Psychological Inquiry
2006, Vol. 17, No. 2, 75–95

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TARGET ARTICLE

Evolutionary Foundations of Cultural Variation: Evoked Culture and Mate Preferences

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We articulate an evolutionary perspective on cultural variation, centering on the concept of evoked culture. We then demonstrate how the framework of evoked culture has been used to predict and explain cultural variation and report new tests of hypotheses about cultural variation in mate preferences. These tests demonstrate the predictive power of ecological variables such as parasite prevalence that are implicated by evolutionary psychological theories. New empirical tests provided little support for the predictions advanced by competing social role theories (e.g., Eagly & Wood, 1999), with some findings running opposite to those predicted by such theories. We propose that a well-articulated evolutionary perspective on cultural variation may be particularly useful because it can specify how variation in cultural practice itself may emerge. We conclude that discussions of cultural variation should move beyond false dichotomies of social versus biological and suggest that evolutionary psychology provides frameworks that transcend these dichotomies.

In the cross-cultural record, two facts stand out. First, people in different cultures vary widely in their behavior, beliefs, and practices. Substantial cultural variation exists in just about every arena of human life, from subsistence strategies, food sharing, and child care arrangements to religious beliefs, body decoration, and leisure time pursuits. Second, human universals underlying this cultural variation abound (Brown, 1991). Thus, although marriage arrangements vary widely across human societies, long-term, culturally recognized, and sanctioned pair bonds occur in all human groups (Murdock, 1949); special terms distinguishing kin exist in all natural languages (Brown, 1991); everywhere, basic facial expressions appear to be interpreted similarly (Ekman et al., 1987); and in all known cultures, men are overwhelmingly the perpetrators of murder (Buss, 2005; Daly & Wilson, 1988).

A comprehensive understanding of human behavior must account for universal features as well as variation between and within cultures. Some theories tended to focus on one or the other. Nativist theories typically emphasize the universals of human life, proposing a basic human nature that is relatively unchanged across time and place (e.g., Lorenz, 1963). Cultural variation, in many of these views, is a thin veneer obscuring a clear view of invariant commonalities. By contrast, social constructionist models generally focus on the particulars of individual cultures and variations among them (e.g., Geertz, 1973, 1983; Shweder, 1990). Because many of these theories propose or imply that the differences in individuals' beliefs and practices across cultures arise from exposure to different cultures, these theories explained the core elements of cultural practice by invoking individuals' experiences rather than intrinsic generative processes of human nature.

Most theorists recognize that genes and environment influence behavior only in a context partly defined by the other, such that a dichotomy between nature and nurture (the idea that influence can be understood through reference to only genes or environment, respectively) is wrongheaded. Behavior results from an underlying, often universal, evolved developmental system (itself consisting of both genetic and environmental components) in conjunction with individual environmental influences, including social experiences. This developmental system gives rise to psychological traits. In some cases (e.g., binocular vision), canalization may be sufficiently strong such that under all normal developmental environments, the traits are universally invariant. In other cases, evolved developmental systems are designed to produce variable phenotypic traits, contingent on variable environments. In all cases, however, universal invariance or variable traits are outcomes of systems. One role of theory is to specify how evolved developmental systems and psychological adaptations translate variable environments into behavioral outcomes, thus creating variation within and between cultures.

This view implies that it is meaningless to place the cause of human behavior either in the individual's essential character or in the environment. Hence, it is misleading to state that behavioral variants are "due to" environmental variation, even when all behavioral variation systematically covaries with environmental variation. We describe several examples throughout this article but consider a simple, nonpsychological example. Variation in skin tanning covaries strongly with amount of environmental exposure to sunshine. A comprehensive understanding of this variation, however, requires knowledge of the underlying biological adaptation for protective tanning that is designed to respond to sunshine by producing melanin. The only way that environmental variation can produce behavioral variation is via an underlying evolved system, which any complete understanding of the behavioral variation must describe. This view also implies that behavioral variation due to environmental variation cannot be construed as a superficial veneer overlying an essential core. When an underlying psychology is designed to produce behavioral variation across different life circumstances, the underlying psychology cannot be separated from the existence of behavioral variation. Humans are essentially neither aggressive nor peaceful, monogamous nor polygynous; rather, humans respond aggressively or cooperatively and mate monogamously or polygynously depending on specific life histories and current environmental arrangements.

Where reasoned debate remains, it largely concerns the precise ways through which evolved systems give rise to universal or variable outcomes. Evolutionary psychology offers one lens through which to view and explore the nature of these systems. Although evolutionary psychology can and has been used to identify and explain psychological features that are universal or near-universal (e.g., Brown, 1991), it can also identify and explain psychological features that are highly variable across cultures.

Most participants in contemporary scientific debates about culture do not propose that genes or environment can operate alone. Nevertheless, there is significant ongoing debate about just what an interactionist perspective on culture entails (Eagly & Wood, 1999; Kasser & Sharma, 1999) as well as how an evolutionary psychological approach can be used to understand cultural variation, if at all (Wood & Eagly, 2000a, 2000b, 2002; Rabinowitz & Valian, 2000).

The primary purpose of this article is to articulate how evolutionary psychological theory founded on specialized psychological adaptations can be used to predict and explain cultural variation. As an illustration, we use cross-cultural data on mate preferences. In our analyses, we test new evolutionary predictions about cultural variation. We argue that an evolutionary psychological perspective on cultural variation can provide a deeper explanation of cultural variation in behavior than alternative theories because it can specify how variation in cultural practice itself may emerge.

Cultural Variation and Evolutionary Psychology

The Evolution of Environmental Contingency

Historically, general learning theories characteristic of the behaviorist approach in psychology emphasized the ways by which environmental arrangements affect behavior (e.g., Hull, 1943). Even these theories did not ignore the nature of an evolved, adaptive system by which environmental influence occurs. Darwin is mentioned on the first page of Hull's (1943) *Principles of Behavior* and a second (and last) time several pages later, where his effect on Hullian theory is revealed: Adaptive adjustments to initial response hierarchies are made through the process of drive reduction, whereby drives are based on fundamental requirements for survival and reproduction, such as food, water, and sex. According to this view, then, organisms make adaptive adjustments to situations through a single evolved process: drive reduction. Subsequent behaviorists such as B. F. Skinner (1981) also recognized the critical role of adaptation and natural selection. Some presented compelling evidence for the existence of multiple evolved learning mechanisms—adaptations for food conditioning, for example, differ qualitatively from those for sexual conditioning (Domjan, 1997; Garcia & Koelling, 1966; Herrnstein, 1977).

Evolutionary psychologists also argue that animals adjust their behavior adaptively in response to the particular environmental arrangements that confront them. In contrast to early general learning theories, however, this approach proposes that adaptive adjustment cannot be accounted for by a single evolved process, as selection is unlikely to favor such an outcome. Though organisms should be designed to behave in ways responsive to their particular environments, "[developmental and psychological] designs that produce 'plasticity' can be retained by selection only if they have features that guide behavior into the infinitesimally small regions of relatively successful performance with sufficient frequency" (Tooby & Cosmides, 1992, p. 101). A contingent patterning of behavior that occupies these small regions of performance is likely to require developmental and psychological adaptations that are specific to particular problem domains (Barrett, 2005; Tooby & Cosmides, 1992).

The problem-specific nature of adaptations can be illustrated with several physiological adaptations. Some skin tissue is designed to callus when abraded. Other skin tissue increases melanin production in response to exposure to sunlight. The pupil of the eye is designed to constrict or enlarge in response to lighting intensities. The immune system has a specific capability to "learn" how to recognize self and attack nonself entities to which it is exposed. These systems share a common feature, environmental contingency, which permits the organism to adaptively adjust to its individual circumstances. This common feature should not obscure the fact that these evolved systems are clearly distinct and responsive in their own highly particular ways to circumstances, which can be understood in terms of the specific problems they evolved to solve (i.e., specific selection pressures that gave rise to them).

The evolutionary psychological perspective argues that brains, too, should consist of adaptations specialized for specific functions in response to particular selection pressures. Only a brain that organizes responses to particular aspects of the environment in an adaptively targeted fashion could be expected to be biologically successful. Hence, adaptations that underlie visual perception and language production should contain specialized design features partly or wholly distinct from adaptations that underlie competition for and selection of mates, which should have design features distinct from those underlying kin recognition, cooperative social relations, or foraging decisions.

Many perspectives acknowledge the existence of distinct psychological systems accounting for adaptive adjustment. Few psychologists would claim, for instance, that the processes underlying color constancy achieved in variable lighting conditions are the same as those underlying language learning. Evolutionary psychology is unique in its argument that discovery of the design of these systems is fostered by the explicit aid of evolutionary theories about the selective environments in which the systems evolved.

Environmental Contingency in Mating Strategies

The heuristic value of the evolutionary approach is illustrated by work on nonhuman species. Behavioral ecologists study how animals adaptively adjust their behavior to their ecologies. They generally assume that adaptive adjustments are problem-specific and involve a multiplicity of adaptations (e.g., Krebs & Davies, 1993). Consider, for example, the collared flycatcher, a bird species on the island of Gotland in the Baltic Sea. Male and female pairs form socially monogamous unions. Nonetheless, about 15% of eggs are sired by extra-pair males. When sexually mature, males develop a patch of white feathers on their foreheads, and males who sport larger patches account for a disproportionate number of the extra-pair fertilizations (Sheldon & Ellegren, 1999). Behavioral ecologists speculated that these males are selected as extra-pair mates because forehead patches are sexually selected indicators of good genes. As predicted by this hypothesis, (a) females whose social mates have relatively small forehead patches are particularly likely to engage in extra-pair copulations (Sheldon, Davidson, & Lindgren, 1999); (b) females tend to seek extra-pair matings when they are most fertile (Michl, Torok, Griffith, & Sheldon, 2002); (c) offspring of males with large forehead patches are in better condition (as measured by standard body weight assessments) compared to their half-siblings who are sired by the female's social mate (Sheldon, Merila, Qvarnström, Gustafsson, & Ellegren, 1997); (d) the offspring of males with large forehead patches tend to be male, the sex that most benefits from having such a sire (Ellegren, Gustafsson, & Sheldon, 1996), which suggests that flycatchers adaptively adjust the sex ratio of offspring depending on their own qualities or the qualities of their mates. It is implausible that the adaptive adjustments of the mating behavior of collared flycatchers are due to adaptations that affect all of their other behavior, such as how they learn and remember food sources or how they engage in other social interactions. Rather, just as specific skin tissue of humans responds to sunlight by producing melanin, specific mating behaviors of collared flycatchers appear to have been specially shaped to be conditional on specific, context-meaningful environmental features. Discovery and understanding of these conditional responses would have been unlikely if not for explicit evolutionary theory about sexual selection on these birds.

Humans should also possess a psychology that is sensitive to a large number of adaptively relevant environmental variables. To illustrate, we consider an example analogous in many ways to the context-specific responses of the collared flycatcher. Recent research has shown that changes in women's sexual preferences and interests are intricately patterned. Fertile women particularly prefer the scent of men who evidence a robust developmental history, as indicated by phenotypic cues such as bodily symmetry (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999b; Thornhill et al., 2003), more masculine faces (Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000), and male behavioral displays of social presence and intrasexual competitiveness (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004). These shifts appear to be specific to when women evaluate men as short-term sex partners, not long-term mates (Gangestad et al., 2004; Haselton & Miller, 2006; Penton-Voak et al., 1999). Yet not all desired traits are more preferred near ovulation. For instance, traits particularly valuable in long-term mates, such as resources, do not show ovulatory increases in female preference (Gangestad, 2004; Haselton & Miller, in press; see also Thornhill et al., 2003). The only explanation as yet proposed to account for these changes is that selection has shaped female preferences for indicators of genetic benefits to offspring in short-term mates to be enhanced mid-cycle—the time when women could have benefited by mating with such partners. Indeed, women appear to show particular sexual interest in men other than primary social partners when they are fertile (Bellis & Baker, 1990; Gangestad, Thornhill, & Garver, 2002; Haselton & Gangestad, 2006; but see also Pillsworth, Haselton, & Buss, 2004). And emerging evidence suggests that women with partners lower on hypothesized fitness indicators are those whose preferences for extra-pair partners are particularly likely to increase as ovulation approaches (Haselton & Gangestad, 2006; Gangestad, Thornhill, & Garver-Apgar, in press).

This same line of research has demonstrated a variety of additional context-specific conditional responses: (a) Women's primary male partners respond contingently based on correlates of their fertility status; men appear to be more vigilant of the whereabouts of partners who are in fertile phases than those same partners in nonfertile phases (Gangestad et al., 2002; Haselton & Gangestad, 2006); (b) women who see themselves as physically attractive particularly prefer masculine faces, presumably because they face smaller trade-offs between qualities advertised by facial masculinity and the effort a partner invests in the relationship, and hence are more able to command both (Little, Burt, Penton-Voak, & Perrett, 2001); (c) when women particularly value investment in a relationship from a man, they may prefer less masculine faces (Penton-Voak, 2001); (d) when women pursue a short-term mating strategy, they show an elevated preference for men who are physically attractive and sexy (Buss & Schmitt, 1993; Greiling & Buss, 2000). In sum, the available evidence points to an intricately designed, environmentally sensitive psychological architecture.

Women's sexual interests are dependent on external factors, such as relationship context (short term vs. long term) and partner quality, as well an important internal cue, her cyclical fertility status. Considered as a whole, the patterning of women's sexual interests and preferences cannot be understood as a set of contingent responses that have been shaped by broad, domain-general learning processes. Rather, the contingent nature of these interests is best explained by invoking the concept of evolved psychological architecture containing design features dedicated to solving specific adaptive problems in the domain of mating.

This area of research provides an example in which variable contemporaneous inputs produce changes in psychological and behavioral outputs. Evolutionary psychologists also expect responses to environmental factors that may developmentally calibrate or condition psychological adaptations, producing more stable differences between individuals occupying different ecologies (Buss, 1991; Tooby & Cosmides, 1990). In short, this conceptual framework points to the possibility of specialized, problem-specific adaptations underlying patterns of within-group similarity and between-group difference—what scientists often refer to as culture.

Evoked and Transmitted Culture

Culture can be conceptualized as sets of practices, beliefs, ideas, values, inventions, artifacts, and attitudes that characterize groups of people. There are at least two pathways through which cultural variation may emerge: transmission and evocation.

First, the elements of culture may be acquired through modeling or social learning and transmitted throughout a population. This is, of course, the dominant view in the social sciences and is likely one major source of cultural variation. For example, the development and retention of cumulative knowledge in the form of technology (e.g., canoe-making, agricultural practices, systems of mathematics) is probably best explained by cultural transmission (see, e.g., Boyd & Richerson, 1985, Henrich & Gil-White, 2001; see also Flinn, 1997).

Second, some variation across cultures may be understood in terms of differences in the social and ecological conditions within which groups live and the specially designed adaptations humans have for responding to them. Tooby and Cosmides (1992) introduced the term "evoked culture" to refer to the fact that these conditions (e.g., war, drought, abundance) provide inputs for a richly responsive domain-specific psychology and thereby "evoke" different behavioral repertoires, forging different elements of culture. The specific content and organization of culture, then, is partly a product of domain-specific phenotypic sensitivities to environmental input in conjunction with specific input. Metaphorically, evoked cultural variation can be understood in terms of a specially programmed jukebox (Tooby & Cosmides, 1992). The jukebox is designed to play a different song depending on environmental inputs (e.g., temperature, population density). As the jukebox is moved from one environment to another (or as environments change temporally), the jukebox plays different tunes. The variable tunes played under specific conditions are due to the jukebox's design in concert with specific environmental inputs (see also Kenrick, Li, & Butner, 2003). To propose that this process accounts for some important forms of cultural variation is not to deny that human learning occurs but rather to shift the emphasis toward understanding how selection has shaped domain-specific phenotypic sensitivities to environmental inputs.

The preceding discussion of specialized contingent responses points to one set of paths by which culture may be evoked. In socioecological circumstances in which women should particularly value male relationship investment, they may prefer less masculine faces; when investment is not especially valued, or when women anticipate only short-term mating, women's preferences may shift to more masculine faces and other characteristics indicative of good genes (Penton-Voak, 2001).

How Cultural Variability May Reflect Evoked Culture

In this section, we discuss in greater detail two examples of how evolutionary scientists predicted and explained cultural variation in terms of specialized adaptations through which particular circumstances evoke different practices and preferences. (For additional examples see Alexander, Hoogland, Howard, Noonan, & Sherman, 1979; Gaulin & Boster, 1992; Holden & Mace, 1999; Mace & Holden, 1999; Schmitt, 2005.)

Mate Preferences and Women's Contribution to Direct Production

Calorie production by men and women. Kaplan, Hill, Lancaster, and Hurtado (2000) argued that a significant aspect of hominid evolution giving rise to long life spans, prolonged investment in juveniles, and large brain size is that, compared to our nearest relatives, humans consume high-quality but difficult to extract resources such as animal protein. Whereas chimpanzees obtain about 95% of their calories from collected foods requiring no extraction (e.g., fruits, leaves), only about 8% of calories consumed by modern hunter-gatherers are from foods requiring no extraction. Both men and women contribute substantially to their own subsistence. In the majority of hunter-gatherer populations studied to date, however, the average male adult generates more calories than he consumes—mostly through hunting. These food resources yield benefits for reproductive women and juveniles by providing extra calories and macronutrients such as protein. Marlowe (2001) estimated that, on average, men produced 64% of the calories in all 95 foraging societies on which sufficient information is available. In Kaplan et al.'s (2000) analysis of studies that carefully measured produced foods in nine hunter-gatherer societies, men generated on average about 66%.[1] No such surplus of calories is generated by male chimpanzees. Women in traditional societies can and do turn the surplus of calories generated by men into production of offspring and thereby reproductively benefit from this surplus generated through male hunting (Marlowe, 2001).

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[1] Broader samples of cultures (such as the widely used 186-culture Standard Cross-Cultural Sample) include societies with more developed forms of agriculture, which may be less relevant to an understanding of human societies prior to the past 10,000 years. Nonetheless, estimates based on them are similar: 65% in the Standard Cross-Cultural Sample (Schlegel & Barry, 1986) and 65% in a broader sample of 499 societies (Sanday, 1973). Wood and Eagly (2002) cited Aronoff and Crano's (1975) mean estimate of 44% of female contribution to subsistence (56% male contribution), based on 862 societies. As was noted in a response by Carroll (1976), this estimate deviates from others, for reasons that an exchange was unable to fully resolve. We noticed that Table 3 of Aronoff and Crano, which reported a grouped relative frequency distribution of female contribution to subsistence across all 862 societies, implies a possible range of 33% to 42% for the mean, with a best guess of 38%—close to other mean estimates. Thus, their calculation appears not to have been the average of all societies' female contributions to subsistence, which probably explains the deviation of their figure from others.

The implications of this surplus for an understanding of human mating and parenting is a matter of debate. Hawkes and colleagues (e.g., Hawkes, 1991; Hawkes, O'Connell, & Blurton Jones, 1991; Hawkes et al., 2001) argued that men in hunter-gatherer groups (e.g., the Hadza and Ache) have little opportunity to direct resources to their own mates and kin, and, hence, their hunting has not evolved as a means of directly providing nutritional benefits to mates and offspring. Kaplan et al. (2000) argued that these male activities have been shaped by selection to partly function as parenting effort. As Hawkes et al. (2001) acknowledged, the wives and children of good hunters in the Hadza are better nourished and, hence, even if male hunting has not evolved for family provisioning, the average ancestral woman could have materially benefited from choosing a man with better access to resources (e.g., through men's enhanced status among men and thereby their ability to protect mates). Indeed, they note that Hadza women prefer to marry good hunters.

Variation in benefits to women through male caloric subsidies. Although women's work is clearly important to child outcomes (e.g., Hawkes et al., 2001), in traditional cultures women's direct production of nutritional resources may interfere with their reproduction by increasing the interval between births and thereby reducing offspring number (e.g., Schlegel & Barry, 1986; see also Kaplan et al., 2000). Hence, across foraging societies, greater male contribution to diet is associated with greater female reproductive success (Marlowe, 2001). Men may also benefit from mating with efficient, industrious mates but not necessarily ones who invest considerable effort into access to resources or status competition. Thus, as Buss (1989) predicted and found, modern women across a range of diverse cultures do appear to place greater emphasis on a mate's access to resources than men do (see also Buss, Shackelford, Kirkpatrick, & Larsen, 2001; Kenrick & Keefe, 1992; Sprecher, Sullivan, & Hatfield, 1994; Wiederman, 1993).

In foraging populations, however, the degree to which women and juveniles benefit from male hunting varies. Indeed, in many groups that particularly rely on gathered (as opposed to hunted) foods, women generate more calories than do men (Kaplan et al., 2000; Marlowe, 2001; Sanday, 1973; Schlegel & Barry, 1986). The variation partly depends on ecological factors (e.g., Marlowe, 2001; Wood & Eagly, 2002). Women can generate dietary resources at a greater rate in some environments than in others (even while caring directly for offspring, e.g., through gathering, horticulture, fishing, or hunting of small animals). In these circumstances ancestrally, the value of men's contribution to producing nutritional resources may have been less, and men may have been selected to shift effort to activities other than hunting and foraging (e.g., alternative activities to compete against men and gain access to mates). Women may still have benefited from choosing men with the ability to produce resources, but these advantages were probably smaller when the diet did not consist of large shares of meat.

Due to varying relative benefits from mate preferences for specific attributes such as access to resources, men and women may have been selected to vary the emphasis they placed on particular mate preferences as a function of the ecological factors associated with the degree of female participation in food production. When men generate a smaller surplus in calories, women may place less emphasis on male resource acquisition abilities. Hence, the sex difference in preference for a mate with high access to resources may be muted in circumstances in which women participate more heavily in direct production (see also Schmitt, 2005).

When women are not involved in direct food production, their work may focus more on domestic tasks such as food preparation. One might also expect, then, that when women do not contribute as much to subsistence, they place fewer demands on a mate to help in these other domains. By contrast, in conditions in which men contribute fewer nutritional benefits to women and offspring, an evoked culture perspective might predict that women choose men on the basis of desirable characteristics other than ability to provision (e.g., status advantages that provide direct benefits mediated through a social network, genetic benefits to offspring; e.g., Gangestad & Simpson, 2000; Low, 1990b). As a result, one should expect effective polygyny (variance in men's sexual access to women) to increase. Moreover, when women depend less on male contributions, they may be more willing to engage in extramarital relations or, relatedly, be less concerned about exhibiting restrictive sexual attitudes to their mates (e.g., Gangestad & Simpson, 2000; Schmitt, 2005). In summary, we might expect that, as a function of women's contribution to subsistence (dictated, at least partly, by ecological factors), a variety of other features, including mate preferences and sexual attitudes, also change as a result of richly responsive, domain-specific psychology sensitive to these variations.

Indeed, the anthropological literature on traditional societies reveals a number of associations between women's contribution to subsistence and variations in mating and sexuality. High levels of female contribution to subsistence are associated with greater degrees of polygyny (e.g., Schlegel & Barry, 1986). And although Schlegel and Barry did not find that levels of extramarital mating in the Standard Cross-Cultural Sample database were significantly associated with female contribution to subsistence in the overall sample, they did find an association with more permissive attitudes toward premarital sex. Detailed studies of a number of these cultures point to high levels of female infidelity (particularly in Oceania, e.g., the Tiwi, Trukese, Trobrianders; Flinn, 1981). These associations are consistent with the idea that aspects of culture are evoked by women's relative contribution to subsistence.

Based on this same reasoning, Low (1989) predicted relations between indexes of women's control of resources and child-rearing practices in the Standard Cross-Cultural Sample. She found that girls' achievement and aggression were more encouraged and obedience less encouraged as female control of resources increased.

Social role theory and variation in women's preference for resources across cultures. Low's (1990b) analysis is also consistent with Eagly and Wood's (1999) recent findings that the sex difference in mate preferences for resource control varies with women's relative empowerment (also see Kasser & Sharma, 1999). The United Nations publishes two indexes used by Eagly and Wood as measures of gender equality: the Gender Empowerment Measure (GEM), a measure of women's access to positions of power (legislative and managerial positions), representation in professional or technical occupations, and women's income relative to men's; and the Gender Development Index (GDI), a complex measure of the relative education, literacy, life expectancy, and income of the sexes.[2] The GEM correlated with the size of the sex difference in preference for a mate with prospects for financial success when the mate preference was assessed by both a rating measure (r = –.29) and a ranking measure (r = –.43). The associations between the GDI and these measures were weaker but in the same direction (–.23 and –.33). The GEM and GDI also predicted the sex difference in mate preferences for domestic skill and age.

Eagly and Wood (1999) explained these findings largely in terms of social roles (see also Buss & Barnes, 1986). In a subsequent article, Wood and Eagly (2002) specifically proposed that male and female divisions of labor are influenced by evolved bodily differences, including the reproductive role of women. They proposed that these bodily differences, and not sexual selection acting directly on men's and women's psychologies, largely explains variation across cultures in male and female preferences, as well as any pancultural sex differences (Wood & Eagly, 2002). That is, the utilities that men and women perceive are based in part on sex-typed physical attributes in conjunction with local settings; these produce differing social roles for men and women through learning. This learning presumably does not involve sex-differentiated learning processes but rather sex-differentiated inputs (Wood & Eagly, 2002; see also Eagly & Wood, 1999). Analogously, tall and short people may learn different repertoires not because they have different psychological adaptations for learning, but rather because they experience different environments.

Although Low's (1990b) hypothesis and Wood and Eagly's (2002) biosocial account each propose that environmental factors adjust mating practices, their explanations for how this adjustment occurs are divergent, and therefore their proposals should be treated as competing hypotheses that may explain the associations Eagly and Wood (1999) documented. Wood and Eagly's account suggested that different cultural practices are evoked by different ecologies: Means of economic production affect sexual division of labor, which thereby affect cultural practices. Low's hypothesis is that humans possess domain-specific adaptations that adjust mating behaviors depending on environmental cues linked with differential fitness payoffs in ancestral environments.

We now turn to a second example of how the concept of evoked culture leads to predictions about cultural variability.

Mate Preferences and Parasite Prevalence

Parasite threat. Pathogens pose threats to the health of any long-lived organism. Although hosts should evolve defenses against pathogens, no solution to the threat of pathogens is final because pathogens themselves evolve to overcome host defenses. It is no surprise, then, that pathogens are major killers of humans, particularly early in the life course. This was almost certainly true in ancestral human groups. In extant hunter-gatherer groups, about 30% to 50% of the population dies before reaching reproductive age, most from disease (e.g., Hill & Hurtado, 1996).

In humans, as well as nearly any host of pathogens, we should expect the evolution of mate preferences designed to discriminate among potential mates on the basis of health. Healthy mates are less likely to pass on pathogens to the mate chooser and are more likely to survive to invest in offspring—investment that is critical to the survival of offspring in human hunter-gather groups (e.g., in the Ache; Hill & Hurtado, 1996). Furthermore, the fact that hosts must continually evolve to remain adapted to pathogens that perpetually evolve themselves has as a consequence that hosts will, at any point in time, differ in their ability to resist pathogens, particularly macroparasites (e.g., Hamilton, 1980). Thus, choosing a mate who is healthy may result in more disease-resistant offspring (Hamilton & Zuk, 1982).

Overt signs of poor health (open sores, oozing pustules, lesions, emaciation, yellow eyes) should be generally disfavored by members of both sexes. There are also subtle signs of health and overall condition. Symons (1979) argued that "physical attractiveness" partly reflects an evolved favorable response to features that function as "health certificates," characteristics associated with healthy condition (see Sugiyama, 2005, for a comprehensive review of the evidence). These characteristics may include those promising a capacity to resist pathogens and hence pathogen-resistant genes giving advantages to offspring.[3]

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[2] One difference between these indexes is that numerical values in the GDI are lower when societies diverge in either direction from gender equality—though, because all variables except life expectancy are always greater for men than women, the measure largely taps the extent to which female outcomes match those of men.

[3] Rhodes et al. (2001) examined the association between components of physical attractiveness (averageness and symmetry) and actual health records and found few relations. As noted by Thornhill and Gangestad (1999a), however, "good condition" is a more general concept in evolutionary biology than in everyday usage. The individual in good condition has an ability to take in and effectively "allocate" nutritional resources to fitness-enhancing activities. Two individuals of equal health may still differ in condition. In fact, under some circumstances individuals in better condition may be more susceptible to pathogens (e.g., when their optimal strategy for allocating energy leads them to actually weaken immune function in favor of alternative fitness-enhancing activities; see Getty, 2002; Kokko, 2001). That this is so should not obscure the fact that their condition gives them reproductive advantages over others.

Parasites and polygyny. Low (1990a) argued that humans living in areas with higher levels of parasites should have higher levels of polygyny. Her argument was that parasites compromise the investment capabilities of some portion of men, rendering fewer men viable mates. As a result, women will more often cross a "polygyny threshold," the point at which becoming a second mate of a man is more desirable than becoming the first mate of the most attractive available unmated man (Orians, 1969). In the Standard Cross-Cultural Sample, her prediction was confirmed; an index of parasite prevalence (including *Leishmania*, *Trypanosoma*, malaria, *Schistosoma*, filaria, spirochetes, and leprosy) predicted the degree of polygyny across cultures.

Parasites and physical attractiveness. In a subsequent study, Gangestad and Buss (1993) asked whether mate preferences shift when individuals occupy ecologies with high levels of parasites. In such circumstances, we might expect individuals to place greater weight on physical attractiveness as a certificate of current health or an indicator of pathogen-resistant genes. Additional analyses of the cross-cultural data from Buss (1989) revealed that, indeed, parasite prevalence is positively correlated with importance of physical attractiveness as a mate preference for both sexes, using culture as the unit of analysis. Gangestad and Buss interpreted these differences as reflecting differences in evoked culture—the cultural patterns were due to responses of an evolved, specially designed mating psychology to ecological factors that moderate the association between certain characteristics (in this case, physical attractiveness) and mate value.

New predictions derived from the parasite hypothesis. Additional predictions can be derived from the preceding logic of the parasite hypothesis. In addition to physical attractiveness, a number of other characteristics from the 37-culture study may be associated with mate value. These predictions are as follows:

1. *Current health.* Signs of current health may indicate low current parasite load and high parasite resistance; hence health should be preferred more in parasite-prevalent environments.
2. *Good heredity and robustness.* Likewise, signs of physical robustness or a family history thereof may indicate low current load and high resistance; hence they should be preferred more in parasite-prevalent environments.
3. *Intelligence and intrasexual competitive abilities.* Low (1990a) argued that sexual selection increases in pathogen-prevalent environments; male reproductive success in particular should vary more in such environments. Increases in sexual selection may increase male attempts to display good condition through successful intrasexual competition. Work using fluctuating asymmetry as a marker of developmental health (asymmetry due to imprecision of development due to perturbations caused by disease, mutations, and toxins) has shown that male social dominance and intelligence are associated with good developmental health (see Gangestad & Thornhill, 1997). In parasite-prevalent environments, intellectual abilities may be compromised by parasites (e.g., Watkins & Pollitt, 1997) and, hence, male intelligence and intrasexual competitive abilities may be particularly valued in pathogen-prevalent environments (see Miller, 2000, for additional arguments for the importance of intelligence as an indicator of pathogen resistance).
4. *Paternal investment.* Mate selection often, if not always, requires tradeoffs. If men are valued for their health because it signals heritable ability to resist pathogens (e.g., as revealed through intrasexual competitive abilities and intelligence), women may compromise their desire to have a mate who is highly investing in offspring for access to a higher value mate (Gangestad & Simpson, 2000). Note that this prediction need not follow if women prefer health because it signals greater ability to invest in offspring. Life history theory indicates that, as adult mortality rates increase, the payoffs to high investment in offspring decrease. High levels of paternal investment, therefore, provide fewer benefits when parasites increase the extrinsic mortality rate (Robson & Kaplan, 2003).

In the cases of both women's access to resources and pathogen prevalence, differences across cultures may reflect differences in evoked culture—in these particular instances, patterns of mate preferences sensitive to cues of which features are especially important to mate value. These patterns reflect special design for adaptively modifying mate preferences based on ancestral fitness utility of cues such as parasite prevalence. It should be noted that, because the two sets of predictions are based on different evolutionary hypotheses, they are logically independent. That is, one evoked culture hypothesis could be correct (e.g., pathogen prevalence), even if the other one is not (e.g., women's access to resources; see Buss, 1995).

Evolution and Evoked Culture: Tests of New Predictions

To assess these evoked culture explanations of some cultural differences, we examined Buss's (1989) cross-cultural data. We were particularly interested in seeing how parasite prevalence (the index developed by Low, 1990a, and used by Gangestad & Buss, 1993) predicted mate preferences and sex differences in mate preferences. We were also interested in examining associations between gender role measures (the GEM and GDI) and mate preferences. Because these features may covary, we used multiple regression analyses that entered both variables rather than simple bivariate analysis.

The GEM and GDI are highly correlated. Eagly and Wood (1999) suggested that the GEM is a better measure of gender equality, though both should reflect it. Hence, we focus on analyses in which it was used but also discuss results employing the GDI. Importantly, we controlled for three additional potential confounds that Eagly and Wood did not control for: (a) we controlled for intercontinental variation and therefore examined associations within Europe, Africa, Asia, the Middle East, and South America rather than variations across them that might be due to large macrocultural variation; (b) we controlled for mean income in the countries in 1986 U.S. dollars; (c) we controlled for degrees latitude from the equator (see also Gangestad & Buss, 1993, who similarly controlled for these potential confounds). Geographical variation may be associated with other important cultural influences of importance such as interdependence versus individualism, degree of social stratification, widespread exposure to mass media sources of the West, religion, and language. Though fully accounting for them with the limited number of cultures available is not possible, these additional statistical controls do ensure that effects of gender equality or pathogen prevalence could not simply be due to differences between, say, Europe and the rest of the world, or countries in the Far East versus all others, effects that could easily be due to confounding variables. In addition, countries are not independent sampling units. Contiguous cultures in particular may influence each other (e.g., through the spread of cultural beliefs by contact). Covariation between variables within sets of geographically connected countries (i.e., when geographical region is controlled) is more impressive evidence for a nonincidental association between the variables (e.g., Murdock & White, 1969).

Affluence is important to control for partly because the samples used to represent the cultures are not equally representative of the general population. Some of the samples were drawn from university populations. In poorer countries in less developed regions of the world (e.g., Africa), a university sample represents a smaller, more elite subpopulation. If some sex differences are enhanced in high-status samples (as has been found in the United States; e.g., Townsend, 1989; Townsend & Levy, 1990), this confound could generate spurious correlations between sex differences and degree of development, as well as any variable associated with degree of development (e.g., gender equality, pathogen prevalence). In addition, affluence itself may importantly affect mate preferences, independent of sexual divisions of labor and pathogen prevalence. Similarly, distance from the equator may be associated with climatic or seasonal variation confounded with pathogen prevalence or, incidentally, gender equality.

Rather than simply examine a few selected mate preferences (as done by Eagly & Wood, 1999, and also in a similar study by Kasser & Sharma, 1999), we explored associations with a broader range of mate preferences. To simplify and increase the power of the analyses, we aggregated across measures for mate preference domains redundantly represented within the data: (a) Health and Heredity (three items; $\alpha = .80$): good health, healthy, and good heredity; (b) Physical Attractiveness (two items; $\alpha = .68$): good looks, physical attractiveness; (c) Intelligence and Education (three items; $\alpha = .39$): intelligence/education, intelligent, college graduate; (d) Status and Status Striving (two items; $\alpha = .77$): ambition/industriousness, favorable social status; (e) Interest in Children (two items; $\alpha = .40$): wants children, desire for home and children; (f) Financial Prospects (two items; $\alpha = .76$): good financial prospects, good earning potential; (g) Domestic Skills (two items; $\alpha = .83$): good housekeeping skills, good cook and housekeeper. In the two cases in which internal consistency was only moderate, the aggregates consisted of preferences characterized by semantically equivalent or highly related terms. In addition, we examined (h) Age preferences (one item). These eight preferences largely cover the domains in which social structural theory or evolutionary perspectives on pathogen prevalence might expect associations, as well as others.

Gangestad and Buss (1993) developed a pathogen prevalence index for 29 cultures. That measure was constructed blind to preference data and the current hypotheses. To establish intercoder reliability, we developed an expanded measure for all countries using two research assistants also blind to the preference data. Each estimated prevalence of seven pathogens (*Leishmania*, *Trypanosoma*, malaria, *Schistosoma*, filaria, spirochetes, and leprosy) in the first half of the 20th century using medical geography maps (e.g., Craig & Faust, 1943; Rodenwaldt, 1952; Simmons et al., 1944–1954) on 1 (*little or none*), 2 (*sporadic or with localized foci*), or 3 (*endemic and widespread through the region*) scales (see Gangestad & Buss, 1993; Low, 1990a). Their ratings were aggregated with those reported in Gangestad and Buss; the pathogen prevalence index was the sum of the mean ratings across pathogens. Correlations across raters were high (mean $r = .93$); alpha for the composite was very high, .97.[4]

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[4] Gangestad and Buss (1993) did not include eight countries because large proportions of the samples were probably not indigenous to the area: United States–Mainland, United States–Hawaii, English Canada, French Canada, Australia, New Zealand, South Africa Whites, Jewish Israelis. At the request of a reviewer, we included these countries here (using pathogen prevalence ratings by the raters we added). Because they share in common the fact that facets of their culture derive from European countries of origin, we classified them in one separate "region," despite the fact that they do not belong to one continent. (Again, a main purpose of controlling for region was to control for shared cultural components arising from common descent, not physical geography, per se.) Excluding these countries from the analyses, however, gave almost identical results. Full results are available on request.

We ran two sets of multiple regression analyses for each preference: one on the total preferences, summed across the sexes, and the other on the sex difference. To interpret significant effects on overall effects or sex differences, we also ran regression analyses on the preferences of men and women separately. We present results in terms of standardized regression coefficients. (All bivariate correlations between variables are listed in the Appendix.)

Regression analyses were performed in two stages. First, we examined the contributions of income, geographical region, and distance from the equator. If a variable accounted for significant variation, it was retained for the second stage of analysis. If it did not, it was dropped from additional analysis. In this way, we controlled for these variables only if they had been shown to be potentially important to control for. Due to small sample size and relatively low power, we used a liberal alpha of .10 (rather than .05) to make these decisions.[5]

We also reduced total preferences and sex differences on these values through principal components analysis (separately for total preferences and sex differences). For total preferences, two components emerged (each with eigenvalues over 1) and were varimax rotated. First, a component on which Status and Status Striving (loading = .92), Health and Heredity (.72), Domestic Skills (.71), Interest in Children (.64), Financial Prospects (.58), Intelligence and Education (.55), and Age (–.45—reflecting interest in younger mates) loaded. As this factor reflects desires for a healthy, competitive mate willing to work hard, we refer to it as General Vigor. The second component reflected a desire for Physical Attractiveness (.84) and, to a lesser extent, Intelligence and Education (.43) at the tradeoff of Domestic Skills (–.45). We refer to this component as Attractiveness.

For sex differences, three components emerged (each with eigenvalues over 1) and were varimax rotated. The first component reflected sex differences in preference for Domestic Skills (.77), Interest in Children (.65), Health (.51), and, negatively, Age (–.88) and Financial Prospects (–.47). We refer to it as Traditional Division of Labor. The second component reflected sex differences in preference for Status and Striving (–.90), Intelligence and Education (–.72), Financial Prospects (–.68), Health and Heredity (–.47), and, in the other direction, Domestic Skills (.46), which we refer to as Male-Biased Status and Resource Seeking. The third component reflected sex differences in preference for Physical Attractiveness (.94) and, to a lesser extent, Health and Heredity (.39). We refer to it as Relative Desire for Female Attractiveness.

We ran regression analyses on these components as well as the individual preference variables.

The Effects of Gender Equality

Standardized regression coefficients are given in Table 1. We first examine the results with regard to the GEM and GDI.

Do the GEM and GDI predict the sex difference in preference for a mate's access to resources? The gender inequality variables were not significantly related to sex differences in preferences for resources in mates. The standardized regression coefficient (.35), however, was similar in magnitude to the effect estimated by Eagly and Wood (1999). The effect of the GDI was also not significant, and the regression coefficient (–.20) was in a direction opposite that reported by Eagly and Wood.

Do the GEM and GDI predict the sex difference in preference for domestic skills? The GEM does predict the sex difference in preference for domestic skills. As the GEM increases, women tended to increasingly care about their mates' domestic abilities, relative to men. The association is largely due to women caring more about a partner's domestic skills as gender equality increases. Once again, the GDI did not significantly predict this sex difference, and the effect actually ran in the opposite direction of that predicted by Eagly and Wood (1999).

Do the GEM and GDI predict the sex difference in preference for a mate's age? The effects for the GEM and GDI were not significant and ran in opposite directions (the effect for the GEM in the direction found by Eagly & Wood, 1999).

Does the GEM predict the sex difference in preference for physical attractiveness? Neither the GEM nor the GDI significantly predicted this sex difference. The directions of the effects were such that, as gender equality increased, the sex difference actually increased. Higher levels of the GEM especially tended to predict lower female preference for men's physical attractiveness, contrary to initial predictions by Eagly and Wood (1999).

Does the GEM predict the sex difference in preference for status and ambition? Neither the GEM nor the GDI significantly predicted sex differences in preferences for status and ambition.

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[5] Forced entry of these controls or use of a .05 level of significance did not alter the results in major ways. In a later section, we discuss individual variables significantly predicted by income and geographical region. Here, we note that, on average, just over one variable was retained. Overall across the analyses, the control variables that were left in the regressions accounted for 47%, 48%, and 54% of the variance in the GEM, parasite prevalence, and the GDI, respectively.

The GEM and overall mate preferences. Gender equality did not significantly predict any overall mate preference.

The GEM, the GDI, and multivariate analyses. We also ran multivariate tests on all overall effects and sex differences, with GEM or GDI, parasite prevalence, income, distance from the equator, and region as predictors. Neither the GEM nor the GDI significantly predicted the overall levels of the eight preferences, $F(8, 18) = .92$ and $F(8, 20) = 1.59$, *ns*. The GEM predicted sex differences at $p < .10$, $F(8, 18) = 2.21$, $p = .077$; for the GDI, $F(8, 20) = 2.54$, $p < .05$. As noted, however, not all sex differences were in the direction expected.

The GEM, the GDI, and principal components of mate preferences and sex differences in mate preferences. The GEM significantly predicted only one principal component: Relative Desire for Female Attractiveness (see Table 1). Contrary to expectations from social role theory (but consistent with our previous analyses), as the GEM increased, men, relative to women, preferred more physical attractiveness in mates. The effect of the GEM on Traditional Division of Labor was in a predicted direction (though it fell short of significance). The effect of the GDI on Traditional Division of Labor, however, was in a direction opposite that predicted and significantly so. Notably, neither the GEM nor the GDI significantly predicted Male-Biased Status and Resource Striving. Both beta weights were close to zero (–.08 and –.05, respectively). In summary, the analyses on principal components offered very little support for predictions that women's access to resources and power predict sex differences in mate preferences.

Summary: Women's Access to Resources

Overall, we found little support for the prediction that women's access to resources and power predict their mate preferences. The analyses for the GEM were somewhat stronger than the analyses for the GDI. As women experience increased access to resources, they place greater importance on men's domestic skills. And, though the effect fell short of significance, they place less emphasis on men's access to resources as they themselves gain access. Effects of the GDI on sex differences on these preferences, however, ran in the opposite direction (though not significantly so). These data provide little support for either the evoked culture hypothesis that women's access to resources affects their desire for a mate who has access to resources or Wood and Eagly's (2002) biosocial approach to sex differences.

Although not significant, the strongest effect of the GEM was on the sex difference in preference for physical attractiveness. In this instance, however, the effects ran in the direction of greater gender equality being associated with greater sex differences. Eagly and Wood (1999) had observed no effect of the GEM and the GDI on the sex difference in preference for attractiveness. They proposed, post hoc, that social structural variables may not predict preferences for attractiveness because there exists a "physical attractiveness stereotype," which conveys attributes such as "social skills," "sociability," and "sexual warmth," and "therefore men's greater valuing of attractiveness might follow from the greater importance of this competence in women's family and occupational roles" (Eagly & Wood, 1999, p. 419). They did not explain the nature of the physical attractiveness stereotype itself, and hence they took it and its content for granted (though evolutionary perspectives do speak to it; e.g., Langlois et al.,

Table 1. *Results of Regression Analyses on Principal Components: Standardized Regression Coefficients*

	Analyses With GEM		Analyses With GDI	
	GEM	**Path. Preval.**	**GDI**	**Path. Preval.**
Principal components of total preferences				
General vigor	–.10	**.61****	–.14	**.52****
Attractiveness	–.01	**.80****	–.14	**.72****
Principal components of sex differences				
Traditional division of labor	–.25	.12	**.37***	**.36***
Male–biased status and resource striving	–.08	.39	–.05	**.42***
Relative desire for female attractiveness	**.53+**	**.46+**	.35	.29

Notes. GEM = Gender Empowerment Measure; GDI = Gender Development Index. For sex differences, positive coefficients reflect increased preference for males relative to females as a function of gender equality or parasite prevalence; negative coefficients reflect increased preference for females relative to males as a function of gender equality or parasite prevalence. For all preferences, significant effects of income, geographical region, or latitude controlled (sex text). Effects with $p < .10$ appear in bold print.

$+p < .10$. $*p < .05$. $**p < .01$. $***p < .001$.

2000). Based on their reasoning, however, one might predict that the greater sex difference in valuation of physical attractiveness with increasing gender equality is due to increased male preference for women's sociability with greater female power. One mate preference participants rated was "sociability." In fact, the correlation between the GEM and male preference for mates' sociability is slightly, though nonsignificantly, negative (–.16; in our regression analyses, partial $r = .02$, *ns*), providing no support for this prediction.

The analyses on the composites of covarying sex differences derived from principal components analysis perhaps most clearly capture the lack of support for predictions regarding women's access to resources and power. Both Low's (1990b) view of evoked culture as a function of women's control of resources as well as Eagly and Wood's (1999; Wood & Eagly, 2002) social structural ideas should expect robust associations between measures of gender inequality in access to resources and power to predict negatively the first two components—one reflecting the extent to which sex differences in preferences reveal a traditional division of labor (men desire greater access to resources; women desire domestic skills, interest in children, and youth), the other reflecting male-biased status and resource striving (men particularly desire resources, status, and status striving and intelligence and education). The mean beta weight for the GEM and the GDI were in the opposite direction in predicting the former, and both variables had near-zero weights in predicting the latter. The GEM did significantly predict the third component, which largely reflected a sex difference in desire for attractiveness—but here, the effect ran in a direction presumably opposite of what these theories should expect (as the GEM increased, so too did the sex difference with respect to desire for a physically attractive mate, with men increasingly wanting this attribute). Overall, these analyses provide absolutely no support for predictions offered by views of evoked culture as a function of women's control of resources or the social structural theory applied to mate preferences.

Given previous support for Low's (1990b) hypothesis, why did our analyses fail to strongly support predictions concerning women's access to resources? There are several possibilities. First, variation in women's participation in labor markets across modern societies may function differently than variation in women's participation in food production across traditional cultures. As discussed earlier, women's contribution to subsistence in the latter cultures does appear to be associated with important aspects of mating (e.g., polygyny). In addition, the effects of women's contribution to subsistence may not be homogeneous, as women's contributions may be a function of multiple factors—pathogen prevalence, the availability and nature of local prey items, horticultural opportunities, and so on—and each of these factors may have somewhat different effects in light of how they specifically affect the sex's contributions to production.

Second, the assumptions of the specific evoked culture model may be wrong. The model assumes that men contributed to diets of their mates and offspring, leading women to prefer men who could provide more. In fact, however, some anthropologists argued that men in foraging societies often have little control over the distribution of the meat they hunt and hence cannot direct meat to mates and offspring (e.g., Hawkes et al., 2001). Women's preference for good hunters in these societies (and possibly ancestral societies), then, may derive from benefits other than direct nutritional resources (e.g., social standing, physical protection, or genetic benefits to offspring; e.g., Hawkes, 2004). If so, the strength of these preferences need not be expected to attenuate when women have greater access to resources. Specific evolutionary hypotheses offer different sets of predictions, and, when one set is not confirmed, alternative hypotheses should be considered.

One difference between the evoked culture account of Low (1990b) and Wood and Eagly's (2002) biosocial model pertains to their assumptions about the nature of ancestral relationships between men and women. Low's evoked culture account assumes that men provided and directed nutritional benefits to women and offspring, leading women to prefer men who could provide (e.g., good hunters) in conditions in which men did provide. Wood and Eagly offered no explicit premise about the nature of men's and women's relationships to which contingent responses to a division of labor are made. They noted that women in traditional societies may value men for their hunting but also noted that men in foraging societies often cannot direct meat to mates and offspring (Hawkes et al., 2001). Anthropologists who claimed the latter point, however, also argued that the implication is that, rather than serving to nurture mates and offspring, men's hunting ancestrally functioned as an effort to gain access to mates (i.e., has been sexually selected). Yet Wood and Eagly explicitly downplayed the role of sexual selection as a cause of psychological sexual dimorphism and, hence, implicitly rejected this implication. As the two explanations in the literature for the fact that men generally hunt are that men's hunting functions to nurture offspring and that it functions to obtain mates, neither of which is endorsed by Wood and Eagly, it is not at all clear how Wood and Eagly explain men's hunting (and hence, how they explain a major component in men's and women's division of labor). In any case, however, it is unclear how Eagly and Wood's theory can explain the pattern of findings we report here.

Finally, we cannot rule out the possibility that we did not detect some associations of the GEM and GDI with mate preferences (controlling for confounds) in a small sample. Given that the overall pattern of results showed virtually no support for predictions, however, it is difficult to imagine that sampling variability could explain but a small piece of the dearth of empirical support. And, again, in analyses on composite principal components, many correlations ran in directions opposite of the predictions. Additional work is needed to fully explain the full pattern of relations.[6]

Hypotheses About Parasite Prevalence and Mate Preferences

We now turn to associations between parasite prevalence and mate preferences. We focus on analyses that used the GEM as a measure of gender equality (see Table 2).

Does parasite prevalence predict preferences for physical attractiveness? The answer is yes, and powerfully so. This result shows that Gangestad and Buss's (1993) finding is robust to the addition of gender equality as a predictor. Both men and women particularly prefer physically attractive mates as parasite prevalence increases. There was a marginally significant trend for the sex difference in preference to increase with parasite prevalence as well, with men's interest in physically attractive mates particularly enhanced when parasites are prevalent.

Does parasite prevalence predict preferences for good health and heredity? Once again, the answer is yes. Overall, the results suggest that individuals particularly prefer mates with good health and heredity when parasites are prevalent. The evolutionary hypothesis most clearly predicts that men and women should particularly favor ancestral cues of health and heredity when parasites are prevalent. Here, we find that they claim to favor these traits themselves under such circumstances.

Does parasite prevalence predict preferences for intelligence and education? Parasite prevalence strongly predicted overall preference for intelligence and education. It robustly predicted the sex difference as well. Sex-specific analyses revealed that women particularly prefer intelligent, educated mates as parasite prevalence increases. Weaker associations were observed for men. Whereas men may assess women's health and disease resistance through physical indicator traits, women may assess men's as much in terms of performance and displays of effectiveness (e.g., Gangestad & Thornhill, 1997; Simpson, Gangestad, Christensen, & Leck, 1999). Although the preference for physical prowess was not directly assessed in this study, one might predict that women's preference for that trait would also increase with parasite prevalence for similar reasons.

Does parasite prevalence predict preferences for status and striving? As pathogen prevalence increased, individuals tended to increasingly prefer status and striving in mates. As observed for preferences for intelligence, this was particularly true of women's preferences. No such preferences were detected in men. (The sex difference was significant when the GDI was controlled and fell short of significant [$p = .101$] when the GEM was controlled.)

Parasite prevalence and other mate preferences. Parasite prevalence predicted one additional mate preference that was not anticipated. With increasing pathogen prevalence, men preferred younger mates. (The sex difference was significant when the GDI was controlled; see the following.) On the one hand, individuals may have been predicted to value youth more when pathogen resistance is high because of direct benefits provided by younger mates due to their greater ability to resist disease. On the other hand, one could have predicted a preference for older mates because survival into older age may advertise ability to resist local pathogens and thereby indirect genetic benefits to offspring (Kokko, 1998). Which effect dominates depends on their relative strengths. The fact that the effect emerged only for men may reflect the fact that child outcomes in ancestral conditions were more strongly affected by maternal than paternal survival (for evidence on the Ache; see Hill & Hurtado, 1996), which would cause the direct benefits of youth to dominate more strongly for men choosing women than vice versa. This should particularly be true if men invest less in offspring as pathogen prevalence increases,

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[6] Readers may wonder why our analyses reduced or eliminated the effect of the GEM and the GDI on sex differences reported in the same data set by Eagly and Wood (1999). Region accounts for 48% of the variation in the GEM. If Region is associated with sex differences in mate preferences merely because of its association with GEM—the variable with true effects—then it should account for less variation in sex differences than the GEM. (If GEM is the variable doing the work, the independent variation in Region should dilute the overlap between Region and sex differences.) But the pattern is precisely the opposite: Sex differences reported by Eagly and Wood are, on the whole, much better predicted by Region than by the GEM, particularly on financial resources: $R^2 = .44$ for Region vs. .16 for GEM; and domestic skills: $R^2 = .66$ for Region vs. .44 for GEM. (This is not the case for preferred age difference; $R^2 = .47$ for Region vs. .52 for GEM). It appears, then, that Region (or some correlate of it) has effects on sex differences due to factors other than those captured by the GEM. (i.e., the GEM itself cannot alone account for the effects of Region.) And if that's the case, it should be important to control for those effects. On a related note, one reviewer suggested that controlling for confounds might reduce the likelihood of finding effects. We disagree. Whether an effect is reduced depends on the extent to which a variable accounts for variation independent of the confound. Region accounted for 51% of the variance in pathogen prevalence, yet pathogen prevalence had effects even with the effects of Region statistically controlled.

Table 2. *Mate Preferences as a Function of GEM and Parasite Prevalence: Standardized Regression Coefficients*

	Gender Equality (GEM)				Pathogen Prevalence			
Mate Preference	**Overall**	**Sex Diff.**	**Men**	**Women**	**Overall**	**Sex Diff.**	**Men**	**Women**
Health and heredity	–.02	–.27	–.13	.00	**.36***	.01	.29	**.33***
Physical attractiveness	–.15	.39	.06	**–.40+**	**.64***	**.52+**	**.69***	**.47***
Intelligence	.16	–.19	**.53***	.19	**.67****	**–.73****	**.46+**	**.84*****
Status and striving	–.06	.30	–.03	–.17	**.34+**	–.42	.16	**.44***
Interest in children	–.04	.05	.01	–.13	.29	.40	.39	.13
Financial prospects	–.02	.35	.17	–.12	-.05	.10	–.04	–.07
Domestic skills	.26	**–.32+**	–.01	**.63***	.15	.00	.18	–.03
Age (relative to self)	–.30	.25	.12	.35	–.45	–.27	**–.43***	.01

Notes. GEM = Gender Empowerment Measure. For overall effects, positive coefficients reflect increased importance of the preference with increased levels of gender equality (GEM) or parasite prevalence. For sex differences, positive coefficients reflect increased preference for men relative to women as a function of gender equality or parasite prevalence; negative coefficients reflect increased preference for women relative to men as a function of gender equality or parasite prevalence. For all preferences, significant effects of income, geographical region, or latitude controlled. Effects with $p < .10$ appear in bold print.

+$p < .10$. *$p < .05$. **$p < .01$. ***$p < .001$.

putting greater effort into seeking mates (e.g., Gangestad & Simpson, 2000; Low, 1990a).

The prediction that women should care less about men's direct investment in offspring as a function of increased pathogen prevalence could not be assessed because no item in the survey directly assessed it.

Analyses using the GDI. In general, the pattern of effects of parasite prevalence on mate preferences remained fairly constant across analyses using the GEM and the GDI (see Table 3). For both men and women, parasite prevalence predicted all of those preferences predicted and found when the GEM was controlled. In addition, the sex differences in preference for status and striving and preference for youth versus an older mate were statistically significant.

As noted, these analyses suffer from low power. Large associations are needed to reject the null hypothesis and, if more cultures had been represented, more associations might have been detected.

Pathogen prevalence and multivariate analyses. Multivariate analyses of covariance revealed strong effects of parasite prevalence on overall preferences, no matter whether the GEM or the GDI was a predictor, $F(8, 18) = 3.34$, $p = .016$, and $F(8, 20) = 4.57$, $p = .003$. Parasite prevalence similarly significantly predicted sex differences when the GEM or the GDI was a predictor, $F(8, 18) = 3.40$, $p = .015$, and $F(8, 20) = 4.77$, $p = .002$, respectively.

Pathogen prevalence and principal components of mate preferences and sex differences in mate preferences. Pathogen prevalence predicted both components of overall preferences: As pathogen prevalence increased, so too did overall preference for General Vigor and Attractiveness. Pathogen prevalence predicted components reflecting sex differences as well, though not consistently across analyses involving the GEM and GDI. These effects on sex differences in preference are consistent with those reported earlier. See Table 1.

Summary: Pathogen Prevalence and Evoked Culture

The analyses provide considerable support for predictions derived from the evoked culture hypothesis concerning pathogen prevalence. Parasite prevalence predicted a number of mate preferences in ways predicted by previously articulated evolutionary hypotheses about the impact of parasite prevalence on the value of health and indicator traits. Moreover, pathogen prevalence had an impact on sex differences that fit with specific evolutionary predictions about differences in indicator traits of health and resistance in men and women and fit with other empirical research conducted with evolutionary psychology.

These effects cannot plausibly be explained by domain-general processes that underlie adaptive adjustment to local ecologies. Rather, just as specialized mating adaptations in collared flycatchers adjust mating behaviors and preferences on the basis of particular environmental cues, specialized mating adaptations in people adjust mate preferences in response to particular environmental cues.

Effects of Income, Latitude, and Geographical Variation

Although not pertinent to our predictions, the effects of income, latitude, and geographical variation (after controlling for pathogen prevalence and the GEM) may be of general interest. As wealth increased, individuals cared significantly less about domestic skills. As distance from the equator increased, they cared more about financial resources. Significant geographical variation was observed for preferences for physical attractiveness (Bonferroni-adjusted contrasts showed greater preference in particularly Europe and European-derived samples relative to Africa, Asia, and South America), health and heredity (greater preference was observed in Asia and the Middle East, particularly for heredity), and status and striving (greater in the Middle East than Europe). Possibly, the greater preference for physical attractiveness in Europe is due to the effects that exposure to attractive models through mass media have on standards of attractiveness (e.g., Kenrick, Gutierres, & Goldberg, 1989). The preference for heredity in Middle Eastern and Asian countries may reflect the fact that several (e.g., Japan, India, Iran) are characterized by high levels of familial social stratification. Several regional effects on sex differences also emerged, and contrasts showed that all involved Asia: financial resources (a greater female–male sex difference in Asia than Europe), domestic skills (a greater male–female sex difference in Asia than Europe, European-derived samples, and South America), and status and striving (a greater female–male sex difference in Asia than in Africa). Controlling for all other variables, then, larger sex differences on several key variables tended to exist in Asia, which may also be due to high levels of social stratification and associated hypergyny in some countries (e.g., Japan). Full results are available from the authors.

The Generativity of the Concept of Evoked Culture

Evolutionary psychology and human behavioral ecology offer the concept of evoked culture as a partial understanding of cultural diversity. Evoked culture arises as a function of specialized, evolved responsivity, which is adaptively contingent on particular environmental features. We have illustrated evoked cultural variation by examining associations between particular environmental and socioecological features and mate preferences.

Evolutionary theory can generate novel predictions about cultural variation and thereby fruitfully guide efforts to investigate cultural diversity. Indeed, associations between pathogen prevalence, polygyny, and mate preferences were unknown prior to Low's (1990a) hypothesis that cultures ought to vary as a function of pathogen prevalence and Gangestad and Buss's (1993) empirical test of the hypothesis, which itself rose out of specific evolutionary theory put forward by Hamilton and Zuk (1982).

Moreover, hypotheses generated from adaptationist theories may provide a deeper level of understanding of cultural differences than many nonevolutionary approaches because they clearly specify the preceding causal conditions. The concept of evoked culture does not merely describe cultural variation; it explains it, at least within certain domains such as those explored in this article.

The perspective we present does not solve all of the complex questions surrounding cultural variation. Evolutionary psychologists have not yet offered explanations for all of the cultural variation now known to exist, such as variations across cultures in individualism–collectivism (e.g., Triandis, 1989; although, see Cashdan, 1980), independence–interdependence (Markus & Kitayama, 1991), and the ways in which people reason about causal events (Choi, Nisbett, & Norenzayan, 1999). Moreover, to date, relatively few evolutionary psychologists have seriously considered the ways by which human developmental systems

Table 3. *Mate Preferences as a Function of GDI and Parasite Prevalence: Standardized Regression Coefficients*

	Gender Equality (GDI)				Pathogen Prevalence			
Mate Preference	**Overall**	**Sex Diff.**	**Men**	**Women**	**Overall**	**Sex Diff.**	**Men**	**Women**
Health and heredity	.17	.15	.15	.06	__.43**__	.31	__.40*__	__.34*__
Physical attractiveness	–.02	.04	.22	–.21	__.68**__	.32	__.67**__	__.62**__
Intelligence	.07	–.20	–.13	.10	__.65**__	__–.72***__	.26	__.76***__
Status and striving	.05	.13	.05	–.03	__.34+__	__–.54*__	.16	__.49**__
Interest in children	.41	.19	.37	.15	.21	__.40+__	.29	.27
Financial prospects	.16	–.20	.24	.11	.04	–.16	.03	.04
Domestic skills	.11	.22	–.03	.23	–.08	.27	.06	–.37
Age (relative to self)	.02	–.16	–.08	–.23	–.22	__–.42*__	__–.49**__	–.23

Notes. GDI = Gender Development Index; GEM = Gender Empowerment Measure. For overall effects, positive coefficients reflect increased importance of the preference with increased levels of gender equality (GEM) or parasite prevalence. For sex differences, positive coefficients reflect increased preference for men relative to women as a function of gender equality or parasite prevalence; negative coefficients reflect increased preference for women relative to men as a function of gender equality or parasite prevalence. For all preferences, significant effects of income, geographical region, or latitude controlled. Effects with $p < .10$ appear in bold print.

+$p < .10$. *$p < .05$. **$p < .01$. ***$p < .001$.

might rely on culturally encoded "scaffolding" (Griffiths & Stotz, 2000), such as sex-specific rearing practices (Low, 1989), to produce typical outcomes (see Geary, 1999). The perspective we described also does not specifically address cultural variation arising as a function of adaptive social transmission processes (see, e.g., Richerson & Boyd, 2005, for a summary), although we would argue that mechanisms of evoked and transmitted culture are unlikely to be completely independent (also see the following). Nonetheless, as we have attempted to illustrate, the evoked culture perspective offers promising conceptual avenues to pursue, some of which have received impressive empirical support (see also Schmitt, 2005).

Conclusions

Psychologists find cultural differences fascinating, and rightly so. Cultural variations allow us to see possibilities we might not otherwise have imagined possible. They allow opportunities to transcend one's own ethnocentrism. They offer the possibility of testing theories about causal influence. And perhaps inevitably, for some, they offer the hope that humans can change, that the current forms of modern cultures do not represent the only ways of being, and that the troubling aspects of modern society might someday be reduced or eliminated.

Some social scientists have viewed culture as a causal force separate from, and independent of, biology. This has been called "the myth of culture as a causal explanation" (Buss, 2001, p. 896). In fact, causal dichotomies that separate biology and culture are false, obscuring more than they reveal. Cultural variation and cultural change are real. But these facts in themselves are not evidence against claims that evolution has played a major role in shaping the mechanisms of the mind, as is mistakenly assumed by some social scientists. Indeed, evolutionary psychology has provided promising conceptual tools needed to present a more coherent theoretical framework for predicting and explaining cultural variation.

This article has focused on evoked culture as one such conceptual tool. The examples of evoked culture described are illustrative rather than exhaustive. We envision many other domains in which the concept of evoked culture can be used to gain insight into cultural variation. Cultures differ, for example, in prevailing levels of causal sex and frequency of mate switching—in the prevailing mating strategies pursued. One hypothesis, anchored in the evolutionary concept of evoked culture, is that variations in sex ratio—the ratio of men to women within the operational mating pool—activate different mating strategies from the universal menu (Pedersen, 1991). In cultures that have a relative surplus of women, such as the Ache of Paraguay, short-term mating strategies are more frequently activated, marriages become more unstable, divorce rates rise, and men become more reluctant to commit to a single woman. In cultures that have a relative surplus of men, such as the Hiwi tribe of South America, long-term mating strategies are more frequently evoked, marriages become more stable, and mate switching diminishes (Buss, 2001). What began as a mysterious phenomenon of cultural variation in mating strategies becomes explicable within an evolution-based hypothesis of evoked culture.

Another example worthy of exploration is cultural variations in rates of marital infidelity. On the hypothesis that jealousy is a complex adaptation that is activated under a delimited set of conditions (e.g., cues to defection; presence of reproductive competitors), an evoked culture hypothesis can make a principled set of predictions. Where infidelity rates are high, jealousy should be more frequently activated, with consequent increases in mate guarding and violence (Buss, 2005). Cultural variations in important domains such as spousal violence and sexual rivalry homicide might be explicable based on a principled evolutionary hypothesis of evoked cultural variations, in this case stemming from variations in infidelity rates. Variation in the degree to which fathers invest in their purported offspring is another factor that may affect male sexual jealousy. In cultures in which fathers do not invest heavily in offspring (e.g., when children are cared for by female kin), activities other than mate guarding pay larger fitness dividends and an evoked culture perspective suggests that jealousy and mate guarding should be evoked less.

Outside of the domain of mating, hypotheses anchored in the concept of evoked culture are also numerous. One pertains to the ecology of resource variance. In cultures with high resource variance, in which resources can be stockpiled and monopolized, men are predicted to engage in greater risk-taking (Daly & Wilson, 1988). Risk-taking in this context can be viewed as an evoked strategy designed either to "win big" or to avoid being shut out entirely. Cultural variations in levels of risk-taking, including violent confrontation, may be traceable to an evolved male psychology that is sensitive to the cultural context of resource variance. Subcultures of inner-city drug gangs may provide a good example. When some live in dire poverty and others can get rich quickly and hence win big, a psychology of risk-taking and violence is evoked.

These examples provide just a few among many future avenues by which the central concept of evoke culture can be explored. The key point is that cultural variation, by itself, is a phenomenon to be explained. Merely describing cultural variation and invoking culture as an explanation without providing a principled hypothesis about causal antecedents provides little more than a redescription of the phenomenon. Hypotheses anchored in the notion of evoked culture offer deeper explanations that reveal how cultural variations originate than explanations that merely invoking culture as an explanation.

We view the concept of evoked culture as critical to understanding some, but certainly not all, forms of cultural variation. Transmitted culture (Richerson & Boyd, 2005; Tooby & Cosmides, 1992), in which ideas, values, attitudes, beliefs, and inventions are communicated from the minds of an individual or group to the minds of other individuals or groups, represents a second promising concept that cultural researchers can successfully utilize. Some social scientists assume that transmitted culture lies outside the province of evolutionary psychology or, more mistakenly, somehow contradicts the tenets of evolutionary psychology. In fact, the only way in which culture can be transmitted from mind to mind is through a foundation of evolved psychological mechanisms. This notion was implicitly recognized decades ago by two pioneers in psychology, Allport and Postman (1947), in the delimited context of rumor: “Rumor is set into motion and continues to travel by its appeal to the strong personal interests of the individuals involved in the transmission” (p. 314). The evolved psychological mechanisms involved in transmitted culture have just begun to be examined (see, e.g., Henrich & Gil-White, 2001) but remain an important conceptual tool, in addition to that of evoked culture, provided by the framework of evolutionary psychology.

A particularly interesting example of transmitted culture was proposed by Nisbett and Cohen (1996) in the context of explaining cultural differences in the frequency with which actual violence is provoked due to insults to status. Nisbett and Cohen’s culture-of-honor theory was developed specifically to explain the homicide rate differences between southern and northern states within America, which are pronounced. Although there are exceptions, the further south the state, the higher the homicide rate. Alabama, Georgia, and Mississippi, for example, have homicide rates of 15.9, 14.8, and 14.3 per 100,000, respectively. Texas tops the list at 17.1. The corresponding rates in Maine, Ohio, and Pennsylvania are 3.2, 7.6, and 7.0, respectively.

According to the culture-of-honor theory, the stress on a man’s public reputation for toughness and physical courage originated in the world’s herding economies. In these economies, herdsmen over the eons confronted the threat of losing their entire wealth if their animals were stolen, as often happened in raiding parties. When all of a herdsman’s resources are stored in the bodies of the herd, he risks catastrophic destitution by being raided. A man’s public reputation may literally have been the key to his economic survival. A public stance of aggressiveness and the courage to defend against these raids became critical to deterring bands of marauding rustlers. According to Nisbett and Cohen’s (1996) theory, the men growing up in herding economies were socialized to act tough, to respond with violence to public insults, and to preserve at all costs their social reputation.

The southern states in the United States were settled primarily by emigrants from such herding cultures, primarily Ireland, Scotland, and Wales, so this culture of honor took root in the South. The northern states, by contrast, were settled primarily by farmers, such as Puritans, Quakers, Germans, and Dutch. Because the economic resources of farmers are tied to their land, they cannot be purloined in one fell swoop, and, through the ages, farmers had less of a mandate to cultivate defensive toughness. Nisbett and Cohen (1996) argued that the higher rates of homicide among white men living in the south are due to the culture of honor that became more prevalent in the South.

Although Nisbett and Cohen (1996) framed their theory as one of transmitted culture, in this case values transmitted through socialization from parents to children, the homicide rate differences could also be an example of a combination of transmitted culture and evoked culture. Cultural values may set different thresholds for activating the evolved mechanisms underlying violence (Buss, 2005). The underlying motives for murders are known to be the same in southern and northern men—public insults to status, sexual rivalry, mate stealing, and so on. Residing in cultures of honor, such as those of the American South, may simply lower the threshold for acting on these universal male motives. If this interpretation is correct, cultural differences in homicide rate differences would be explained by a combination of transmitted culture (values transmitted vertically from parents to children) that set thresholds for activating evolved psychological circuits of violence (i.e., evoked culture).

According to the evolutionary psychological metatheory, humans have evolved psychological adaptations that are specifically designed to receive and process variable social and cultural input. Evolutionary psychology thus suggests that biological potentialities permit a wide range of psychological, behavior, and sociocultural outcomes and do not dictate singular outcomes. Hence, evolutionary psychology provides a theoretically grounded unifying framework for understanding how and why humans are so exceptionally responsive to their cultural environments.

Notes

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We thank Alita Cousins, Corey Fincher, Melissa Franklin, Shelly Gable, Christine Garver-Apgar, Gian Gonzaga, Anne Peplau, Matt Pirritano, Chris Radi, Glenn Scheyd, and the Gable–Haselton–Peplau relationships lab group for helpful comments on earlier drafts of this article.

References

Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M., & Sherman, P. W. (1979). Sexual dimorphism and breeding systems in pinnepieds, ungulates, primates and humans. In N. A. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective* (pp. 402–435). North Scituate, MA: Duxbury.

Allport, G. W., & Postman, L. (1947). *The psychology of rumor.* New York: Holt.

Aronoff, J., & Crano, W. D. (1975). A re-examination of the cross-cultural principles of task segregation and sex role differentiation in the family. *American Sociological Review, 40,* 12–20.

Barrett, H.C. (2005). Enzymatic computation and cognitive modularity. *Mind and Language, 3,* 259–287.

Bellis, M. A., & Baker, R. R. (1990). Do females promote sperm competition: Data for humans. *Animal Behaviour, 40*, 997–999.

Boyd, R., & Richerson, P. (1985). *Culture and the evolutionary process.* Chicago: University of Chicago Press.

Brown, D. E. (1991). *Human universals.* New York: McGraw-Hill.

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences, 12,* 1–49.

Buss, D.M. (1991). Evolutionary personality psychology. In *Annual Review of Psychology* (pp. 459–491). Palo Alto, CA: Annual Reviews.

Buss, D. M. (1995). Evolutionary psychology: A new paradigm for psychological science. *Psychological Inquiry, 6,* 1–49.

Buss, D. M. (2001). Human nature and culture: An evolutionary psychological perspective. *Journal of Personality, 69,* 955–978.

Buss, D. M. (2005). *The murderer next door: Why the mind is designed to kill.* New York: Penguin.

Buss, D. M., & Barnes, M. F. (1986). Preferences in human mate selection. *Journal of Personality & Social Psychology, 50,* 559–570.

Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: A contextual evolutionary analysis of human mating. *Psychological Review, 100,* 204–232.

Buss, D. M., Shackelford, T. K., Kirkpatrick, L. A., & Larsen, R. J. (2001). A half century of mate preferences: The cultural evolution of values. *Journal of Marriage and the Family, 63,* 491–503.

Carroll, M. P. (1976). On Aronoff and Crano's re-examination of the cross-cultural principles of task segregation and sex role differentiation in the nuclear family. *American Sociological Review, 41,* 1071–1072.

Cashdan, E. A. (1980). Egalitarianism among hunters and gatherers. *American Anthropologist, 82,* 116–120.

Choi, I., Nisbett, R. E., & Norenzayan, A. (1999). Causal attribution across culture: Variation and universality. *Psychological Bulletin, 125,* 47–63.

Craig, C. F., & Faust, E. C. (1943). *Clinical parasitology.* Philadelphia: Lea & Febiger.

Daly, M., & Wilson, M. (1988). *Homicide.* New York: deGruyter.

Domjan, M. (1997). Behavioral systems and the demise of equipotentiality: Historical antecedents and evidence from sexual conditioning. In M. E. Bouton & M. S. Fanselow (Eds.), *Learning, motivation, and cognition: The functional behaviorism of Robert C. Bolles* (pp. 31–51). Washington, DC: American Psychological Association.

Eagly, A. H., & Wood, W. (1999). The origins of sex differences in human behavior: Evolved disposition versus social roles. *American Psychologist, 54,* 408–423.

Ekman, P., Friesen, W. V., O'Sullivan, M., Chan, A., Diacoyanni-Tarlatzis, I., Heider, K., et al. (1987). Universals and cultural differences in the judgments of facial expressions of emotion. *Journal of Personality & Social Psychology, 53,* 712–717.

Ellegren, H., Gustafsson, L., & Sheldon, B. C. (1996). Sex ratio adjustment in relation to paternal attractiveness in a wild bird population. *Proceedings of the National Academy of Sciences USA, 93,* 11723–11728.

Flinn, M. V. (1981). Uterine and agnatic kinship variability and associated cousin marriage preferences. In R. D. Alexander & D. W. Tinkle (Eds.), *Natural selection and social behavior: Recent research and new theory* (pp. 439–475). New York: Chiron.

Flinn, M. V. (1997). Culture and the evolution of social learning. *Evolution and Human Behavior, 18,* 23–67.

Gangestad, S. W. (2004, May). *Special design in women's sexual preferences and interests: When during their cycles women want what.* Paper presented at the annual meeting of the American Psychological Society, Chicago.

Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology, 14,* 89–96.

Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences, 23,* 675–687.

Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, P. N. (2004). Women's preferences for male behavioral displays change across the menstrual cycle. *Psychological Science, 15,* 203–207.

Gangestad S. W. ,& Thornhill, R. (1997). Human sexual selection and developmental stability. In J. A. Simpson & D. T. Kenrick (Eds.), *Evolutionary social psychology* (pp. 169–195). Mahwah, NJ: Lawrence Erlbaum Associates, Inc.

Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preference for the scent of symmetrical men. *Proceedings of the Royal Society of London, Series B, 265,* 927–933.

Gangestad, S. W., Thornhill, R., & Garver, C. E. (2002). Changes in women's sexual interests and their partners' mate retention tactics across the menstrual cycle: Evidence for shifting conflicts of interest. *Proceedings of the Royal Society of London, Series B, 269,* 975–982.

Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2005). Female sexual interests across the ovulatory cycle depend on primary partner developmental instability. *Proceedings of the Royal Society of London, Series B, 272,* 2023–2027.

Garcia, J., & Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science, 4,* 123–124.

Gaulin, S. J., & Boster, J. S. (1992). Human marriage systems and sexual dimorphism in humans: Is there any variance to be explained? *American Journal of Physical Anthropology, 89,* 467–475.

Geary, D. C. (1999). Evolution and developmental sex differences. *Current Directions in Psychological Science, 8,* 115–120.

Geertz, C. (1973). *The interpretation of cultures.* New York: Basic Books.

Geertz, C. (1983). *Local knowledge: Further essays in interpretive anthropology.* New York: Basic Books.

Getty, T. (2002). Signaling health versus parasites. *American Naturalist, 159,* 363–371.

Greiling, H., & Buss, D. M. (2000). Women's sexual strategies: The hidden dimension of short-term extra-pair mating. *Personality and Individual Differences, 28,* 929–963.

Griffiths, P. E., & Stotz, K. (2000). How the mind grows: A developmental perspective on the biology of cognition. *Synthese, 122,* 29–51.

Hamilton, W. D. (1980). Sex versus non-sex versus parasite. *Oikos, 35,* 282–290.

Hamilton, W. D., & Zuk. M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science, 218,* 384–387.

Haselton, M. G., & Gangestad, S. W. (2006). Conditional expression of female desires and male mate retention efforts across the human ovulatory cycle. *Hormones and Behavior, 49,* 509–518.

Haselton, M. G., & Miller, G. F. (2006). Women's fertility across the cycle increases the short-term attractiveness of creative intelligence compared to wealth. *Human Nature, 17,* 50–73.

Hawkes, K. (1991). Showing off: Tests of a hypothesis about men's foraging goals. *Ethology and Sociobiology, 12,* 29–54.

Hawkes, K. (2004). Mating, parenting, and the evolution of human pair bonds. In B. Chapais & C. M. Berman (Eds.), *Kinship and behavior in primates* (pp. 443–473). Oxford, England: Oxford University Press.

Hawkes, K., O' Connell, J. F., & Blurton Jones, N. G. (1991). Hunting patterns among the Hadza: Big game, common goals, foraging goals and the evolution of the human diet. *Philosophical Transactions of the Royal Society of London, Series B, 334,* 243–251.

Hawkes, K., O' Connell, J. F., & Blurton Jones, N. G. (2001). Hunting and nuclear families—Some lessons from the Hadza about men's work. *Current Anthropology, 42,* 681–709.

Henrich, J., & Gil-White, F. (2001). The evolution of prestige: Freely conferred status as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior, 22,* 1–32.

Herrnstein, R. J. (1977). The evolution of behaviorism. *American Psychologist, 32,* 93–603.

Hill, K., & Hurtado, A. M. (1996). *Ache life history: The ecology and demography of a foraging people.* New York: deGruyter.

Holden, C., & Mace, R. (1999). Sexual dimorphism in stature and women's work: A phylogenetic cross-cultural analysis. *American Journal of Physical Anthropology*, *110,* 27–45.

Hull, C. L. (1943). *Principles of behavior: An introduction to behavior theory.* New York: Appleton-Century.

Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: Evidence for hormone mediated adaptive design. *Evolution and Human Behavior, 21,* 251–267.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology, 9,* 156–185.

Kasser, T., & Sharma, Y. S. (1999). Reproductive freedom, educational equality, and females' preference for resource-acquisition characteristics in mates. *Psychological Science, 10,* 374–377.

Kenrick, D. T., Gutierres, S. E., & Goldberg, L. (1989). Influence of erotica on ratings of strangers and mates. *Journal of Experimental Social Psychology, 25,* 159–167.

Kenrick, D. T., & Keefe, R. C. (1992). Age preferences in mates reflect sex differences in reproductive strategies. *Behavioral and Brain Sciences, 15,* 75–133.

Kenrick, D. T., Li, N. P., & Butner, J. (2003). Dynamical evolutionary psychology: Individual decision rules and emergent social norms. *Psychological Review, 110,* 3–28.

Kokko, H. (1998). Good genes, old age, and life history trade-offs. *Evolutionary Ecology, 12,* 739–750.

Kokko, H. (2001). Fisherian and "good genes" benefits of mate choice: How (not) to distinguish between them. *Ecology Letters*, *4,* 322–326.

Krebs, J. R., & Davies, N. B. (1993). *An introduction of behavioural ecology* (3rd ed.). Oxford, England: Blackwell.

Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin, 126,* 390–423.

Little, A. C., Burt, D. M., Penton-Voak, I. S., & Perrett, D. I. (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society of London, Series B, 268,* 39–44.

Lorenz, K. (1963). *On aggression.* New York: Harcourt Brace Jovanovich.

Low, B. S. (1989). Cross-cultural patterns in the training of children: An evolutionary perspective. *Journal of Comparative Psychology, 103,* 311–319.

Low, B. S. (1990a). Marriage systems and pathogen stress in human societies. *American Zoologist, 30,* 325–40.

Low, B. S. (1990b). Sex, power, and resources: Male and female strategies of resource acquisition. *International Journal of Contemporary Sociology, 27,* 49–73.

Mace, R., & Holden, C. (1999). Evolutionary ecology and cross-cultural comparison: The case of matrilineal descent in sub-Saharan Africa. In P. C. Lee (Ed.), *Comparative primate socioecology* (pp. 385–403). Cambridge, MA: Cambridge University Press.

Markus, H. R., & Kitayama, S. (1991). Culture and self: Implications for cognition, emotion, and motivation. *Psychological Review, 98,* 224–253.

Marlowe, F. (2001). Male contribution to diet and female reproductive success among foragers. *Current Anthropology, 42,* 755–760.

Michl, G., Torok, J., Griffith, S. C., & Sheldon, B. C. (2002). Experimental analysis of sperm competition mechanisms in a wild bird population. *Proceedings of the National Academy of Sciences USA, 99,* 5466–5470.

Miller, G. F. (2000). *The mating mind.* New York: Doubleday.

Murdock, G. P. (1949). *Social structure.* New York: Free Press.

Murdock, G. P., & White, D. R. (1969). Standard cross-cultural sample. *Ethology, 8,* 329–339.

Nisbett, R. E., & Cohen, D. (1996). *Culture of honor: The psychology of violence in the South.* Boulder, CO: Westview.

Orians, G. H. (1969). On the evolution of mating systems in birds and mammals. *American Naturalist, 103,* 589–603.

Penton-Voak, I. S. (2001, December). *Cross-cultural differences in attractiveness judgments of male faces: Results from rural Jamaican and urban UK samples.* Paper presented at the third Göttingen Freilandtage, Göttingen, Germany.

Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically—Further evidence. *Evolution and Human Behavior, 21,* 39–48.

Penton-Voak, I. S., Perrett, D. I., Castles, D., Burt, M., Koyabashi, T., & Murray, L. K. (1999). Female preference for male faces changes cyclically. *Nature, 399,* 741–742.

Pedersen, F. A. (1991). Secular trends in human sex ratios: Their influence on individual and family behavior. *Human Nature, 2,* 271–291.

Pillsworth, E. G., Haselton, M. G., & Buss, D. M. (2004). Ovulatory shifts in female sexual desire. *Journal of Sex Research, 41,* 55–65.

Rabinowitz, V., & Valian, V. (2000). Sex, sex differences, and social behavior. *Annals of the New York Academy of Sciences, 907,* 196–207.

Rhodes, G., Zebrowitz, L. A., Clark, A., Kalick, S. M., Hightower, A., & Hightower, R. (2001). Do facial averageness and symmetry signal health? *Evolution and Human Behavior, 22,* 31–46.

Richerson, P. J., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution.* Chicago: University of Chicago Press.

Rikowski, A., & Grammer, K. (1999). Human body odour, symmetry, and attractiveness. *Proceedings of the Royal Society of London, Series B, 266,* 869–874.

Robson, A. J., & Kaplan, H. S. (2003). The evolution of human life expectancy and intelligence in hunter-gatherer economies. *American Economic Review, 93,* 150–169.

Rodenwaldt, E. (Ed.). (1952). *World atlas of epidemic diseases.* Washington, DC: Bureau of Medicine and Surgery, Navy Department.

Sanday, P. R. (1973). Toward a theory of the status of women. *American Anthropologist, 75,* 1682–1700.

Schlegel, A., & Barry, H., III. (1986). The cultural consequences of female contribution to subsistence. *American Anthropologist, 88,* 142–150.

Schmitt, D. P. (2005). Sociosexuality from Argentina to Zimbabwe: A 48-nation study of sex, culture, and strategies of human mating. *Behavioral and Brain Sciences, 28,* 247–311.

Sheldon, B. C., Davidson, P., & Lindgren, G. (1999). Mate replacement in experimentally widowed collared flycatchers (*Ficedula albicollis*): Determinants and outcomes. *Behavioral Ecology and Sociobiology, 46,* 141–48.

Sheldon, B. C., & Ellegren, H. (1999). Sexual selection resulting from extrapair paternity in collared flycatchers. *Animal Behaviour, 57,* 285–898.

Sheldon, B. C., Merila, J., Qvarnström, A., Gustafsson, L., & Ellegren, H. (1997). Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. *Proceedings of the Royal Society of London, Series B, 264,* 297–302.

Shweder, R. (1990). Cultural psychology: What is it? In J. Stigler, R. Shweder, & G. Herdt (Eds.), *Cultural psychology* (pp. 1–43). Cambridge, England: Cambridge University Press.

Simmons, J. S., Whayne, T. F., Anderson, G. W., Horack, H. M., & Thomas, R. A. (1944–1954). *Global epidemiology: A geography of disease and sanitation.* Philadelphia: Lippincott.

Simpson, J. A., Gangestad, S. W., Christensen, P. N., & Leck, K. (1999). Fluctuating asymmetry, sociosexuality, and intrasexual competitive tactics. *Journal of Personality & Social Psychology, 76,* 159–172.

Skinner, B. F. (1981). Selection by consequences. *Science, 213,* 501–504.

Sprecher, S., Sullivan, Q., & Hatfield, E. (1994). Mate selection preferences: Gender differences examined in a national sample. *Journal of Personality & Social Psychology, 66,* 1074–1080.

Sugiyama, L. S. (2005). Physical attractiveness in adaptationist perspective. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 292–343). New York: Wiley.

Symons, D. (1979). *The evolution of human sexuality.* New York: Oxford University Press.

Thornhill, R., & Gangestad, S. W. (1999a). Facial attractiveness. *Trends in Cognitive Sciences, 3,* 452–460.

Thornhill, R., & Gangestad, S. W. (1999b). The scent of symmetry: A human sex pheromone that signals fitness? *Evolution and Human Behavior, 20,* 175–201.

Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., McCollough, J., & Franklin, M. (2003). MHC, symmetry and body scent attractiveness in men and women (*Homo sapiens*). *Behavioral Ecology, 14,* 668–678.

Tooby, J., & Cosmides, L. (1990). On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation. *Journal of Personality, 58,* 17–68.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides, & J. Tooby, (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York: Oxford University Press.

Townsend, J. M. (1989). Mate selection criteria: A pilot study. *Ethology and Sociobiology, 10,* 241–253.

Townsend, J. M., & Levy, G. D. (1990). Effects of potential partners' physical attractiveness and socioeconomic status on sexuality and partner selection. *Archives of Sexual Behavior, 371,* 149–164.

Triandis, H. C. (1989). The self and social behavior in differing cultural contexts. *Psychological Review, 96,* 506–520.

Watkins, W. E., & Pollitt, E. (1997). "Stupidity or worms": Do intestinal worms impair mental performance? *Psychological Bulletin, 121,* 171–191.

Wiederman, M. W. (1993). Evolved gender differences in mate preferences: Evidence from personal advertisements. *Ethology and Sociobiology, 14,* 331–351.

Wood, W., & Eagly, A. H. (2000a). A call to recognize the breadth of evolutionary perspectives: Sociocultural theories and evolutionary psychology. *Psychological Inquiry, 11,* 52–55.

Wood, W., & Eagly, A. H. (2000b). Once again, the origins of sex differences. *American Psychologist, 55,* 1062–1063.

Wood, W., & Eagly, A. H. (2002). A cross-cultural analysis of the behavior of men and women: Implications of the origins of sex differences. *Psychological Bulletin, 128,* 699–727.

Appendix
Correlation Matrix

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1. GEM	.74	–.78	.75	.63	–.35	–.14	–.38	.30	–.21	–.35	–.13	–.57	–.42	–.35	–.38	–.61	.27	.40	.22	–.27	.38	–.48	–.66	.20	.72
2. GDI		–.69	.75	.65	–.58	–.25	–.28	.44	–.08	–.28	.07	–.51	–.40	–.13	–.39	–.60	.45	.31	.13	–.06	.30	–.38	–.59	.13	.59
3. Pathogen prevalence			–.74	–.66	.36	.26	.21	–.32	.34	.36	.09	.61	.62	.31	.38	.63	–.42	–.34	–.01	.20	–.58	.56	.62	–.27	–.70
4. Income				.49	–.34	–.21	–.22	.19	–.28	–.15	.06	–.43	–.46	–.37	–.59	–.54	.28	.11	.21	–.10	.31	–.54	–.53	.01	.59
5. Latitude					–.38	–.28	–.13	.75	–.46	–.56	.27	–.52	–.42	–.26	–.37	–.63	.23	.48	–.05	–.20	.24	–.54	–.62	.10	.64
6. Region contrast 1						–.10	–.09	–.26	–.09	.02	–.14	.10	.04	.03	.37	.26	–.53	–.14	–.05	.21	.08	.18	.35	.22	–.55
7. Region contrast 2							–.10	–.30	–.10	.24	–.33	.55	–.02	.13	.27	.25	–.06	–.52	.13	–.29	–.45	.25	.54	–.49	.07
8. Region contrast 3								–.26	–.09	.05	.20	.54	.39	.12	.05	.46	–.05	–.12	.03	.26	–.15	.30	.32	.09	–.24
9. Region contrast 4									–.26	–.41	.33	–.50	–.17	–.25	–.23	–.65	.18	.54	–.04	–.16	.21	–.46	–.54	.24	.32
10. Region contrast 5										.30	–.32	.01	.21	.22	.15	.20	–.01	–.07	–.09	.06	.03	.28	–.01	.08	–.21
11. Financial prospects											.08	.42	.17	.25	.20	.52	–.17	–.55	.00	.22	–.25	.27	.37	–.21	–.38
12. Physical attractiveness												.00	.19	.07	–.20	–.02	–.07	.16	.11	.32	–.17	–.10	–.14	–.12	–.12
13. Health and heredity													.33	.23	.35	.70	–.19	–.52	.08	.20	–.44	.61	.71	–.24	–.43
14. Intelligence														.20	.23	.49	–.26	.03	–.02	.28	–.51	.42	.24	–.10	–.38
15. Interest in children															.56	.53	–.11	–.14	.12	.35	–.22	.44	.42	.03	–.28
16. Domestic skills																.56	–.32	.02	.03	.17	–.10	.57	.43	.22	–.36
17. Status and striving																	–.33	–.41	.00	.42	–.44	.57	.68	–.15	–.57
18. Age																		.08	–.14	–.29	.22	–.01	–.15	.03	.28
19. Sex diff: Financial prospects																			–.04	.04	.44	–.24	–.68	.56	.39
20. Sex diff: Physical attractiveness																				.19	–.13	.07	–.01	.14	.06
21. Sex diff: Health and heredity																					–.03	.10	.06	.36	–.38
22. Sex diff: Intelligence																						–.33	–.42	.60	.22
23. Sex diff: Interest in children																							.54	–.05	–.39
24. Sex diff: Domestic skills																								–.33	–.61
25. Sex diff: Status and striving																									.04
26. Sex diff: Age																									

$p < .05$.

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