shiwiar informants regularly express preference for higher female body fat (within the local range), and experimental results confirm that higher-weight line drawings are found more sexually attractive, healthy, fertile, young, and preferable as spouses (Sugiyama, 2004a). Studies among Hadza foragers of Tanzania and Machiguenga forager-horticulturalists of Peru show similar results (Wetsman & Marlowe, 1999; Yu & Shepard, 1999). However, measures of subcutaneous body fat indicate that even the “fattest” Shiwiar woman has lower body fat than average U.S. female college students. Most Shiwiar (and Machiguenga) have probably never seen an obese individual, and their assessment system has never observed the link between obesity and other cues of poor phenotypic quality, such as shortness of breath, impaired

gait and mobility, and increased susceptibility to disease. Pettijohn and Jungeberg's (2004) Playmate study indicates that within societies, preferences for higher weight correlate with economic indicators of "hard times." So, while body-weight preference varies across cultures and time, it does so in predictable ways, and nowhere have experimental studies found obesity considered the height of attractiveness. Conversely, even among Western college students, extreme thinness is not found most attractive, nor preferred (e.g., Tovée & Cornelissen, 2001).

BMI, or weight scaled for height (measured as kg/m^2), captures two relevant features of somatic growth: determinate skeletal growth and more fluctuating changes in body weight. In a series of experimental studies in which subjects were presented with female body images produced in various ways, BMI was reported to account for about 80% of the variance in female body attractiveness (e.g., Tovée & Cornelissen, 1999, 2001; Tovée et al., 1998, 1999; 2002;). Tovée and Cornelissen (2001) had male and female undergraduates rate color digital 24-bit photos of 50 real women (18–42 years of age, mean age 26, s.d. 8 years) standing in uniform poses wearing standard tight gray leotards and leggings on a zero- (lowest) to nine- (highest) point attractiveness scale. Each subject rated 10 women's front and side view pictures from each of five BMI categories taken from obesity literature: emaciated (BMI <15), underweight (15–19), acceptable (20–24), overweight (25–30), and obese (>30). Men and women showed an indistinguishable pattern of results. Peak attractiveness ratings were for BMI of 19, with ratings falling precipitously for both higher and lower BMI figures. Front and side view results were highly correlated, suggesting they were generated by the same underlying assessment. However, this study has limited evolutionary ecological validity (EEV): It presents subjects with a narrow range of evolutionarily relevant morphological variation by presenting a limited range of female age, parity, fecundity, and current pregnancy (see Tovée & Cornelissen, 1999, 2001).

The actual perceptual cues used in weight-related assessment are not currently known. Fan et al., (2004) suggest that it is assessed via analysis of volume-to-height index (VHI), and that low female VHI is preferred. This is unlikely given the well documented preferences for higher body weight in some cultures. Given, however, that marriage arrangements are often made prior to female reproductive maturity and

wooing a long-term mate may take some time, we might alternatively hypothesize that low volume-to-height index (VHI) is associated with female prepubescence and that adaptations generating attraction to this female life stage would under some circumstances increase male fitness by targeting females when their reproductive value is high and there is still time enough to secure mating access before fertility onset (see, e.g., Symons, 1979, 1995). The observed male preference for relatively long legs to height (Fan et al., 2004), a ratio that in females is most pronounced at the onset of puberty, would support this contention. In industrialized societies, low VHI (and BMI) is associated with prepubescence (and nubility); in some forager societies, however, relatively higher BMI or VHI is associated with nubility. In sum, female body weight (or close correlates thereof) is an important cue to female reproductive value but what it indicates about reproductive value varies between populations. Relative weight preferences vary across populations in evolutionarily predictable ways and may vary within populations in predicted ways as well.

For males, fitness effects of growth differ from those for females. There is a positive relationship between Aché male body weight and fertility. The increase in fertility with body weight is steeper for males than for females to about 66 kg, upon which it declines with the few males over 67 kg. While 65 kg is the predicted optimal weight for Aché males to stop growing and begin reproduction given the mortality, growth rate, and impact of body size on fertility in this group, there may be a trade-off between optimal reproduction and foraging body size. Large Aché males could be more effective in intrasexual conflict, but they achieve lower hunting return rates (kg/hr) than average-size males, probably due to problems that larger men have moving efficiently in dense tropical forest (Hill & Hurtado, 1996).

Chagnon (1988) reports that Yanomamö men who are *unokai* (i.e., men who have undergone ritual ceremony as a result of participation in a killing) have higher RS than men who have not. In a society in which reputations for fierceness are valued, *unokai* status is public recognition that an individual is willing and able to defend his coalitional interests. Similar evidence is reported for Jivaroan men (Patton 2000). Nevertheless, it is clear that willingness and ability to defend one's interests is an important component of male political leadership in small-scale societies. One venue

where possible correlates of male aggressive formidability have been investigated is sports performance. Ritualized fighting such as Yanomamö chest pounding, side slapping, or club fighting, are duels with normative rules that can reduce mortality risk, yet can serve to settle disputes and provide a (usually) sublethal outlet for physical aggression (Chagnon, 1997). Androgens, particularly testosterone, have developmental effects on spatial abilities, cardiovascular efficiency, speed, endurance, strength, muscle mass, and personality traits associated with aggressiveness (Bardin & Catterall, 1981; Dabbs, 2000; Manning & Bundred, 2000)—traits expected to be correlated with fighting formidability and physical dominance. Physical contests (e.g., wrestling, racing, weight throwing or carrying, ritualized fighting) are common cross-culturally and may serve as proxies of, training for, and/or advertisements of fighting ability (e.g., Chagnon, 1997; Chick & Loy, 2001; Hill, 1984; Manning & Taylor, 2001). Manning and Taylor (2001) suggest that sports serve as useful proxies for fighting ability because they require speed, endurance, strength, and good spatial skills. These traits are expected to correlate with phenotypic quality more generally and are required to some extent in hunting, although knowledge-based skills may be more important in determining hunting success (Kaplan et al., 2000), and strength peaks earlier than hunting return rates (Walker et al., 2002).

Faurie et al. (2004) found that male and female college students who participated in competitive sports or were enrolled in sports curricula reported higher numbers of opposite-sex sex partners than those who were not involved with sports. High-level competitors reported more previous-year opposite-sex partners than lower level competitors. For males but not females, BMI was positively associated with reported previous-year mates, although it could not be analytically separated from the sports participation variable. Manning and Taylor (2001) found evidence that level of sports performance is positively associated with testosterone markers. The ratio of the second to fourth digit, 2d:4d (index finger/ring finger), is generally lower in males than in females and appears to be a correlate of prenatal testosterone concentration (Manning, 2002; Manning et al., 1998, 1999). Lower 2d:4d ratio is associated with higher level performance or competition in middle distance running (Manning & Pickup, 1998); running speed (Manning, 2002); sports generally (including running, football, and

soccer); and martial arts, rugby, racquet sports, swimming, and hockey (Manning & Taylor, 2001). It is also associated with better mental rotation performance (Manning, 2002). Low 2d:4d is associated with testosterone-related personality traits such as aggression but also with intelligence (Manning, 2002). Both men and women can rate the attractiveness of hands. Longer fourth digits are also associated with prenatal testosterone, and when photocopied dorsal and ventral hand surfaces were presented to subjects, digit length was positively correlated with rated attractiveness and sexiness of male and female hands (Manning, 2002). In men, fourth-digit length, attractiveness, and height are positively associated, but there was a negative association between fourth-digit length and male weight. Since the stimuli were from Western subjects, the latter result could be due to obesity: all else equal fatter males may have shorter fourth digits than their peers. Replication among a natural-fertility population of foragers or subsistence horticulturalists (among whom weight will be more closely associated with muscle mass and height) is warranted because other studies show positive correlations among size, strength, and attractiveness.

Sexual jealousy adaptations are expected to be expressed in situations where an individual perceives a threat to his or her relationship (Buss et al., 2000). The traits expected to evoke jealousy are therefore expected to reflect the outcome of self-to-other comparisons based on cues of relative mate value. Dijkstra and Buunk (2001) had subjects list the traits in a mating rival that would make them feel most jealous. The only specific morphological traits listed as jealousy-evoking in a rival were those cues associated with intrasexual competition. Among the traits listed as jealousy-provoking by males were rivals being bigger, stronger, taller, more heavily built, more muscular, and having broader shoulders than self (Dijkstra & Buunk, 2001). In line with predictions about sex differences in the value placed on certain cues to mate value (e.g., Buss, 1989; Buss & Schmitt, 1993; Symons, 1979), heterosexual males regarded each of these traits as being significantly more jealousy-provoking in a sexual rival than did females. Moreover, these traits loaded together in a principal components analysis of 56 different jealousy-evoking traits, suggesting that they are important interrelated features of male intrasexual competition.

Waist-to-Hip Ratio

There are pronounced postpubertal sex differences in the ratio of waist circumference to hip circumference (WHR; Jones et al., 1986; Singh, 1993a, 1993b). In females, estrogen during puberty stimulates fat deposition on the thighs, hips, and buttocks, and inhibits deposition around the abdomen. It is also associated with the widening of the female pelvis. Women's WHR increases with pregnancy, number of births, and high intestinal parasite loads. Western women with normal WHR (.67–.80) are at reduced risk for primary infertility and various health problems (e.g., cardiovascular disorders, female carcinoma), independent of overall level of body fat (Bjorntorp, 1988; Marti et al., 1991; Singh, 1993a, 1993b). Conversely, adult male WHR averages about .9 and is associated with androgen hormonal profile. Singh therefore argues that selection shaped men's mating psychology to prefer low female WHR, regardless of overall preferences for body fat (Singh, 1993a, 1993b) and women's mating psychology to prefer male WHR of .9. To test these ideas, Singh had subjects examine 12 line drawings of female figures depicting four levels of WHR (0.7, 0.8, 0.9, and 1.0) and three levels of body weight (normal [N], low [L], and overweight [O]). When young White and Hispanic men ranked the figures for attractiveness, youthfulness, healthiness, sexiness, and capability of and desire for reproduction, they strongly preferred the normal weight figures (Singh, 1993a, b, 1994a, b). Within each body-weight category, lower WHR was preferred to higher WHR, with 0.7 WHR preferred overall (Singh, 1993a, b, 1994a, b). Ratings of college-age males and females agreed on the relative attractiveness of stimuli based on WHR (Singh, 1993b). Results were not simply the byproduct of current fashion trends (in the simplistic cultural determinist sense). Analyses of body weight and WHR of *Playboy* *Playmates*, Miss America Contest winners (Singh, 1993a), and British fashion models (Morris et al., 1989) show that while weight decreased over time, WHR remained in the .68 to .72 range (Singh, 1993a). British males and African American, Hispanic, White, and Indonesian males in the United States also prefer lower WHR among women of normal weight within the normal Western range, but some variability exists in the preferred level of WHR across studies depending on the method used, specific questions asked, and population tested: Average-weight female figures with 0.7 WHR are usually judged most

positively, but WHRs of 0.6 and 0.8 are sometimes judged most attractive as well (Furnham et al., 1997; Henss, 1995; Singh, 1993a, 1993b, 1994a, 1994c, 1999; Singh & Luis, 1995). Idealized female WHR depicted in art also varies across cultures, but within cultures is consistently lower than idealized male WHR (Singh & Haywood, 1999). As predicted, subjects also rate male figures with 0.9 WHR (in the normal range for Western males) most attractive (Henss, 1995; Singh, 1994c).

Ancestral environmental variability and empirical data suggest that WHR assessment is more complex than an “invariant preference” for a specific WHR, or a rule specifying “the lower a woman’s WHR, the better” (e.g., Marlowe & Wetsman, 2000; Singh, 1993a, 1993b; Sugiyama, 1996, 2004a; Symons, 1995; Tassinari & Hansen, 1998; Wetsman & Marlowe, 1999; Yu & Shepard, 1998). By Western standards, women in foraging populations have high numbers of pregnancies, high parasite loads, and high caloric dependence on fibrous foods (e.g., Kelly, 1995), all of which can increase WHR. These factors vary cross-culturally, suggesting that, across ancestral populations: (1) the normal range of female WHR was often higher than in Western populations, (2) what constituted locally “low” WHR varied, and (3) average WHR of nubile females and of females at peak fertility varied. Thus, a WHR that indicates pubertal onset, sex, fertility, parity, hormonal irregularities, and/or differentiates male from female in one population may not do so in another. Environmental conditions that fluctuate over an individual’s lifetime could affect the relationship between local cues of reproductive value associated with age, sex, health, fertility, and body morphology, including WHR. WHR preference likely targets local distribution of female WHR and updates and recalibrates preferences as local conditions change. WHR of <Playboy> Playmates of the Year does appear to positively correlate with yearly indicators of economic stress, but so, too, does weight, and the effect of WHR controlling for weight was not addressed in that study (Pettijohn & Jungeberg, 2004).

The hypothesis that WHR affects assessments of attractiveness does not necessarily mean that WHR assessment is based on output from a psychological WHR calculation device of waist to hip per se. WHR could be assessed by a curve-detector mechanism, for instance. And because health and reproductive studies measure WHR in circumference, but experimental stimuli predominantly use front and back views, they

lack some of the relevant health and reproductive value cues that WHR is hypothesized to provide. Further, the cues to female health and reproductive value hypothesized to be indexed by WHR are multidimensional. For example, pelvic width and angle were critical changes in female hominid morphology to accommodate the passage of large-headed babies through the pelvic opening. The developmental widening of women's pelvic bones is not complete until about 18 years of age, and it then increases with parity, while gynoid fat distribution appears at puberty. Yet, among Shiwiar and Aché women, body fat appears to decrease with age after first reproduction. These two aspects of WHR may therefore index different aspects of female mate value and independently contribute some of the variance in attractiveness assessment.

A reliable, efficiently functional mate-preference psychology using cues associated with WHR or body shape more generally should take as input the observable range of female WHR and body fat, based on analysis of the following critical WHR subcomponents: (1) pelvic width, shape, and angle; (2) hip width and circumference; (3) hip shape; (4) buttocks extension; (5) buttocks shape; (6) waist width and circumference; (7) waist shape; (8) stomach shape; and (9) stomach extension in relation to (10) other aspects of skeletal structure—such as shoulder and/or ribcage width, distance from pelvis to shoulder, and length of long bones (which provide reference points for assessing pelvic width and fat deposition)—in relation to overall growth, developmental health, and biomechanical efficiency (e.g., Sugiyama, 1996, 2004a). In sum, instead of uniform, cross-cultural preference for a specific WHR, lower WHR relative to the normal female range to which a man is exposed should be preferred. Because at some level low WHR will appear as a deformity, lower limits of WHR attractiveness are also expected (Symons, 1995). Additionally, men exposed to a higher range of healthy nubile female WHR should find higher WHR more acceptable than men exposed to a lower range of female WHR, and lowering the natural range of WHR to which men are exposed should predictably lower their expressed WHR preference, at least within the limits of the reaction norm for these adaptations (Sugiyama, 2004a).

The only studies that have tested WHR preferences in EEV small-scale, subsistence-economy populations report conflicting results (Sugiyama, 2004a; Marlowe,

2001; Wetsman & Marlowe, 1999; Yu & Shepard, 1998). These studies provide a useful illustration of the need for, but potential pitfalls of, cross-cultural testing of hypotheses about psychological adaptations (for an in-depth discussion, see Sugiyama 2004a). The Matsigenka are a case in point. Of six female line drawings depicting two WHRs (0.7 and 0.9) and three body weights (overweight, normal, and low weight), more isolated Matsigenka men of Peruvian Amazonia ranked figures O.9, O.7, N.9, N.7, U.9, and U.7 in order of descending preference for attractiveness, health, and desirability as spouse (Yu & Shepard, 1998, 1999). In contrast, more acculturated Matsigenka ranked the figures O.7, O.9, N.7, N.9, U.7, and U.9 in descending order for attractiveness and desirability as spouse. Yu and Shepard (1998) conclude that the Matsigenka preference for low WHR is an artifact of “culture”—namely, Western media exposure. However, this argument fails to explain why Matsigenka men should prefer the body shape of women from a foreign culture to that of women from their own—that is, how and why exposure to another culture interacts with the psychological design that produces WHR preferences.

Experimental stimuli must reflect local conditions. WHR of Matsigenka women is higher than that of Western women (Yu & Shepard, 1998), yet the experimental stimuli used did not symmetrically bracket this range. The WHR considered “high” in the Matsigenka study is the Shiwiar female average (Sugiyama, 2004a). No Shiwiar females had WHRs lower than .8, and the mean female WHR was .92. Labeling 0.9 WHR “high” under these circumstances is misleading, and using only .7 and .9 WHR (i.e., abnormally low and average) increases the probability that high body-weight preference will swamp any effects of WHR preference (Sugiyama, 1996, 2004a). Moreover, acculturated Matsigenka are exposed to a lower range of female WHR than are unacculturated Matsigenka. This exposure presents lower WHR in association with other cues to high female mate value in the bodies and faces of the nubile young women on beer posters and similar advertisements to which acculturated Matsigenka are exposed. We should expect WHR assessments to be updated across the life span in response to changes in the local cue structure of WHR. Yu and Shepard’s (1998) finding that more acculturated Matsigenka are exposed to a lower range of and prefer

lower relative female WHR than less acculturated Matsigenka is consistent with the context-sensitive WHR-assessment algorithm outlined above.

When I presented the standard 12-stimuli array to Shiwiar men, I found significant effects of weight on a series of attractiveness-related measures, but no significant effects of WHR. However, when I reduced the variance in weight of line drawings presented, and compared preferences to local distribution of female and male WHR, Shiwiar men chose lower- than- locally average WHR figures as more sexually desirable, youthful, and healthy than locally high-WHR figures. When asked to pick the most sexually attractive, fertile, best mother, and wife, Shiwiar men never chose locally high-WHR figures more often than locally low-WHR figures, and when asked to pick the least desirable on these traits, locally low-WHR figures were always chosen more often than locally high-WHR figures. However, sample size was small and replication with a larger sample is necessary (Sugiyama, 2004a).

Marlowe (2004) hypothesized that waist-to-buttocks ratio (WBR) was a critical feature used in female body shape attractiveness assessment. His results show that Hadza men, who show no preference based on frontal views of WHR, do find lower WBR more attractive: Specifically, buttocks extension was found to be a variable in attractiveness assessment. Although I did not test this dimension directly, my Shiwiar informants spontaneously noted that low WHR drawings had “no buttocks”—that is, low buttocks extension—and “no” or “straight waists.” Cross-cultural tests of preferences for this aspect of female morphology are warranted, but no more so than pelvic angle detection, relative pelvic width to shoulder width, and so on.

WHR does explain some of the variance in attractiveness ratings of women’s bodies, both in static front, back, and side views (Thornhill & Grammar, 1999; Grammar et al., 2002; Tovée & Cornelisson, 2001; Tovée et al., 2002) and in three-dimensional rotation (Fan et al., 2004), but body shape accounts for less of the variance in attractiveness ratings than BMI. Tovée and colleagues have reported a series of studies in which subjects assess the attractiveness of women’s bodies. They conclude that female WHR, and body shape generally, accounts for relatively little of the variance in female body attractiveness, perhaps, they suggest, because BMI and WHR covary, and BMI assessment is less variable than WHR depending on an individual’s

view (front versus side versus back). Conversely, when photos of men are assessed using the same methods, upper body shape accounts for the largest amount of variance in rated attractiveness (Maisey et al., 1999).

As noted earlier, studies based on photos of Western women over 18 (mean age 26, s.d. 8 years) present a limited range of the morphological variance to which WHR assessment is a hypothesized mate choice solution. WHR is hypothesized to distinguish pre- from postpubertal females, males from postpubertal females, pregnant from nonpregnant postpubertal females, relative parity, postpubertal females who are fertile from those suffering primary infertility, and fertile from postmenopausal women. Only the latter three issues could even potentially be tested in the Tovée and similar studies (e.g., Fan et al., 2004). In the population of women used as models, moreover, the number of women suffering primary infertility, the number of postmenopausal women, and variability in parity are all small. Determining the variance in reproductive value assessments accounted for by WHR requires subjects to compare figures encompassing the entire range of relevant stimuli: males and females of all ages and females of all levels of parity, primary infertility, and stages of pregnancy in a natural fertility population. In addition, the ecological reality of mating (and other social value) decisions seems to be better captured by choices between people, not abstract relative ratings along a Likert scale. Forced-choice methods may reveal effects of cues to social value that are obscured by having subjects rate stimuli on a scale.

Finally, the fitness effects of differences in attractiveness produced by particular reproductive value assessment adaptations targeting a specific cue can be associated with significant behavioral and fitness effects, even if the cue in question accounts for a relatively small proportion of the variance in attractiveness. Hughes and Gallup (2002) measured WHR of college men and women (none of whom were pregnant) and asked them to fill out a sexual history survey. Females with low WHR and males with WHR closest to .9 reported earlier age at first intercourse and more sex partners, extrapair copulations (EPC), and sex with individuals who were already in a relationship. This concurs with a study by Mikach and Bailey (1999) finding that women with lower WHRs engage in more short-term sex than those with higher WHR. In related research that replicated and extended Hughes and Gallup (2002) to test relationships between vocal

attractiveness and body morphology, the only association found between BMI and sexual behavior was that female age of first sexual intercourse was later among college women with higher BMI (Hughes et al., 2004).

Upper Body Morphology: Shoulders, Chest, and Breasts

Males and females exhibit sexual dimorphism in skeletal morphology and muscle mass as well as body fat distribution. One such feature is the circumference of the shoulders relative to that of the hips (shoulder-to-hip ratio [SHR]). Broad shoulders are associated with developmental effects of testosterone, such that men tend to have broader shoulders than women (Evans, 1972; Kasperk et al., 1997). In their sexual history study, Hughes and Gallup (2002) measured SHR as well as WHR of college men and women. Male SHR accounted for more of the variance in reported sexual behavior than did WHR. Men with high SHR reported earlier age at first intercourse, more sex partners, more EPCs, and more instances of being the extra-pair partner of a woman's EPC. Conversely, there was no association between female SHR and any of the sexual history measures. These findings bolster the claim that women find moderately broad shoulders and chests in men attractive (i.e., an inverted triangular shape of the upper torso) as long as they are not too "muscle bound" and that male shoulder width is a feature used by men in assessment of their rivals (e.g., Dijkstra & Buunk, 2001; Franzoi & Horvath). Horvath (1979) found shoulder width positively correlated with male attractiveness, and female ratings of color photos of male bodies show that waist-to-chest ratio (WCR) accounted for more of the variance in male body attractiveness than either WHR or BMI (see also Maisey et al., 1999). In their study of jealousy-provoking traits, Dijkstra and Buunk (2001) found that high SHR men were perceived as more attractive, and rivals with high SHR provoked greater jealousy in men than in women. But both sexes found rivals with higher SHR more physically and socially dominant.

While female SHR shows little effect on ratings of female attractiveness, breast shape and size do. Human breasts are highly sexually dimorphic, and women's breasts are large compared to closely related primate species. As such, they are likely the product of sexual selection. In natural fertility populations, breast morphology provides more powerful cues to age, parity, and pregnancy status than in nonnatural fertility

populations (Symons, 1979): Budding breasts are associated with pubescence; developed, firm, high breasts are associated with nubility; engorged breasts indicate lactation; and degree of breast “sagginess” and lack of fullness tracks increasing parity and declining reproductive value. The changes before and after first pregnancy are particularly striking. Large breasts may more clearly manifest these changes, such that larger breasts could provide honest cues to reproductive value. Symons (1979) predicted that firm breasts that point slightly up and out (angle of axis) with small areola would be more attractive because they are associated with young women (i.e., high reproductive value). All else equal, larger breasts show higher levels of asymmetry, so breast size may provide honest (costly) signals to phenotypic quality (Manning, 1997; Møller et al., 2004). In a study presenting college men with female line drawings that varied in WHR, weight, and breast size, Singh and Young (1995) found that slender, low-WHR figures with large breasts were judged most attractive, feminine, healthy, and desirable for both short- and long-term relationships. In their study of attractiveness based on body and facial traits of nude female photographs, Grammar et al. (2002) found significant positive correlations between breast size and attractiveness and negative association between areola size and attractiveness. Principal components factor analysis for 36 traits predicted to be associated with attractiveness showed that in a four-factor solution, there was high positive loading of breast size and angle of axis and negative loading of areola size on the factor Grammar et al. conclude is associated with nubility. Møller et al. (2004) looked at the relation among breast size, FA, and measures of female attractiveness and fecundity in two populations (United States and Spain). They found higher breast FA in women with large breasts than in women with small breasts and negative association between breast FA and age-independent fecundity (Manning et al., 1997, 2004). However, when expected symmetry was allometrically scaled to breast size, larger breast volume was associated with lower than expected symmetry (Manning et al., 1997). Breast asymmetry appears to be negatively associated with fitness (number of offspring) and positively associated with later age at first reproduction (Manning et al., 1997). Manning et al. (1997) conclude that women with higher levels of body fat have higher levels of estrogen (which reduces immune function), producing larger breasts, but that this tends

to increase asymmetry. Only women with high phenotypic quality can produce large symmetrical breasts, so large symmetrical breasts provide honest (costly) signals of high phenotypic quality.

Conclusions

My goal in presenting an outline of social value in human life history perspective was to present the foundation on which physical (and nonphysical) attractiveness across different domains of social value can most usefully be based and from which those conducting research on physical attractiveness could generate more specific adaptationist hypotheses and empirical tests. This should be axiomatic: Understanding of the mating preferences, differential parental solicitude, kin-based cooperation, and coalitional dynamics of all other species except *Homo sapiens sapiens* is based on advances in evolutionary life history theory, particularly those developed over the past 40 years. Adaptationist hypotheses about male and female mate value assessment explicitly start with consideration of this aspect of social value in evolutionary life history perspective (e.g., Buss, 1989; Buss & Schmitt, 1993; Gangestad & Thornhill, 1997a; Grammar et al., 2002; Manning, 1997; Møller et al., 2004; Sugiyama, 2004a; Symons, 1979, 1995; Thornhill & Gangestad, 1994, 1999; Thornhill & Grammar, 1999b), just as hypotheses about offspring phenotypic condition assessment explicitly start from parental investment theory (e.g., Apicella & Marlowe, 2004; Daly & Wilson, 1988; DeBruine, 2004; Hrdy, 1999, 2002; Mann, 1992; Platek et al., 2002, 2003, 2004; Trivers, 1972, 1974).

The study of physical attractiveness has gained significantly in theoretical and methodological sophistication over the past quarter century. Research on sexual attractiveness has progressed most (arguably) because theoretical development on mate choice in biology has a long history and because the adaptationist approach provided a clear, cross-species, theoretical basis for its investigation in humans. The adaptationist approach explicitly links theory and evidence that are normally disciplinarily partitioned (e.g., by departments or fields of biology, anthropology, psychology), which gives it a powerful integrated dimension. Symons's *The Evolution of Human Sexuality* (1979) is a benchmark in this regard: Since its

publication, an explicitly adaptationist approach to sexual attractiveness has increasingly informed research on human attractiveness in psychology. Further development of theory concerning the trade-offs involved in alternate sexual strategies in humans (e.g., Buss & Schmitt, 1993) has focused attention on context-sensitive mate selection for specific cues of reproductive value and phenotypic quality. For example, research on potential fitness trade-offs between female short-term and extra-pair mating strategies on the one hand and long-term mating strategies on the other led to the prediction and finding that women's mate preferences shift in the importance given to "good genes" traits and "good father" traits during the fertile and nonfertile phases of the ovulatory cycle (e.g., Franklin & Johnson, 2000; Johnston et al., 2001; Penton-Voak & Perrett, 2000). Prior to these predictions, research on female assessment of male attractiveness yielded contradictory results: Sometimes women preferred masculine and sometimes feminine faces. From now on, all research on women's attractiveness preferences must include data on ovulatory phase or else results will be confounded by these changes in preference. Similarly, Gangestad has shown individual differences in general mating strategies—what he calls <I>sociosexual orientation.</I> People with more "closed" sociosexual orientation tend to seek long-term mateships, have fewer mates, and begin having sex later in relationships, while those who have more "open" orientations show opposite tendencies. These tendencies could be mediated by hormonal effects during embryonic development and/or in "strategic" response to environmental effects during juvenile development (e.g., Belsky et al., 1991; Gangestad 1993). Because mate choice preferences change along the short- to long-term strategy continuum, all future research should include a soci-sexual orientation measure, or else results from open and closed orientation subjects may wash out the results. In sum, we have identified numerous adaptive problems associated with mate-value assessment, which have been used to generate hypotheses regarding the physical cues targeted by mate-value assessment mechanisms. Tests of these hypotheses have yielded a rich data base for further exploration. Researchers are beginning to address how much of the variance in sexual attractiveness each of these cues accounts for, as well as the context-sensitive design of the mechanisms that take these cues as input. A next stage of research would profit from including a more

evolutionarily relevant range of variation in experimental stimuli and regularly including subject data on known sources of systematic variability in mating preferences (e.g., fertility, sociosexual orientation, own attractiveness, short- versus long-term mateship).

Research into the relationship between attractiveness and cooperative, kin, and coalitional social value has progressed slowly, partly because an explicitly life history evolutionary approach has not been employed. Cunningham et al. (2002) present a multiple fitness model of attractiveness assessment, based on the observation that different physical traits may signal different qualities, but they do not explicitly organize their model in terms of different domains of human sociality in evolutionary life history perspective, nor do they ground their predictions in the relevant data from human evolutionary ecology. Keating (2002) and others note that social and physical dominance are important features in attractiveness assessment that can be assessed via physical cues, but they haven't grounded this observation in the evolutionarily relevant aspects of dominance behavior. Zebrowski and Rhodes (2002) suggest that because there are many types of attractiveness, measurement instruments should distinguish among them, yet most studies rely on "global 'attractiveness' rating scales" (p. 264).

In this chapter, I have tried to indicate what is known about the evolution of human life history as it relates to social value, in the hope that more psychologists will be stimulated to read the primary anthropological literature on this topic. The value of this approach to the study of attractiveness is highlighted by the questions that no study has asked, yet that seem obvious to evolutionary anthropologists interested in parsing social relations in small-scale, egalitarian societies (e.g., Patton, 2000; Sugiyama, 1999; Sugiyama & Scalise Sugiyama, 2003). Distal concepts such as physical cues to physical and social dominance have been investigated, but no study of attractiveness has asked whom subjects would rather be attacked by, attack, fight, go to war with, seek revenge against, or have on their side in a fight. No study has asked whom subjects would rather have seeking vengeance against them or whom they would rather have defend them against attackers. Although a few studies have asked whom subjects would rather have as friend or roommate and a number have investigated the hiring, salary, and other advantages of physical attractiveness, no one has yet asked with

whom subjects would most like to share food or who would be most likely to share food with the subject. No study has asked subjects whom they would rather have take care of their children, aid them in childbirth or in time of temporary disability, or establish trade relations with. And I have yet to find a study asking parents whom they would prefer their daughters or sons to have as friends, date, marry, have sex with, and so on based on physical appearance.

Complex information-processing adaptations are often expected to use informational cues from the environment to generate different psychological and behavioral outputs in response to different conditions. Therefore, hypotheses concerning such adaptations must delineate specific psychological properties (or their byproducts) that process local social and environmental cues to generate the intra- and intercultural similarities and differences found in attractiveness standards for different domains of evolutionarily relevant social value. Among the contextual variables that social value assessment adaptations are expected to include in their calculations are assessor's and assessee's sex, developmental stage, health, reproductive and mating status, aggressive formidability, alternative social options, and social value in different domains, which should influence the social strategies being deployed by the individual. Even though the underlying functional design of attractiveness-assessment adaptations is expected to be universal, we should expect to see strategic variation in its behavioral expression at the population, group, and individual levels.

Human physical attractiveness assessment is generated by adaptations functioning to evaluate evolutionarily relevant cues to human social value across multiple domains of interaction. Evolutionary human life history theory is instrumental in generating predictions about these domains and their associated cues. Unfortunately, the field of psychology continues to pay little attention to our best sources of data concerning the life history trade-offs that formed the selective parameters in which the adaptations comprising our social adaptations evolved and the likely range of variability across which they were selected to function: the ethnographic, archaeological, and paleo-anthropological record of natural fertility, small-scale societies. With relatively few exceptions (e.g., Jones & Hill, 1993; Wetsman & Marlow, 1999; Grey & Marlow, 2004; Sugiyama, 2004a; Yu & Shepard, 1999), direct tests of adaptationist hypotheses

concerning physical attractiveness have not been conducted in small-scale, natural fertility populations, and anthropologists either conducted or collaborated on all of these studies. Conversely, the vast majority of anthropologists have not been trained to think about psychological processes in a way that would allow them to produce reasonable procedural hypotheses about how psychological adaptations might plausibly function (in a procedural cognitive sense). Of those who have, human behavioral ecologists have the scientific, empirical, and adaptationist expertise (see Hill & Hurtado, 1996; Smith et al., 2001) that make them natural research allies for psychologists (e.g., Jones & Hill, 1993; Wetsman & Marlow, 1999; Sugiyama et al., 2002; Barrett et al., 2004). An apparent impediment to this kind of collaboration seems to be a common misperception that an evolutionary psychological approach predicts universality at the level of psychological or behavioral output instead of at the level of the functional organization of the information-processing system.

For example, in their interpretation of the observed cross-cultural variation in female height, RS, and marriage patterns, Sear et al. (2004) contrast their interpretation of the evolutionary psychology argument that complex cognitive adaptations will usually be universally distributed in a species with their (behavioral ecological) approach, stating:

We believe that a much more satisfactory approach to the study of human behavior is to take social and ecological conditions into account, and to test evolutionary hypotheses across a variety of different cultures. . . . Given . . . the . . . wide range of ecological conditions that humans are able to live in, we think that human variation is, in any case, far more interesting to research than are human universals. (Sear et al., 2004, p. 12)

It is indeed true that more cross-cultural research is needed to test hypotheses about evolved mental function, and it is also true that the hypotheses about psychological design must include consideration of the ancestral range of variability in socioecological environments that constitute selection pressures and the cue structures

with which the adaptations function to produce locally contingent behavioral expression (e.g., Sugiyama, 1996, 2004a; Sugiyama et al., 2002; Tooby & Cosmides, 1989, 1992). However, the larger message of Sear et al. mischaracterizes the evolutionary psychology approach, leading to what appears to be wholesale dismissal of the programme. To reiterate, evolutionary psychology predicts or expects the following: (1) complex information processing adaptations of the mind will usually be universally distributed in the species, (2) these adaptations will take local environmental information as input such that their outputs will differ depending on specific features of local conditions (what behavioral ecologists refer to as “reaction norms”), and (3) adequately characterized cognitive adaptations will specify how specific kinds of local environmental information are used by the adaptation in question to produce the variability in behavior that we observe (e.g., Sugiyama, 2004a; Tooby & Cosmides, 1989, 1992). My discussion of the design features necessary in a WHR-like assessment adaptation provides a case in point, as does research on menstrual shift in mating preferences and variation in weight preferences. Cross-cultural research is critical to this enterprise (e.g., Buss, 1989; Jones & Hill, 1993; Marlowe & Wetsman, 2001; Sugiyama et al., 2002; Sugiyama, 2004a; Tooby & Cosmides, 1989, 1992). Studying variability without considering it in terms of underlying information-processing regularities (and their decision-making outcomes) makes understanding of the generation of cross-cultural variation impossible. What is needed, then, is for psychologists to collaborate in cross-cultural research with evolutionary anthropologists and, conversely, for evolutionary anthropologists to more generally recognize that evolutionary psychological hypotheses should often predict context-dependent variation (e.g., Sugiyama, 2004a; Sugiyama et al., 2002; Tooby & Cosmides, 1992) just as behavioral ecological models do (e.g., Hill & Hurtado, 1996; Smith et al., 2002). Anthropologists can advance psychologists’ appreciation of variability in local cues and behavioral outputs; in turn, psychologists can design their hypotheses to account for this variability and design their studies to include an ecologically relevant range of stimuli. I can’t think of any aspect of human attractiveness research, evolutionary psychology, or psychology more generally, that wouldn’t benefit from this approach. Because all normal conspecifics are expected to share complex adaptations

or a facultative developmental programs that builds them, for evolutionary psychologists, this cross-cultural testing is a requisite component of our research program.

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