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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 qualita-

tively 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, *in press*; 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, 2005; 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, 2005; 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, 2005); (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, 2000; 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, *in press*.)

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).

¹Broader 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, in press).

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, in press). 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 (xxxx) 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 (XXXX) 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.

²One 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.

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

³Rhodes 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 asym-

metry 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

⁴Gangestad 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.

⁵Forced 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 ac-

cess 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

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. FEM = 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.

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

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., 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 (XXXX) 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 (XXXX) 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 contri-

bution 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 (XXXX) 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 compo-

nent 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 evi-

⁶Readers 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*

Mate Preference	Gender Equality (GEM)				Pathogen Prevalence			
	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.

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

dence 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, 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, Gutierrez, & 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 responsiveness, 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

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

Mate Preference	Gender Equality (GDI)				Pathogen Prevalence			
	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.

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

(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 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, *in press*).

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 (Petersen, 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 evoked culture can be explored. The key point is that cultural vari-

ation, 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, herdsman over the eons confronted the threat of losing their entire wealth if their animals were stolen, as often hap-

pened 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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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																									

$p < .05$.

COMMENTARIES

Parasites, Behavioral Defenses, and the Social Psychological Mechanisms Through Which Cultures Are Evoked

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Let's talk first about parasites. Given the persistent influence that bacteria, viruses, and other parasites have had on human evolution (Van Blerkom, 2003), it's astonishing that so little scientific attention has been devoted to their impact on human psychology and human culture. There are extensive bodies of research documenting the role of parasites on evolved patterns of animal cognition and behavior. Many studies reveal that mammals are sensitive to signs of parasitic infection in potential mates and avoid mating with individuals who show those signs (e.g., Kavaliers, Colwell, Braun, & Choleris, 2003). These kinds of effects are not restricted to mating contexts either. Bullfrog tadpoles selectively prefer to swim near healthy tadpoles, while avoiding tadpoles that carry parasitic infections (Kiesecker, Skelly, Beard, & Preisser, 1999). Closer to home (phylogenetically speaking), chimpanzees react with unusual violence toward other chimpanzees that show the physical symptoms of debilitating diseases (Goodall, 1986). It is likely that the human mind too is characterized by mechanisms designed to recognize and respond negatively to individuals who show signs of parasite infections—and to do so especially under conditions in which the risk of parasitic infection is especially high (Kurzban & Leary, 2001; Schaller, Park, & Faulkner, 2003).

In recent years, empirical studies have documented the presence of just such mechanisms and their consequences on social cognition and behavior. Some of these consequences are straightforward: We stigmatize and avoid sick people, especially when we perceive their sickness to be contagious (Crandall & Moriarty, 1995). Additional consequences are more subtle. We not only stigmatize people who really are sick; we also stigmatize people who may be perfectly healthy but who—on the basis of some superficial feature—appear to pose a risk of parasite transmission. And we do so especially under conditions in which we feel especially vulnerable to parasitic infection. Xenophobic reactions to foreigners are stronger

among folks who feel personally vulnerable to germs and disease (Faulkner, Schaller, Park, & Duncan, 2004). Individuals with deviant or nonprototypical morphological features—people who are disfigured or disabled, or who are grossly obese—are similarly stigmatized, and, again, this stigmatization seems to occur especially strongly among people who are personally concerned about their own vulnerability to disease (Park, 2005; Park, Faulkner, & Schaller, 2003). The preference for physically attractive mates might also be understood within this context. Physical *unattractiveness* is based substantially on perceived deviations from a population prototype (Langlois & Roggman, 1990). Consequently, the subjective assessment of unattractiveness may serve as a cue indicating the potential presence of a parasitic infection at the moment, as well as a cue indicating potential susceptibility to parasitic infections in the future. Within this conceptual context, it is no surprise that people care about the physical attractiveness of someone with whom they are destined to spend a lot of time with and that they care especially within populations that have historically been more vulnerable to debilitating parasitic infections (Gangestad & Buss, 1993). Now, in the results reported by Gangestad, Haselton, and Buss (this issue), we encounter even more impressive evidence that parasite-prevalence influences mate-selection preferences, and this influence occurs across an even broader set of preferences.

The Behavioral Immune System

It is because of results such as these that I am increasingly convinced that there evolved a sort of behavioral immune system that serves as an organism's first crude line of defense against potentially harmful parasites and pathogens. (It would probably be more apt to refer to this as the "psychological immune sys-

tem,” because the system involves emotions and cognitions as well as behavior, but that term has appeared already in the psychological literature, referring metaphorically to a different set of processes that have nothing to do with parasite defense; see Gilbert, Pinel, Wilson, Blumberg, & Wheatley, 1998.) The behavioral immune system is triggered by the perception of specific kinds of stimuli (e.g., morphologically unusual appearance). When such stimuli are perceived, there ensues the automatic activation of the specific emotions and cognitions (e.g., disgust; automatic inferences about disease-connoting traits) that facilitate functional behavioral reactions (e.g., avoidance, social exclusion).

Of course, there are costs as well as benefits associated with the activation of this suite of reactions, and so the behavioral immune system is functionally flexible, responsive to information bearing on these costs and benefits. Relevant information may lie in temporary features of the immediate situation, and so these discriminatory reactions may be triggered in some situations more strongly than in others. Relevant information may also lie in chronic individual differences, and so these reactions may be triggered among some people more strongly than among others. Finally, relevant information may also lie in chronic aspects of the ecological context, and so these reactions may be triggered in some populations more strongly than in others.

That last remark—about the effect of ecological contexts and differences across populations—provides a point of transition into a bigger, broader point about universal evolutionary mechanisms and cross-cultural differences. I devote the rest of my remarks to this issue. The question I want to grapple with more fully is this: Just how are different cultural norms “evoked” under different ecological circumstances?

Questions Lurking Within the Concept of Evoked Culture

The notion of evoked culture is easily extrapolated from what we know already about evolved plasticity and environmental contingency. Those concepts are so well accepted within the biological sciences that, as concepts, they are almost boring. Not boring at all, of course, are the discoveries that result from the recognition that these concepts matter.

Consider the many wonderful examples that illustrate the operation of evolved plasticity and environmental contingency. Gangestad et al. (this issue) mention several (e.g., contingent mating strategies among collared flycatchers). I have a few other favorite examples. The tendency for cannibalistic spiders to selectively avoid eating their own kin is contingent on the extent to which alternative sources of food are

available (Bilde & Lubin, 2001). Genetically-identical butterflies may take on entirely different appearances depending on local climatic conditions during the larval stage of development (Beldade & Brakefield, 2002). And, among several families of tropical fishes, changes in local sex ratio and social density may lead individuals to actually change from male to female or vice-versa (Godwin, Luckenbach, & Borski, 2003). Not only are these examples fascinating and fun in their own right, they offer a sort of standard against which we can judge the plausibility of evoked differences in human populations. If ecological variables can trigger such profound phenotypic variability in spiders and butterflies and fishes, it is hardly surprising that powerful ecological forces posed by parasites might evoke somewhat different mating preferences in a species as famously flexible as *Homo sapiens*.

The other thing that is definitely not boring about any environmental contingency in the biological sciences is the process through which it occurs. Interesting scientific stories lie not only in the observation that phenotypic differences are evoked under different ecological contexts; they lie also in the sophisticated programs of research that attempt to answer the question of exactly how this actually happens. These answers take us beyond the observations of zoology and behavioral ecology and deep into the realms of functional genomics and developmental biology (e.g., Hofman, 2003; Godwin et al., 2003; for a discussion of applications to human cognition, see Marcus, 2004). The documentation of an evolved environmental contingency is not a conclusion; it is an introduction. It opens the door to an enormous world of scientific exploration.

The same is true when the concept of evoked culture is introduced into conversations among psychologists and other social scientists. Evoked culture is not really an explanation for cultural variation. It is an observation that seeks explanation and offers logical clues to the sorts of theories that might be generated to provide those explanations. If indeed certain kinds of cultural norms are evoked by certain kinds of ecological circumstances, how does this actually happen? What are the actual psychological mechanisms involved? And what are the evolutionary roots of those mechanisms?

We are still a long way from having satisfactory answers to those questions. There is neither surprise nor shame in that. It is difficult enough to arrive at convincing answers to questions that address just the psychological level of analysis. It is even more difficult when connecting the psychological with either an evolutionary or a cultural level of analysis. And to connect all three levels of analysis together, coherently and convincingly—well, that is going to take some time and serious collective effort.

The Importance of Social Transmission Processes

As one step toward that goal, it will be valuable to sidestep the rhetorical baggage that sometimes accompanies the concept of evoked culture and explicitly integrate it with the concept of transmitted culture.

The baggage to which I refer is an ideology-tinged tendency to view evoked and transmitted culture as alternative theoretical approaches to the emergence of cultural differences. The presence of this baggage may help explain why some folks mistakenly believe that evidence of cultural transmission argues against the plausibility of evoked culture, and other folks mistakenly believe that evidence of evoked culture argues against the importance of social learning, interpersonal communication, and other modes of cultural transmission. This baggage might be traced, in part, to the manifesto-like tone of the chapter in which Tooby and Cosmides (1992) introduced the concept of evoked culture and contrasted their evolutionary perspective against the so-called standard social science perspectives that focused merely on domain-general learning and transmission processes. I have nothing against manifestos (in fact I rather like them), and that rhetorical approach probably made sense at the time. But it doesn't anymore. No longer is it necessary to argue that the principles of evolutionary psychology can be applied usefully to questions about culture. The intervening years have supplied plenty of evidence establishing that point. (Gangestad et al.'s, this issue, article offers one nice example. For other examples, see Atran & Norenzayan, 2004; Henrich & Boyd, 1998; Kameda, Takezawa, & Hastie, 2003; Kenrick, Li, & Butner, 2003; Krebs & Janicki, 2004; Norenzayan, Schaller, & Heine, *in press*). What is necessary now is to document more exactly the mechanisms through which evolved psychological processes actually do influence culture.

Here is where we need to take seriously an important point that Gangestad et al. (this issue) make toward the end of their article: that the mechanisms of evoked and transmitted culture are unlikely to be completely independent. I would hit that point even harder: The mechanisms of transmitted culture are integral to the process through which different cultures are evoked under different ecological circumstances. Just as biologists cannot fully understand environmentally contingent differences in the morphology of fishes without attending to the developmental mechanisms through which these differences emerge, we cannot fully understand the process of evoked culture without attending to the mechanisms of social transmission. Let me try to explain why.

A Few Thoughts on Social Learning

If I had a bit more space (and a lot more expertise), I might go into detail on ways in which social learning mechanisms are implicated in the process through which cultures are evoked. Instead, I just make a few quick points that suggest the need for closer attention and future elaboration. Basic mechanisms of social learning—mimicry, imitation, conformity—have deep evolutionary roots, operate automatically, and are ubiquitous aspects of the contemporary social landscape (Lakin & Chartrand, 2003; Moore, 2004; Henrich & Boyd, 1998). Many other evolved psychological systems employ basic learning mechanisms as a necessary means of facilitating adaptive behavior. One example is found in the set of mechanisms that comprise a sort of “fear module,” endowing individuals with the adaptive tendency to respond fearfully toward potentially dangerous things. A fundamental part of that fear module is an evolved capacity to learn specific stimuli that signal danger, and it appears that there may be an innate preparedness to learn certain fears—such as a fear of snakes—especially quickly (Öhman & Mineka, 2001). These fears can be learned through entirely nonsocial associative mechanisms, but social learning is implicated as well. Rhesus monkeys, for instance, learn to fear snakes simply from observing other monkeys' fearful reactions to snakes (Cook & Mineka, 1990; see also Whiten, 2000). Just as social learning mechanisms are implicated in the process through which individuals acquire the capacity to react fearfully to potentially dangerous stimuli, it is also likely that social learning mechanisms are implicated in the process through which the behavioral immune system acquires the capacity to respond aversively to deviant morphological features and the process through which individuals acquire the capacity to distinguish desirable mates from less desirable ones.

Finally, just as other evolved psychological mechanisms (such as those that comprise the behavioral immune system) are triggered more strongly under specific kinds of circumstances, these learning mechanisms may be functionally flexible as well. Under conditions of high parasite prevalence, one might display an especially strong expression of disgust on encountering some stranger who is disfigured or otherwise unattractive. Under these same conditions, another person might be especially vigilant to those expressions of disgust and might be especially quick to form a learned association linking physical unattractiveness with social disapproval. Under conditions of low parasite prevalence, these associations may be learned more weakly.

The Causes and Consequences of Communication

Now let's talk about communication. The basic mechanisms that underlie interpersonal communication are activated and applied across every imaginable domain of social life. Over time, simple acts of communication exert a dynamic cascade of consequences that result, inevitably, in the emergence of different cultures defined by different norms (Harton & Bourgeois, 2004; Latané, 1996).

If we just left it at that, it might appear that communication processes create cultural differences independent of the sorts of evolutionary pressures described by Gangestad et al. (this issue). But we cannot leave it at that. People do not just talk; they talk about specific things, and the specific contents of communication have cultural consequences (Schaller, 2001). Plus, people make strategic decisions (not always consciously) to talk about some things and not others. Those decisions may reflect the role of functionally flexible psychological adaptations: In ancestral populations, strategic acts of interpersonal communication are likely to have had consequences on the communicator's reproductive fitness.

To appreciate this last point, it is helpful to bear in mind the important evolutionary concept of inclusive fitness, whereby any individual's fitness is affected not merely by his or her own individual outcomes, but also by the outcomes of others who share the same genes. Assume, for a moment, that you and I are living in some ancestral environment. To the extent that you and I are related, my inclusive fitness can be influenced by my decisions to tell you about some things, rather than others. If you are my sibling, for instance, my own inclusive fitness (or, if you prefer, the fitness of my genes) may be influenced by my decision to alert you to the danger posed by a poisonous berry or by the appearance of a stranger with peculiar-looking pustules on his face. If you are my child, my own inclusive fitness may be influenced by my decision to advise you to choose a symmetrical man for your mate, rather than some goofy-looking guy with a goopy eye.

Furthermore, within any highly social species, an individual's fitness may be influenced by the outcomes of other members of a coalitional ingroup, even if those members are not immediate kin. My own well-being, and thus my reproductive fitness, is likely to be adversely affected if you—a fellow group member with whom I expect regular social contact—become infected with a contagious parasite that I might then catch from you. Thus it would not only be in your best interests, but also in the best interest of my genes, for me to warn you against interactions with anyone who might already be infected. And, of course, it would be adaptive to err on the side of caution (Haselton & Nettle, *in press*; Nesse, 2005), encouraging you to seek in-

teractions with folks who appear to be healthy (e.g., attractive people) rather than with those who might not be.

A couple of interesting implications emerge from this line of reasoning. First, it suggests that our behavioral immune system may be designed not merely to protect ourselves but to protect the broader population of individuals whose outcomes have implications for the reproductive fitness of our genes. Second, to accomplish that goal, the behavioral immune system is designed to produce specific kinds of communicative signals that alert those people.

This line of reasoning is not specific to the behavioral immune system. It can be applied to many other domains of social life and the psychological adaptations that apply to them. And so, generally speaking, the contents of communication are likely to follow the same principles that we commonly see in the operation of evolved cognitive processes. Just as we observe the selective activation of emotions and cognitions that are instrumental in guiding adaptive patterns of behavior (e.g., the tendency for morphologically unusual people to elicit disease-relevant cognitions), we are likely to observe that people selectively communicate fitness-relevant information to kin and other coalitional ingroup members. And just as the selective activation of emotions and cognitions occurs more strongly under some circumstances (e.g., morphologically unusual people elicit more disease-relevant cognitions under circumstances in which the perceived risk of contagion seems especially high), the selective communication of fitness-relevant information is likely to be exaggerated under the same circumstances.

These general points are perhaps illustrated by recent findings reported by Bangerter and Heath (2004) on the prevalence of media reports about the so-called Mozart effect—the alleged, but actually nonexistent, effect whereby children who listen to classical music become more intelligent. These results showed that the prevalence of these transmissions was especially high within populations in which there was greater collective anxiety about the quality of early childhood education. The prevalence of these transmissions may reflect an overgeneralization of the presumably adaptive tendency to provide kin with information that is instrumental in raising children with qualities, such as intelligence, that might enhance their fitness. If so, it follows that this tendency would be exaggerated under conditions in which there is greater reason to worry about their acquisition of such qualities. I am speculating, of course. But if there is any merit to this speculation, then these results document a sort of evoked cultural difference, and communication mechanisms play an essential role in the process through which these cultural differences are evoked.

We can apply the same logic to help understand how interpersonal communication may be an essential

mechanism through which parasite prevalence evokes different cultural norms. People are more likely to communicate about others' traits and characteristics that more clearly connote potential threat or lack of threat (Schaller, Faulkner, Park, Neuberg, & Kenrick, 2004). People are also especially likely to transmit urban legends—which often serve as cautionary tales—that most strongly elicit disgust, the emotion that serves as a cue for potential contagion (Heath, Bell, & Sternberg, 2001). Although it has not yet been documented, I bet that the latter effect would be especially strong under conditions in which parasite prevalence, and thus the potential risk of contagion, was especially high. Similarly, under conditions of high parasite prevalence, people may be especially likely to advise their family and friends to selectively interact with healthy or healthy-looking (i.e., attractive) individuals and to avoid interactions, especially in mating relationships, with sickly or unattractive folks.

Advice on interpersonal relationships is not merely communicated through private conversations among family and friends; it is also embedded in the folk tales, fairy stories, and other narratives that comprise the oral traditions of any culture. The handsome knights, beautiful maidens, and loathsome trolls that populate these tales are not merely stock characters. They also serve as prototypes, instructing children (and other individuals whose outcomes influence our own fitness) about what sorts of folks to avoid, what sorts of folks to spend time with, and what sorts of folks are suitable mates. Some narratives are more likely than others to be told and retold. This selectivity is influenced, in part, by memory mechanisms (Norenzayan, Atran, Faulkner, & Schaller, in press). In addition, I suspect that some of this selectivity is the function of the extent to which a narrative offers implicit lessons about the features that discriminate between the healthy and the ill, the fit and the unfit, the desirable mate and the mate that just won't do. And this selectivity is likely to be even more pronounced under conditions in which parasites are especially prevalent.

The point is clear, I hope: Different ecological circumstances are likely to evoke different decision rules that have direct consequences on the contents of interpersonal communication. It is through deeper inquiry into this mechanism of transmission that we can more fully understand what's going on when we talk about evoked culture.

Envoi

The biological sciences can be great sources of inspiration to people who study human psychology, culture, and other social sciences. (The spark of inspiration travels in the reciprocal direction as well; let's not forget that Darwin's evolutionary insights were influ-

enced, in part, by his reading of Malthus; see Hull, 1988). Behind the concept of evoked culture lurk many wonderful findings from research on evolutionary theory and behavioral ecology. Those findings themselves pose deeper questions, which are addressed in other domains of biological inquiry (e.g., functional genomics) that focus on underlying mechanisms. It is probably premature to turn to genomics for answers to questions about evoked culture. But it is not premature to follow an analogous path and to dig more deeply into the actual mechanisms through which culture is evoked. When we do this digging, we discover that interpersonal transmission processes (social learning, interpersonal communication) are not alternative routes to culture; they are important links in the coherent causal chain through which evolutionary processes create culture. Then, by trying to figure out the specific details, we discover whole new realms within which to develop theories and conduct empirical research at the intersection of the biological and social sciences. I reckon that'll keep us busy for a while.

Notes

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Evolutionary Psychology: Resistance Is Futile

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The Borg is an imaginary federation of Star Trek creatures who conquer other beings not by annihilation but by incorporating them into a larger collective. Thus, the strengths of former foes become assets for an ever-enlarging and ever-strengthening network. When a member of the Borg alliance encounters opposition, he responds with a simple declaration: "Resistance is futile. You will be assimilated."

For several decades, a Borg-like federation of researchers in several disciplines has been working toward a fully integrated perspective for the behavioral sciences. This increasingly inclusive perspective melds insights from evolutionary psychology, cognitive science, and dynamical systems theory (Cosmides, Tooby, & Barkow, 1992; Kenrick, Li, & Butner, 2003; Kenrick et al., 2002). Attacking individual proponents of this integrative perspective is akin to attacking individual ants—it may bring a temporary sense of relief, but it will do little to slow the growth of the colony, and it may result in a surprisingly effective counterattack.

Gangestad, Haselton, and Buss's (this issue) article illustrates why years of frequent and persistent attack have not caused evolutionary psychology to crumble. Evolutionary psychologists used the many attacks to fortify strengths, jettison weaknesses, and borrow the best weapons of their enemies. This is of course nothing more than science-as-usual. Incorporating criticism into newer and stronger theories is what makes scientific approaches resilient in a way that has perennially annoyed proponents of dogmatic belief systems.

Evolutionary Epistemology and Coevolutionary Arms Races

Evolutionary psychology is simply the scientific study of thought, emotion, and behavior, in light of a general adaptationist framework. This framework includes two general assumptions: (a) All organisms living today are descendents of ancestors efficiently designed to survive and (more important) reproduce, and (b) successful survival and reproduction is usually accomplished most efficiently by living systems composed of domain-specific mechanisms. Domain-specific mechanisms are features such as the special breathing apparatus, fins, and sonar communication capacities of whales, each efficiently designed to accomplish a different function. Evolutionary psychologists assume that, like physical traits, cognitive and behavioral mechanisms are most efficient when designed to deal differently with different problems (such as

avoiding poisonous foods vs. learning language vs. choosing mates vs. making economic decisions involving kin).

Adaptationist reasoning can be applied to any aspect of psychology. Much of the early research applying evolutionary models to human behavior focused on sex differences in mating and intrasexual competition. These topics were chosen not randomly, but because they were conceptually low-hanging fruit. Sex differences in mating strategies are ubiquitous in the animal kingdom, and men and women manifest a number of obviously different physical features linked to mating. It follows that men and women should manifest behavioral and psychological characteristics that correlate with those physical differences (see Geary, 1998; Kenrick, Trost, & Sundie, 2004, for reviews).

The process of natural selection itself is partly driven by a coevolutionary arms race between any given species and its enemies (e.g., Dawkins & Krebs, 1979). Animals surviving today inherited complex defenses designed to respond not only to particular threats but also to flexibly redesign new defenses for new attacks. At the phylogenetic level, sexual reproduction may have evolved to reshuffle physiological structures to keep one step ahead of cell-sized enemies (such as viruses and bacteria; Hamilton, Axelrod, & Tanese, 1990; Ridley, 1993). At the ontogenetic level, the immune system works in this way, flexibly responding to attacks from previously unknown enemies.

Evolutionary epistemologists assume scientific theories are subject to a process analogous to natural selection (e.g., Campbell, 1974). Good theories compete more successfully for intellectual territory, and better theories emerge from a process of variation and selective retention. Some theories are completely eliminated by better alternatives, but even the survivors are continually evolving. Critics sometimes complain that evolutionary psychologists won't stand in one fixed place long enough to let them get in a good shot. But committing to one rigid and immobile posture is not how science works. Instead, evolutionary psychologists, like all working scientists, respond to criticisms with empirical and theoretical attempts to remove weaknesses and to build a stronger and more incorporative intellectual architecture. The foundation of Darwinian adaptationist assumptions has proven itself remarkably capable of supporting an ever-larger and more elaborate empirical edifice.

To the criticism that early research in evolutionary psychology focused too heavily on male psychology, feminist-inspired evolutionary theorists responded

with an increasing consideration of topics such as the role of female choice in mating, female alliance formation, mothering, and grandmothering (e.g., Hawkes, 1999; Hrdy, 1999; Taylor et al., 2000). To the criticism that early work ignored the complexities of ongoing human cognition, there has been increasing research on evolutionary social cognition (Becker, Kenrick, Guerin, & Maner, in press; Haselton & Funder, in press; Krebs & Denton, 1997; Maner et al., 2003; Park & Schaller, 2005). To the criticism that evolutionary psychology has focused too narrowly on sex and aggression, there is an increasing emphasis on a wide range of topics, including racism and stereotyping (e.g., Cottrell & Neuberg, 2005; Schaller, Park, & Faulkner, 2003), positive psychology (Buss, 2000), health psychology (Taylor et al., 2000), social influence (Sundie, Cialdini, Griskevicius, & Kenrick, in press), and social dilemmas (Kenrick & Sundie, in press; VanLange & VanVugt, in press). And to the criticism that evolutionary psychologists ignored the complexities of culture, there has been an increasing integration of cultural and evolutionary psychology (e.g., Norenzayan, Heine, & Schaller, in press; Tooby & Cosmides, 1992).

Why have researchers in an increasing number of subareas of psychology started investing time in exploring evolutionary hypotheses? A commonly stated reason is broad intellectual appeal: The perspective connects the subdisciplines of psychology and makes our work mutually informative with developments in other fields such as biology and anthropology. But broad ideas do not count for much by themselves. In the economy of scientific ideas, data talks. The general Darwinian or adaptationist framework has been a rich mine of productive hypotheses about a wide range of behavioral and cognitive phenomena. This makes sense given that animals, including *Homo sapiens*, are designed by natural selection to do something, and to do it relatively well. Hypotheses that consider ultimate function stand a better chance of being on the right track than those that presume behavior and cognition stems from arbitrary and random causes (cf. Alcock, 2000).

The increasing exploration of domain specificity has also helped make evolutionary hypotheses more interesting. According to this view, qualitatively different processes apply to different aspects of thought, feeling, and behavior. It bypasses the classic “goldfish problem” that can make domain-general approaches boring. In the apocryphal story, a graduate student proposes a dissertation based on the following reasoning: Researchers had already demonstrated conditioning in rats, mice, humans, cockroaches, and even one-celled organisms, but no one had ever demonstrated it in a goldfish. As psychologists began exploring how conditioning is differentially linked to each organism’s evolutionary history (e.g., Garcia & Koelling, 1966;

Wilcoxon, Dragoin, & Kral, 1972), things simply got more interesting.

A less frequently stated aspect of this intellectual breadth is evolutionary psychology’s capacity to embrace the research topics and methods of its critics. Despite the wishful thinking of those who have not yet joined the alliance, evolutionary psychology does not involve a narrow commitment to one set of topics, one set of methods, or one dogmatic way of interpreting data. Evolutionary psychology involves simply a call to consider the adaptive background of whatever behavioral phenomenon one chooses to study. Thinking about adaptation generates a reasonable ratio of empirical hits but of course plenty of misses as well (Alcock, 2000; Kenrick, 1995). Like all good scientific frameworks, the evolutionary perspective is strengthened and expanded by considering phenomena that first appear to be exceptions to the current way of viewing things. Even if all current evolutionary hypotheses are replaced, they will likely be replaced by hypotheses that better correspond to actual evolved mechanisms. The only limiting condition would be if the majority of behavioral phenomena ultimately prove to be governed by mechanisms that operate outside the realm of natural selection. So far, that does not appear to be the way things are looking. Consider the class of phenomena generally known as “cultural influences” on behavior.

The Culture of Evolutionary Psychology

Evolutionary theorists have been considering the interaction between culture and evolution for several decades (e.g., Campbell, 1972; Lumsden & Wilson, 1981). A glance at the literature on coevolution will quickly negate any stereotyped ideas that postulating evolved mechanisms means proposing an “alternative” to cultural influences on behavior (see Janicki & Krebs, 1998, for a review). Perhaps an evolutionary perspective is sometimes misperceived in this way because proponents do, in fact, (a) tend to doubt that culture is something that arises independent of human nature, (b) tend to believe that a number of psychological universals may lie beneath apparent cultural variations in manifest behavior, and (c) take issue with the popular practice of attributing behavioral phenomena to culture without considering any cross-cultural evidence whatsoever. If anyone reads those three points as denying that there is such a thing as culture, or as implying that it is unimportant, he or she should read again. Indeed, an evolutionary perspective inspires more rather than less interest in conducting cross-cultural psychology (e.g., Daly & Wilson, 1988; Kenrick & Keefe, 1992; Norenzayan & Heine, 2005; Schmitt & International Sexuality Description Project, 2003). The creation of culture is surely one of the more fascinating

features of our species, and questions about how cultural variations emerge from, interact with, and shape the development of evolved psychological mechanisms are some of the most important questions in the behavioral sciences.

The notion that some cultural variations are manifestations of flexible adaptations (i.e., evoked culture) is only one of the interesting ideas from the literature on coevolution, and the jukebox-like evocation of a flexible adaptation is only one of several logical coevolutionary relations. Another is the possibility that some cultural norms represent self-amplification of evolved mechanisms in a group context. For example, young men are more physically violent from the early years, a phenomenon that is found not only in humans but also in many other vertebrates. This sex difference seems to be an early life-history manifestation of differential parental investment and sexual selection (e.g., Geary, 1998). The innate differences between male and female found in many other species, however, may be enhanced in human societies by cultural practices such as training in martial arts for boys versus home economics for girls (Kenrick, 1987). Another possibility is that evolved mechanisms exert important influences on the selection of cultural practices. For example, attempts to raise children separately from their biological parents (as practiced in Israeli kibbutzim for some time) would be expected to be less likely to persist than arrangements in which children are kept in close proximity to parents and siblings. Yet another possibility is cultural practices designed to control selfish evolved mechanisms. Laws against nepotism, theft, rape, and gang warfare are examples of such group-designed reactions to universal selfish tendencies (Campbell, 1972; Jones, 2001). Once one begins to consider the diverse ways evolved predispositions can be reflected in, amplified by, and opposed by cultural practices, one is led to question any default assumption that culture regularly operates “independently” of evolved mechanisms.

Jukeboxes and Coloring Books

Cosmides and Tooby’s jukebox metaphor is useful for describing certain examples of evoked culture. For example, polyandry, though rare, tends to be associated with resource scarcity at the ecological level and to involve brothers at the social structural level. This follows from the differential costs of cuckoldry on men versus women and from the lowered fitness costs associated with investing in a sibling’s offspring. Polygyny, on the other hand, tends to be more pronounced when there is a steep social hierarchy (such that some families control many more resources than others) and when there is occasional famine such that poorer families may occasionally fall below the resource threshold needed to provide for children (Crook & Crook, 1988).

Sometimes, however, evolved constraints influence the development of cultural norms in a more flexible and complex manner. For such cases, a coloring book may a slightly more apt metaphor than a jukebox. A coloring book involves not so much a fixed set of outcomes but a flexible possibility space for which biological predispositions provide the predrawn lines and for which local social and physical ecology provides a palette of tints with which to color in the open spaces. The eventual picture drawn on the page of a coloring book is not completely determined, but neither is it completely arbitrary.

Consider for example, the Tiwi of North Australia. According to a classic ethnography on this group, most men did not get married until they were in their twenties or thirties, at which point they married elderly widows (Hart & Pillig, 1960). At first glance, this pattern poses problems for all existing accounts of gender differences in age preferences. To begin with, the practice of young men marrying older women flies in the face of data Keefe and I (Kenrick & Keefe, 1992) collected from a number of societies that suggested a universal mutual attraction between powerful older men and attractive younger women. According to our evolutionary life history perspective, women are attracted to status and material wealth rather than seniority. Men across human societies do not contribute physiological resources directly from their bodies, as women do, but instead contribute indirect resources, such as food and shelter. The ability to provide such resources correlates with a man’s status and material wealth, which in turn tend to increase with age. On the other side, age-linked changes in female fertility are universal, with puberty and menopause forming lower and upper limits on the years of peak fertility in all societies. Data from a large number of societies around the world indeed indicated that men, regardless of their own age, are attracted to women in the years of peak fertility (Kenrick & Keefe, 1992).

The Tiwi pattern of young men marrying older women, however, is directly contrary to this general worldwide pattern and seems to defy the general evolutionary life history model. It also fits poorly with the other models discussed by Gangestad et al. (this issue). Eagly and Wood (1999) reported that the preference for young women was more pronounced in relatively more patriarchal societies and took this to support their social role theory. If this theory applied here, we would expect to find that the usual patriarchal rules found in European societies (which are normally stronger in most third-world cultures) do not apply to Tiwi society. But Tiwi society is actually highly patriarchal. Tiwi men, for example, decide not only who their daughters will marry but even make such decisions for their widowed mothers. Gangestad and colleagues demonstrate that the simple correla-

tion between patriarchy and age preference disappears when parasite prevalence is considered. Yet the Tiwi do not seem to support their parasite model either. When the classic ethnography was written, the Tiwi lived in something close to a hunter-gatherer lifestyle in a semitropical climate. The best bet is their parasite load is rather unlike modern Europeans living in Sweden, hence the preference for female attractiveness (and youthful characteristics) ought to be especially pronounced rather than reversed.

On closer examination, the Tiwi marriage patterns suggest a dynamic interaction between two sets of sex-differentiated evolved mechanisms—one involving competition for status (which results in the worldwide construction of patriarchies) and the other involving the male preference for relative youth. It turns out that Tiwi men are, like men in other societies, strongly attracted to young women as sexual partners (Hart & Pillig, 1960). If so, why don't young Tiwi men marry younger women, as do men in most of the world's other societies? The answer has to do with the exaggerated patriarchal power over Tiwi mating arrangements. To begin with, Tiwi society is polygynous, and only much older men get to exercise their attraction to younger women. This is because power in Tiwi society is largely monopolized by the older polygynous men. Those older patriarchs tend to betroth their young daughters to other patriarchs, who are in a position to reciprocate. Young men, with no daughters to offer, are thus excluded from obtaining young wives. A young man caught having an affair with a young woman could be punished by expulsion from the group or by being gored with a hunting spear.

The fact that older men use coercive means to monopolize the younger women explains why younger men and women do not marry but not why young men and older widows marry. The explanation for that custom lies in other features of the Tiwi social system. All Tiwi women (but not all men) are required to be married. At birth, an infant girl is betrothed to a powerful older man, and a widow must remarry on her husband's death. But older widows are less desirable to powerful older men once they have acquired young wives. A young man who marries an older widow, though, cements alliances with her relatives and gains some rights in determining who her daughters marry if they become widowed early. As a consequence, a young man takes the first step toward gaining status when he marries an older widow, and, as a consequence, he is later more likely to acquire desirable younger wives (Hart & Pillig, 1960).

Men from the Mardudjara tribe, another Australian aborigine group, also reportedly prefer younger wives as sexual partners (Tonkinson, 1978). But young wives are hard to find, as girls are frequently betrothed to powerful older men. Again, a young man may marry a

widow as his first wife, thereby increasing his status and social connections and increasing his chance of later attracting younger wives. The pattern is less pronounced than that found among the Tiwi because the Mardudjara do not require all women of all ages to marry.

There is likely a wide range of individual variation among men and women and across societies in attraction toward relatively older versus younger partners. But it would be difficult to imagine a monogamous society in which young men were only attracted to elderly women and in which only older women could find partners. If such a society ever existed, it would have been short lived, given the constraints on reproduction posed by female reproductive life history. Instead, the Tiwi pattern suggests a dynamic interaction between evolved psychological mechanisms (male attraction toward women in the years of peak fertility, female attraction toward men who have acquired status) and local social ecology (a geriatric patriarchy that monopolizes younger women, in combination with a rule that all women must be married).

Dynamical Evolutionary Psychology: Emergence by Domains

To understand how evolved mechanisms and cultural norms interact with one another, the traditional evolutionary approach can incorporate some of the insights of a dynamical systems perspective (Kenrick et al., 2000, 2003). Dynamical systems theory is concerned with complex, multicomponent systems (ranging from the microscopic [e.g., genes within the developing organism or networks of neurons within the brain] to the macroscopic [e.g., animals and plants within a particular ecosystem, or the millions of consumers within an economic market]). A key feature of many dynamical systems is bidirectional causality. In a laboratory, an animal may be given a distinct and unconfounded choice between two carefully controlled types of food. In a natural ecosystem, the food may take steps to avoid being eaten or even bite back. Dynamical systems theorists believe that studying bidirectional causality, though more difficult than studying isolated variables, is essential to understanding many natural phenomena.

Observations of complex dynamic systems have yielded a pair of critical insights. First, great complexity can arise spontaneously from the interaction of just a few simple parameters. Second, self-organization often arises out of initially random interactions of dynamically linked components (Nowak & Vallacher, 1998). Self-organization refers to the spontaneous emergence of new structures and patterns of behavior

that were not programmed into the system but that arise from the combined activity of multiple components following simple rules.

Human cultures are complex dynamical systems in which the individual parts often rearrange themselves into something novel. As in all dynamical systems, the rearrangements emerge from the initial decision rules used by the interacting elements in the system. An evolutionary perspective is useful in suggesting the initial decision rules that affect the emergence of important social norms—the social norms that surround mating, sharing with friends versus family members, gaining status, negotiating with ingroup versus outgroup members, and so on (Kenrick et al., 2003). For example, inclusive fitness considerations make the standard assumptions of market economics largely irrelevant within families and very different for men and women seeking mates than for friends sharing food or information (Kenrick & Sundie, in press). Evolved decision-rules are important not only in affecting social norms but also in shaping social structures: Different natural geometries emerge from the decision-rules associated with friendship networks, mating arrangements, families, and status hierarchies (Kenrick et al., 2002). For example, intrinsic conflict over genetic interest makes it easier to maintain a stable alliance of six or seven same-sex friends than six or seven men married to the same woman. In terms of our earlier metaphor, the mind is a coloring book with multiple pages: Different patterns of lines and different color palettes influence the picture that emerges within each different domain.

Qualitatively different dynamic principles likely apply to coevolutionary processes at several different levels of analysis (Kenrick et al., 2002). Over phylogenetic time spans, for example, the physical traits and psychological preferences within a species will influence one another (internal gestation and nursing young correlates with high selectiveness in choosing mates, for example) and can influence the evolution of traits of conspecifics (selectivity in one sex selects for intrasexual competitiveness in the other, for example). Over the individual lifespan, the existence of particular traits within one person will constrain the development of other traits in that individual (e.g., high physical attractiveness and symmetry in a man facilitate a relatively more unrestricted mating strategy, Gangestad & Simpson, 2000). Over relatively shorter time spans, random variations in decision-biases within the local population will influence the formation of local norms (a relatively high number of local women willing to compromise male commitment for good genes will affect the mating choices of local men and other women who might have otherwise favored more restrictive local norms).

Why Do Some Continue to Resist Assimilation to the Integrationist Program?

If an evolutionary perspective is flexible enough to incorporate all the different research topics of social and personality psychology, dynamic enough to incorporate the broadest questions about the emergence of human cultural diversity, and powerful enough to keep generating new and interesting empirical hypotheses, why do some psychologists still fight tooth and nail to resist assimilation? The answer to this question is probably fairly complex, but I believe a good part of the answer is this: Resisters still regard the Blank Slate position as somehow morally superior. Many resisters will no doubt insist that they are not Blank Slate theorists. Yet even when they acknowledge the research evidence demonstrating that the slate is not blank, resisters often give away a strong preference for a slate that is as blank as possible, particularly when it comes to their own research neighborhoods.

Consider Eagly and Wood's position on sex differences in mating preferences. Their general position is roughly this: Cross-cultural variations in the size of sex differences in mate preferences cast doubt on the necessity of evolutionary models and instead support an alternative account in which differences in male and female role assignments account for women's preferences for older, high-status men and men's preferences for younger, attractive women. They acknowledge that certain features of these role assignments stem from biological differences—women carry and nurse the offspring; men are physically larger and stronger (Eagly, Wood, & Johannesen-Schmidt, 2004). This is itself one form of an evolutionary model, but it sticks as close to a Blank Slate as possible, yielding only on a few obvious facts about morphology whose denial would strain credibility. Eagly and Wood resist considering how animals' brains and bodies tend to coevolve, so that where there is a structure, there is usually some programming to run it. They also resist considering the many parallel sex differences found in other species (such as intramale competitiveness). And they resist a full consideration of how those sex differences in other species are accompanied by hormonal differences between the sexes and why those hormones are coincidentally also found in humans. If Eagly and Wood merely made the coevolutionary argument that sex role assignments exacerbate initial biological differences between men and women, evolutionarily oriented psychologists would have few problems with their model. But it is clear in reading Eagly and Wood that they find it somehow preferable to yield as little ground as possible to a brain that does not operate like a Blank Slate (indeed, it is only the bodily structures outside the brain that are sex differentiated; male and female nervous systems are presumed to operate in virtually iden-

tical ways as people absorb the culturally assigned roles their particular societies create around the external morphological differences).

Eagly and Wood are surely among the more enlightened of evolutionary psychology's critics; they do their best to argue from data and to keep their political and moral sentiments out of sight. In a recent *American Psychologist* article, Hyde (2005) was more explicit about the moral and political preferences that make resistors long for a slate that is as blank as possible. Hyde advocated that the default position for psychologists ought to be a "sex similarities hypothesis." She acknowledged, with what appears to be some reluctance, that there are a few sex differences that cannot be denied, such as those involving aggression and sexuality, but preferred to focus on a number of forms of affect and cognition for which the sexes do not appear to differ much, if at all. It is noteworthy that the article does not even consider the massive evolutionary literature on why there are sex differences in some areas and similarities in others. Is Hyde unfamiliar with this literature? It is hard to keep up with every research literature tangential to one's own interests, but Hyde is a prominent sex differences researcher who has published chapters in several books right alongside evolutionary accounts of sex differences. Did the *American Psychologist* editor choose reviewers unfamiliar with the pertinent evolutionary literature or biased in ways that led them to ignore it all? In the closing sections of Hyde's article, she argued that even talking about sex differences may be harmful, presumably because it might provide justification for conservative forces who would block women's career progress.

Resistance Is Self-Righteous But May Be Self-Defeating

It seems as if resistors to an evolutionary perspective like to view themselves as freedom riders, valiantly crusading against the massive civil rights setbacks that would ensue if the Darwinian adaptationists got out of hand. But they may be unintentionally a bit more like folks with Confederate flags on their pickups, or like fundamentalist Christians who oppose sex education because they think kids won't do it if they are not made to think of it.

Let's consider a recurrent and rather insulting claim made by opponents of evolutionary psychology, as recently stated by Rose and Rose (2000): "the political agenda of EP [evolutionary psychology] is transparently part of a right-wing libertarian attack on collectivity, above all the welfare state" (p. 8). Is there any truth to this claim? Having attended the annual meetings of the *Human Behavior and Evolution Society* and the *Society for Experimental Social Psy-*

chology, it seems to me that the only political difference is that the evolutionary group includes more Sierra Club types. My informal observations are consistent with a systematic study comparing political values of graduate students in evolutionary psychology and other areas (Tybur, Miller, & Gangestad, 2005). Although a tiny minority of the nonevolutionary students (8.6%) favored George W. Bush before the 2004 election, not a single evolutionist did. Considering a range of other political attitudes, the general picture was the same for both groups: overwhelmingly liberal.

So evolutionary theorists are not themselves political right-wingers, transparently or otherwise. But could it nevertheless be true that their research on sex differences produces results that should be suppressed, or at least deemphasized, because they may be ultimately harmful to egalitarian goals? There are several logical flaws in this argument. It presumes for one thing that right-wing political ideologues really care a lot about scientific facts. A more important problem is that the argument contains a dangerous premise: that equitable treatment of men and women should be based on the lack of psychological differences between the sexes. On that premise, then unless we can suppress all evidence of psychological sex differences, any that gets out to the politicians can be used as a justification for inequity. And is it possible to censor data or theory without losing credibility as scientists? Pinker (2002) eloquently laid out a number of serious problems with the various continuing political misconceptions that have kept the Blank Slate perspective in business long after most psychologists have become convinced that it is factually incorrect. At the very least, there are a lot of reasons to question the default political assumptions that have been used to justify inequitable treatment for research findings that support evolutionary assumptions.

Because evolutionary theorists have been accused for decades of facilitating nefarious political developments (see Segerstrale, 2000, for a review), it seems only fair to consider the other side of this argument. In recent years, the Christian Right has been increasingly championing the position that schoolchildren ought to be required to learn about so-called Scientific Creationism, also known as "intelligent design." Indeed, their president—G.W. Bush—recently came out with public support for this position. Biblical creationists frequently cite the writings of Gould, Rose, and other long-term critics of sociobiology and evolutionary psychology. They use the critiques to argue that the theory of natural selection is still being debated by scientists. Of course, most antievolutionists probably care little about the logic of the scientific debate; they simply have strong moral convictions that it is good to censor the evidence to which innocent minds are exposed. Sound familiar?

Will All the Resistors Be Assimilated?

The fictional Borg statement that “resistance is futile” is followed by the proclamation that “you will be assimilated.” It is of course doubtful that all the individuals who have resisted evolutionary psychology will themselves be assimilated into the integrationist federation. Indeed, vast social psychological literatures suggest that strongly held opinions to which people are publicly committed are very difficult to change, and evidence against such opinions is likely to fall victim to various forms of schema-biased processing. But if the adaptationist approach continues in the current direction, it will persist in incorporating the good ideas of those who resist it and thereby expand into a more inclusive and integrative perspective. If resistors are open-minded, they will cease persecuting adaptationists as though criminals and eventually join the federation themselves. If not, the useful aspects of their intellectual culture will eventually be absorbed, and the next generation will learn that we are all in this scientific universe together.

Notes

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Causal Explanations of Human Behavior: From Culture to Psychology or From Psychology to Culture?

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At the beginning of the 21st century, there continues to be much debate regarding the extent to which evolution by natural selection has shaped the diversity of human psychology in the same way it has shaped human physiology and other living systems (e.g., Lewontin, Rose, & Kamin, 1984; Pinker, 2002). There are many sides to this debate, two of which include (a) those who do not employ the principles of evolutionary biology to explain human behavior and, instead, adopt (more or less) the tenets of a standard social science model (SSSM) of psychology (Tooby & Cosmides, 1992) and (b) those who use the logic of natural selection to guide investigations of the human cognitive architecture and the diverse array of behavior it generates. Whereas the former position privileges culture and social structure as causal forces shaping human psychology, the latter position allows for investigations of how evolved psychological adaptations pattern individual behavior and cultural phenomena. What follows is a brief overview of these two perspectives leading into a discussion of another active front in the behavioral sciences in which causality is being debated: inbreeding avoidance in humans. In the same way cultural patterns of mate preferences reflect the operation of evolved psychological

programs that calibrate according to specific environmental contingencies (see target article), culturally expressed sentiments relating to incest, the other side of mating, are also products of our evolved psychological architecture (Lieberman, Tooby, & Cosmides, 2003). Data discussed in the target article by Gangestad, Haselton, and Buss (this issue) as well as those discussed in this article suggest that, at least for some aspects of human behavior, the arrow of causality points from evolved psychological adaptations to culturally manifest behaviors.

The SSSM of Human Psychology

According to Tooby and Cosmides (1992), the SSSM is a set of assumptions that has shaped (and isolated) the social sciences throughout the last century. Briefly, proponents of the SSSM view social and cultural factors as primary, if not sole, causal forces shaping human behavior (e.g., Frazer, 1908/1910; Geertz, 1973; White, 1948). That is, the diversity of human behavior is a product of few domain-general psychological processes such as “learning,” “imitation,” and “so-

cialization” that guide the absorption and transmission of local rules and norms (i.e., culture; see Tooby & Cosmides [1992] and Pinker [2002] for a thorough discussion of this perspective and its assumptions about human nature). Though many researchers within psychology would not readily categorize themselves as proponents of the SSSM as defined (e.g., stating in objection that they believe the mind does contain specialized “hard-wired” systems for perception and language), many still assume that the arrow of causation regarding human social behavior—including any sex differences that may exist—points from the outer world (e.g., culture, social structure, norms, and so on) to individual behavior and preferences.

One modern instantiation of the SSSM is the biosocial perspective (also known as the social structural theory, social role theory, or social learning theory) discussed by Halpern (2000) and Eagly and Wood (1999). For example, according to Wood and Eagly (2002), “the origins of sex differences are best understood from a biosocial perspective that gives priority to the interaction between the bodily specialization of each sex and the attributes of societies’ economy, social structure, and ecology” (p. 718). The bodily specializations discussed include physiological processes such as placentation and lactation (e.g., Eagly & Wood, 1999) and neuronal pathways and associated neurochemical processes (e.g., Halpern, 2000).

Perhaps most scientists, evolutionary and social learning included, would agree that the production of any phenotype is an interaction between many components, including one’s ecology, social structure, hormonal condition, and sex. However, for bodily specializations (e.g., female specializations for childbearing and men’s greater size and strength) to impact behavior in specific ways as Wood and Eagly (2002) suggested, there have to be information-processing procedures that use this information (e.g., time and energy costs associated with childbearing), integrate it with specific information from the environment (e.g., pathogen load or indexes of effort and skill required for obtaining a particular resource), and motivate certain behaviors over others (e.g., motivations for seeking a mate with resources). What is needed is a rigorous description of the kinds of cognitive programs and information-processing procedures involved in the production of behavior. This level of analysis (i.e., an algorithmic level of analysis [Marr, 1982]) is absent from biosocial accounts. Rather, proponents of this view rely on domain-general learning programs to describe how a function is achieved. And although it may be acknowledged that humans and other animals are equipped to learn certain contingencies faster than others, social learning theorists suggest that the

ing experiences and the neurochemical processes that allow learning to occur (release of neurotransmitters) and change in response to learning. ... Thus, learning depends on what is already known and on the neural structures and processes that undergird the learning and remembering processes. (Halpern, 2000, p. 16, italics added)

That is, explanations are deferred to prior learning experiences, whatever they may be, and are framed in terms of the physical arrangement of our neural system—an important level of analysis, but by no means the only one necessary. Throwing together a bunch of neurons and neurotransmitters within a particular ecology does not a social creature create; social behavior is produced by virtue of the information-processing procedures that, for our species and many others, are instantiated in neuronal pathways and that allow for the interaction with specific components of the ecology, social structure, and so on.

Neural structures in the brain process information, and a complete explanation of a particular behavior requires a description of the kinds of information represented and processed. This can be done independent of any knowledge of the physical instantiation of such processes. It seems theorists who privilege the physical organization of neural structures (e.g., the kinds of hormones and neurotransmitters) and physiology to explain human social behavior jump right over an analysis of the information-processing programs required and in its stead insert placeholders such as “learning” or “socialization.” Any attempt to rigorously specify the kinds of information-processing structures required to perform a particular function (e.g., choosing a mate based on certain environmental and physiological contingencies) would quickly reveal that the processes of learning and socialization are severely underspecified and that specialized systems are required to reliably tailor behavioral responses to local conditions. Specialized systems, however, are highly improbable orderings of matter (e.g., see Tooby, Cosmides, & Barrett, 2003) and require an explanation for their existence. Evolution by natural selection is the only known causal force that can build complex functional designs—the kind that would be required to “learn” complex behaviors or modify behavior based on environmental contingencies. And so this requires knowledge of how and why complex functional mechanisms come into existence.

An Adaptationist Perspective of Human Psychology

In contrast to the SSSM and more recent social structural models of human psychology, an evolutionary framework suggests the human mind consists of infor-

predisposition to learn some behaviors or concepts more easily than others is determined by *prior learn-*

mation processing neural circuitry that was selected due to the effects such neural circuitry had on the probability of reproduction and survival over our species' evolutionary history (Tooby & Cosmides, 1990). Recurring selection pressures (e.g., pathogens, individuals of the opposite sex, deleterious recessive mutations, patterns of parental investment, predators, and close genetic relatives) led to the evolution of specialized psychological as well as physiological structures and processes that conferred a selective advantage with respect to each pressure. For example, the presence of pathogens over our species' evolutionary history not only led to physiological processes (e.g., elements of the immune system) for rapid detection and elimination but also psychological processes for avoiding contact with substances that were reliably associated with disease causing organisms such as feces, rotten meat, and spoiled milk (e.g., the cognitive program of disgust).

Pathogens are also hypothesized to have exerted a selection pressure on our mating psychology in at least two ways. First, as discussed in the target article, pathogens are capable of perturbing evolutionary developmental programs, one visible result being a body plan that more greatly deviates from perfect bilateral symmetry (see Gangestad & Thornhill, 1997). Consequently, circuitry guiding mate selection is hypothesized to take this information into account and motivate mateships with individuals displaying fewer cues signaling the presence of pathogens (Gangestad & Buss, 1993). Second, pathogens are hypothesized to have been a selective force in shaping inbreeding avoidance mechanisms (i.e., negative mate preferences; Tooby, 1982). Individuals of close common descent are more likely to share similar internal biochemistries. That is, by virtue of having an increased probability of sharing underlying genes, the internal biochemistry of, say, a brother and sister are more similar than the biochemistry of the sister and an unrelated man. Because pathogens are better able to adapt to environments that remain constant from generation to generation (i.e., they become better able to sequester resources, replicate, and evade components of the immune system), mating with a close genetic relative would have produced offspring that were more susceptible to the harmful effects of pathogens. This is one reason why inbreeding avoidance mechanisms are thought to have evolved (Tooby, 1982).

The purpose of this discussion is to demonstrate how an adaptationist perspective generates hypotheses regarding the kinds of phenotypes (physiological and psychological) that are likely to exist given recurring features of our ancestral past. Furthermore, it allows for the development of potential models of our cognitive architecture. For example, given that pathogens posed the adaptive problem of avoiding contact with and ingestion of substances associated with disease-causing organisms, how did our ancestors know

which substances to avoid? What cues correlated with the presence of pathogens? What motivation systems used this information to direct food choice? In general, fleshing out the kinds of information-processing systems required to direct behavior away from random can fortify investigations of human behavior and any variation (e.g., individual or cultural variation) that may arise.

Explaining Individual and Cultural Variation From an Adaptationist Perspective

An understanding of our evolved cognitive architecture provides a legend for interpreting the kinds of variation found within and between groups. For example, many of our psychological adaptations are hypothesized to be sensitive to context and generate behavioral and physiological responses contingent on contextual information. One consequence is that different environments may produce different phenotypes. This has been termed *evoked culture* (Cosmides & Tooby, 1992), and two examples are discussed in the target article (see also Cosmides & Tooby [1992] on patterns of social exchange based on resource variance). As mentioned in the target article, another way groups can become different from one another is through cultural transmission, that is, the passing of information between individuals. But not all information is transmitted—only a subset of all possible beliefs, skills, practices and so forth are transmitted and retained. This narrow state space has led some researchers to suggest that the study of cultural transmission is akin to the study of the epidemiology of representations (Sperber, 1994). If cultural transmission relies on the kinds of representations humans generate and communicate, then an understanding of culture entails the investigation of our cognitive architecture, including the nature of the representations used to process information and guide behavior, a level of analysis not utilized by social learning theorists.

The debate over whether evolutionary principles can be applied to understanding patterns of human behavior seems to become more charged the closer one comes to social behavior (e.g., mating behavior and moral sentiments). For instance, few scientists would likely object to recent findings showing that cultural variation in food preparation is intimately tied to the pathogen load of the environment. Billing and Sherman (1998) sought to understand “why some like it hot” and investigated the use of 43 spices in the meat-based cuisines of 36 cultures. They reasoned that because spices vary in their antimicrobial effects, cultures exposed to greater pathogen loads would utilize a greater number of more potent spices and, specifically, those spices best able to combat the local pathogen composition. They found that as mean annual tempera-

ture increased (an index of environmental pathogen load), so too did the percentage of recipes including spices, the number of spices used in total and per recipe, as well as the use of the most potent antimicrobial spices. They tested many alternate hypotheses and concluded that spices help protect foods from pathogens, rendering them safer to eat, and that this is reflected in cross-cultural patterns of food preferences. This example demonstrates how evolutionary hypotheses regarding the kinds of selection pressure that affected human survival and reproduction can help generate hypotheses regarding behavioral variation at the cultural level. If it is possible to explain food choice using these principles, then surely it is possible to apply the same principles to understand other domains of human behavior such as mate choice and moral sentiments.

Summary

Social learning theorists and adaptationist-minded researchers approach the study of human behavior from radically different perspectives. Whereas social learning theorists privilege culture and social structure as the prime causal forces shaping human behavior, adaptationist-minded researchers start with the same biological principles used to study nonhuman behavior to investigate human psychology, including cultural patterns and individual differences. The target article by Gangestad et al. (this issue) discusses how cultural patterns of mate preferences can be explained by considering the kinds of selection pressures that shaped male and female mating psychology (e.g., patterns of parental investment and environmental pathogen load). Oddly, social learning theorists that have voiced strong opposition to this perspective (e.g., Wood & Eagly, 2002) privilege differences in bodily specializations as direct causal forces in shaping mating behavior yet deny the causal role of parental investment theory. But where do they think different bodily specializations came from? Parental investment patterns played a heavy hand in shaping physiological structures (e.g., see Trivers, 1972), and if natural selection can differentially shape physical structures in men and women, surely it can also differentially shape psychological processes. In any event, social learning theorists maintain that the culturally derived social roles of men and women shape mating preferences; where roles are more disparate, mating preferences should differ, and where roles are more equal, mating preferences should be more similar. However, Gangestad et al. found little support for this perspective in explaining patterns of cross-cultural mating preferences.

The remainder of this commentary looks at another aspect of mating that can open a window onto the causal factors that play a role in the generation of culturally expressed variation: inbreeding avoidance and the incest taboo. Where do our sentiments relating to

incest come from? Does culture or social structure fashion our attitudes relating to incest in the same way proposed for mating preferences (e.g., see Eagly & Wood 1999), or does our evolved psychological architecture pattern moral sentiments and attitudes relating to incest?

Causal Explanations of Human Incest Avoidance: Social Learning or Evolved Psychology?

A Short History of Explanations of Inbreeding Avoidance and the Incest Taboo

At the end of the 19th century, Edward Westermarck (1891/1922), a Finnish social scientist, proposed an explanation for the commonplace observation that family members rarely find one another sexually appealing. Having noted the injurious effects of inbreeding in many species, Westermarck hypothesized that early childhood association, which typically occurs among genetic relatives, serves as an inbreeding avoidance mechanism by triggering the development of a sexual aversion that becomes manifest later during adulthood (Westermarck 1891/1922). This has come to be known as the Westermarck Hypothesis (WH).

In addition to proposing a specialized mechanism that functions to reduce the probability of choosing a close genetic relative as a sexual partner, Westermarck (1891/1922) also proposed an explanation for the origin of the culturally manifest incest taboo. He claimed that the biological systems responsible for the development of sexual aversions between close kin were also responsible for the culturally expressed incest taboo. That is, the explicit cultural prohibitions regarding incest were hypothesized to be a by-product of the natural sexual disinclination that develops between near relatives.

Westermarck's (1891/1922) explanation of the incest taboo differed drastically from the reigning social learning theories of his day, which privileged the cultural incest taboo as the origin, not the consequence, of sexual avoidance behaviors (e.g., Frazer, 1908/1910). In what has become a well-known quote, Westermarck addressed the shortcomings of this alternate explanation:

Moreover, the [social learning] theories in question imply that the home is kept free from incestuous intercourse by law, custom, or education. But even if social prohibitions might prevent unions between the nearest relatives, they could not prevent the desire for such unions. The sexual instinct can hardly be changed by prescriptions; I doubt whether all laws against homosexual intercourse, even the most draconic, have ever been able to extinguish the peculiar desire of anyone

born with homosexual tendencies. Nevertheless, our laws against incest are scarcely felt as a restraint on individual feelings. And the simple reason for this is that in normal cases there is no desire for the acts that they forbid. Generally speaking, there is a remarkable absence of erotic feelings between persons living very closely together from childhood. Nay more, in this, as in many other cases, sexual indifference is combined with the positive feeling of aversion when the act is thought of. *This I take to be the fundamental cause of the exogamous prohibitions. Persons who have been living closely together from childhood are as a rule near relatives. Hence their aversion to sexual relations with one another displays itself in custom and law as a prohibition of intercourse between near kin.* (pp. 192–193; italics added)

Though initially well received, the WH and Westermarck's (1891/1922) explanation of the incest taboo gradually fell into disfavor. There were, perhaps, many reasons for this. One main reason was the widespread adoption of the SSSM of human psychology (see Tooby & Cosmides, 1992; Pinker 2002). Whereas the WH implies the existence of content-rich psychological mechanisms designed by natural selection to regulate behavior in adaptive ways, according to the SSSM, the mind is akin to a content-free blank tape that, through processes such as enculturation and socialization, records "relevant" ambient signals from the surrounding social environment, which, in turn, shape an individual's behaviors and attitudes. Applied to the domain of incest, the SSSM (which captures the social learning theories discussed by Westermarck and more recent authors [e.g., Eagly & Wood, 1999]) claims that mere exposure to norms relating to incest automatically generates feelings of sexual disinterest toward family members. The function of this taboo-generated sexual disinterest was thought to have less to do with the dangers of sexual relations within the family (as Westermarck proposed) than the establishment of cooperative relationships between families via cultural practices such as exogamy (e.g., see Frazer, 1908/1910; Levi-Strauss, 1960; White, 1948).

An Adaptationist Perspective of the WH

From an adaptationist perspective, the WH makes good sense. Due to the selection pressures posed by deleterious recessive mutations and short generation pathogens (Bittles & Neel, 1994; Tooby, 1982), individuals who avoided mating with a close genetic relative and instead chose as a sexual partner someone who did not share a recent common ancestor would have produced healthier, more viable offspring. For this reason, inbreeding avoidance mechanisms are hypothesized to exist in any species, including humans, in which close genetic relatives frequently interacted over

the lifespan. Indeed, such mechanisms have been found in a number of nonhuman species (Fletcher & Michener, 1987; Hepper, 1991).

What might a human inbreeding avoidance system look like? At least two systems would be required: one that computed genetic relatedness (i.e., a kin detection system) and one that regulated sexual avoidance based on the computed estimates of relatedness. Because it is not possible to directly compare DNA (at least it was not ancestrally), evolution is hypothesized to have shaped kin-detection mechanisms that took as input cues that correlated with relatedness under ancestral conditions. One ancestrally reliable cue to relatedness would have been patterns of childhood coresidence, as the WH suggests. Another cue that would have signaled genetic relatedness is seeing one's biological mother pregnant and caring for (e.g., breastfeeding) a newborn. Indeed, recent investigations have found support for the WH showing that childhood coresidence duration predicts the development of sexual aversions as well as the incidence of sexual behaviors between siblings (e.g., Bevc & Silverman, 2000; Fessler & Navarrete, 2004; Lieberman et al., 2003; Walter & Buyske, 2003; Wolf, 2005). Furthermore, recent evidence suggests that exposure to one's mother caring for a newborn also serves as a cue to siblingship (Lieberman, Tooby, & Cosmides, under review). Certainly, other cues to siblingship may exist (e.g., facial similarity [e.g., DeBruine, 2002], and olfactory cues based on MHC composition [e.g., Wedekind & Furi, 1997]) and it is possible different cues may be used to detect different categories of kin.

The Incest Taboo: Cause or Consequence?

Was Westermarck (1891/1922) correct? Are culturally manifest attitudes (e.g., moral sentiments) relating to incest a by-product of systems guiding the development of sexual aversions toward one's own family members? Or, as suggested by traditional SSSM accounts of incest prohibitions, are our moral sentiments a result of the unbiased adoption of ambient cultural norms? These are empirical questions, capable of being explored using the tools of modern behavioral science. If Westermarck was indeed correct and culturally expressed moral sentiments relating to incest are a reflection of underlying biological systems for inbreeding avoidance, then the cues the human mind uses to detect kin and to regulate sexual avoidance should explain the patterns of moral sentiments relating to incest. If, on the other hand, social learning theorists (e.g., Eagly & Wood, 2002) are correct and individuals "learn" preferences based on their social role, then these cues should not necessarily explain patterns of moral sentiments. Rather, culturally transmitted val-

ues, either from one's peers or from one's family members, should predict an individual's moral sentiments.

In recent studies, coresidence duration with an opposite-sex sibling has been found to predict the level of moral opposition to third-party sibling incest (Fessler & Navarrete, 2004; Lieberman et al., 2003). These findings support Westermarck's (1891/1922) original notion that the culturally manifest incest taboo and related sentiments are a product of the same mechanisms guiding the development of a sexual aversion toward one's own family members. However, this finding could be marshalled as support for social learning theories: Coresidence duration may predict moral sentiments not because it regulates the development of sexual aversions based on estimates of kinship, but rather because coresidence duration tracks opportunities for the cultural transmission of norms. An alternate hypothesis, then, is that the cultural transmission of sexual attitudes from parents and peers should predict moral sentiments relating to incest. However, as Lieberman et al. have shown, they do not: Parental attitudes regarding sexuality and an individual's own attitudes regarding sexuality, attitudes that may have been shaped by peers or family members, do not predict moral sentiments relating to incest. In contrast, coresidence duration does predict moral sentiments relating to incest, even after the effects of parental and personal attitudes are statistically removed.

Social learning theorists could suggest, however, that family social structure is the important dimension, not coresidence duration *per se*. Families with more traditional values and structures may be less likely to divorce, leading to greater coresidence periods for the children. If this is the case, then the sex of the children should not matter; traditional family structure or not, sex is determined by a genetic coin flip. Consequently, coresidence with same- and opposite-sex siblings should generate similar patterns of moral sentiments. They do not. Whereas coresidence duration with an opposite-sex sibling predicts moral sentiments, coresidence duration with a same-sex sibling does not (see Lieberman et al., 2003). Although difficult to explain from a social learning perspective, this makes sense based on evolutionary hypotheses: Systems regulating sexual behavior should target members of the opposite sex (assuming heterosexuality).

One last possibility is that social learning theorists might suggest family composition matters such that, in families in which both sons and daughters exist, parents are communicating different rules about sexual behavior compared to families in which only sons or only daughters exist. If this is the case, then to the extent that coresidence tracks a separate variable having to do with the communication of norms, it should do so regardless of birth order. That is, coresidence (as a proxy for this other variable) should predict moral sen-

timents regardless of whether an individual in an opposite-sex sibling pair is older or younger. However, adaptationist hypotheses suggest that coresidence duration may be a cue used to detect older siblings and not, necessarily, younger ones. This is because other, more reliable cues may have been available for detecting younger siblings, namely, seeing one's mother pregnant and breastfeeding a newborn. Because the arrow of time forbids younger siblings from seeing their older siblings being born or breastfed, coresidence may be the best cue available for assessing the relatedness of older siblings. Therefore, coresidence duration with an older sibling should predict moral sentiments relating to incest whereas coresidence duration with a younger sibling should not. And this is exactly the pattern found. Moreover, it holds after controlling for sibling age to ensure that opposition is not a result of the presence of prepubescent siblings (see Lieberman et al., *under review*). Taken together, these findings militate against social learning hypotheses and suggest that evolved psychological adaptations for guiding mating behavior pattern culturally expressed sentiments relating to incest and not the other way around.

Conclusion

From a social learning perspective (e.g., Eagly & Wood, 1999), mating preferences, including any sex differences that might arise, are due to interactions between physiological specializations and particular attributes of the environment. To the extent there is any scientific merit to this approach, this interaction should specify the entire scope of mate preferences, from those traits preferred in a mate (see target article) to those avoided. That is, the interaction between physiology and the environment (e.g., culture and local resources) should explain the patterns of sexual avoidance and related attitudes in the same way it explains the patterns of sexual preferences and related attitudes. But, as the target article and this discussion suggest, social learning theories do not explain the patterns of variation found in mate preferences or moral sentiments relating to incest.

The structure of mate choice in humans as well as other social behaviors in humans will, of course, rely on a multitude of factors. However, specific hypotheses are required to rigorously investigate why and how various factors influence behavior and related attitudes. The principles outlined by an adaptationist framework provide a robust set of guidelines for the generation of specific hypothesis regarding ultimate causation as well as the generation of cognitive models specifying proximate procedures that give rise to the array of individual behaviors and, consequently, patterns of cultural variation.

Note

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Cultural Influences on Human Mating Strategies: Evolutionary Theories, Mechanisms, and Explanations of Change

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Gangestad, Haselton, and Buss (this issue) offer a compelling case for viewing much of human culture as reflecting, amplifying, and ultimately resulting from our evolved psychological architecture—our human nature. At times, this human nature produces cultural universals (e.g., language acquisition, emotional expressions, incest avoidance; see Brown, 1991). Domain-general learning mechanisms and the standard social science model simply cannot account for the breadth of observed cultural universals, especially when these universals are compared to the “ethnographic hyperspace” of human cultural possibilities (Cronk, 1999). Other times, our universal human nature interacts with environmental contingencies and personal circumstance and results in cultural variation. For example, preferences, norms, and values in the realm of mating culture can vary as a result of human nature responding in specially designed ways to local ecological information (Gangestad & Simpson, 2000; Schmitt, 2005). Gangestad et al. show that the cultural emphasis on physical attractiveness and intelligence in mate preferences intensifies (i.e., is evoked) when local ecologies are high in pathogens, precisely when both physical attractiveness and intelligence would provide critical adaptive insights into a potential mate’s genetic quality.

Unfortunately, most psychologists seem unable or unwilling to acknowledge evolutionary or natural explanations of cultural variation. Any confirmation of a trait’s cultural variability is, instead, taken as *de facto* evidence that nature is largely irrelevant and the trait’s origins reside solely within the realm of nurture. It is only when features of humanity demonstrably transcend 100% of all cultures (an exceedingly stringent requirement given the limitations of the ethnographic method, the conditional nature of many psychological adaptations, as well as basic measurement error; see Schmitt & Pilcher, 2004) that the potential influence of nature is recognized. The calls of Gangestad et al. (this issue) for finally dispensing with this false “nature versus nurture” dichotomy that plagues academic psychological thought are welcome, and one hopes they will be heeded.

There are additional problems with the way psychologists have thought about culture and cultural variation. Historically, social scientists have conceived of culture as the transmission and sharing of patterns of human cognition, emotion, and behavior. For most cross-cultural psychologists, culture is also viewed as a prospective explanatory force, a first cause. Culture ex-

ists, and then human psychology results. Several serious problems exist with this standard view of culture. First, there are definitional and circularity issues. Cultures cause the sharing of human psychology, but cultures *are* the sharing of human psychology. Second, not all people within a culture share the same features of human psychology. Variations within cultures along the dimensions of sex, age, and status lead to skepticism about the legitimacy of culture as a causal force. Third, all cultures change over time. Without a mechanism for explaining why cultures change, any theory of culture and its influence on human psychology is necessarily incomplete (Cavalli-Sforza & Feldman, 1981; Ross, 2004).

Because of these and other serious limitations, many social scientists during the middle of the last century became disenchanted with culture as an explanatory tool. Culture became an “essentializing” concept that failed to acknowledge multicultures, cocultures, and cultural change. Fortunately, evolutionary approaches to culture offer a legitimizing reason to revive the study of culture, both as a cause and as a consequence of human nature. This is because evolutionary perspectives on culture provide three important improvements from classic cross-cultural psychology and cultural anthropology. First, evolutionary psychology offers theories for why cultures vary in the ways that they do. Gangestad et al. (this issue) theorize that cultural variations in the desire for physically attractive mates result from ecological differences in pathogen prevalence. Second, evolutionary psychology perspectives offer mechanisms for why cultural variations exist. Gangestad et al. explain the mechanism of cultural variation in mate preferences is a conditional if–then adaptation within our universal psychological repertoire. If environments have high pathogen prevalence, then our mating desires adaptively emphasize physical attractiveness. If the local environment has low pathogen prevalence, then our adaptive desires de-emphasize physical attractiveness in potential mates. Third, evolutionary psychology perspectives offer explanations of cultural change. When levels of pathogen prevalence shift, the corresponding emphasis on physical attractiveness should shift as well.

In my own research on psychological adaptations toward short-term mating (Schmitt, 2005), evolutionary perspectives offer explanations for within-cultural variability (e.g., sex and individual differences in seeking multiple short-term mates; Buss & Schmitt, 1993), between-cultural variability (e.g., female-biased sex

ratios lead relatively rare men to have more relational power, and they are able to successfully insist on short-term mating; Pedersen, 1991), and cultural change over time (shifts in sex ratios as well as the need for paternal investment can lead to shifts in short-term mating; Gangestad & Simpson, 2000). All of these evolutionary perspectives possess the ability to explain cultural universals and variations, something very much missing from standard psychological accounts of short-term mating (Schmitt, 2005).

If psychologists continue to treat culture as simply an independent variable that is a first cause of human cognition, emotion, and behavior, the psychological science of culture will linger. Neither should social or cultural causes be treated as independent of biological or evolved causes. Instead, we need to fully explore and ultimately acknowledge the evolved psychological architecture that constitutes human nature and recognize that the conditional nature of human psychological adaptation gives rise to predictable forms of cultural variability. It is not the case that every evolutionary theory of cultural variation will turn out to be correct, as Gangestad et al. (this issue) demonstrate with the disconfirmation of Wood and Eagly's (2002) biosocial theory of human sexuality and culture. Neither will all aspects of culture (e.g., unique historical events) be subject to evolutionary explanation, at least in terms of genetic evolution. However, at this point in time all psychologists should dispense with dichotomous nature–nurture explanatory thinking and fully recognize that evolutionary psychology has the potential to transcend the tired old paradigms of the standard social science model and its view of learning culture as a first and only cause. Only by combining genetic and cultural levels of evolution in sophisticated ways will a more complete explanation of human psychology be possible (Boyd & Richerson, 1985; Lumsden & Wilson, 1981).

Finally, in addition to evoked and transmitted aspects of culture mentioned by Gangestad et al. (this issue), further thought within evolutionary psychology needs to be given to anticipated culture. That is, many psychological adaptations were designed to function in foraging cultures, and the development of fully functioning adaptations may require contact with certain environmental inputs particular to those cultures. Many aspects of modern culture are certainly similar to foraging cultures, but the differences need to be more fully incorporated into evolutionary theories of culture

and psychology. Moreover, our human nature likely anticipates being exposed to reliable nurturing from human culture (e.g., language acquisition adaptations anticipate exposure to language). In this way, important aspects of human culture may be considered extensions of our evolved phenotype. Just as webs are an extension of the phenotype of spiders, just as nests are to birds and dams are to beavers, cultures (both universal and variable) are extensions of the evolved phenotype of humans (Dawkins, 1982).

Note

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Cross-Cultural Universals and Variations: The Evolutionary Paradox of Informational Novelty

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Psychological Universals and Adaptive Variation

The identification of universals in a species is an important method for inferring adaptive design (Mayr, 1982). Among humans, large (~1300cc) brains and habitual upright bipedal locomotion are ubiquitous traits that distinguish us from our primate relatives, providing important clues about hominin evolutionary history. The identification of psychological universals is similarly useful (Brown, 1991; Ekman, 1993; Norenzayan & Heine, 2005) and has been emphasized by the evolutionary psychology paradigm (e.g., Buss, 1995; Tooby & Cosmides, 1990).

The identification of variation can also be a powerful scientific tool. For example, different color morphs of *Heliconius* butterflies suggest advantages for distinctive aposematic color patterns (Langham, 2004), maintaining allelic diversity at relevant loci. In addition to genetic differences, phenotypic variation usually involves ontogenetic responses to the environment (West-Eberhard, 2003). Gangestad, Haselton, and Buss (this issue) note the flexible production of melanin in melanocytes in response to solar radiation. Other classic examples include seasonal changes in cryptic fur coloration in the arctic hare, production of a protective shield in *Daphnia* in response to predation risk (Agrawal, LaForsch, & Tollrian, 1999), and the canalization of migratory locusts into short-winged nondispersing or long-winged dispersing adult morphs contingent on exposure to crowded conditions as juveniles (for a general discussion, see Schlichting & Pigliucci, 1998). Learning constraints follow similar “reaction norms” (e.g., Garcia, 1974). The phenotypic variations associated with human culture, however, present some added complexities for inferring evolutionary design.

The Problem of Culture

Vygotsky (1978) observed that children are especially tuned to their social worlds and the information that it provides. More recent evolutionary theorists of the mind suggest a complementary adaptive logic: The social world is a rich source of useful information for cognitive development. The human brain has been designed by natural selection to take advantage of this bonanza of data (e.g., Alexander, 1979; Belsky, 2005; Bjorklund & Pellegrini, 2002; Tooby & Cosmides,

1992). Some, perhaps in a gesture of appeasement to the cultural *tabula rasa* old guard, would have culture running off in its own evolutionary system with its own separate (but linked!) inheritance mechanisms (for reviews, see Dawkins, 1982; Durham, 1991; Henrich & McElreath, 2003; Richerson & Boyd, 2005). Others advocate a more restrictive grounding in the biology of learning (e.g., Galef, 2004; Gottlieb, 2002; Shettleworth, 1998; Tomasello, 1999), viewing culture as a rather special type of phenotypic plasticity (Alcock, 2005; Coe, 2003; Flinn, 1997; Flinn & Alexander, 1982). Gangestad et al (this issue) exemplify this latter paradigm, modeling culture—with mate choice as a specific component—as a compilation of flexible responses by individuals to specific environmental contingencies, analogous to the biological concept of reaction norms and consistent with the basic premises of evolutionary psychology (e.g., Daly & Wilson, 1983).

Here I aim to push this evolutionary perspective beyond the concept of “evoked culture” as constrained response to variable environments guided by specialized psychological modules. Startling advances in the understanding of the evolutionary basis of the phenotype, captured in part by the emergent field of “evo-devo” (evolutionary developmental biology) and its re-emphasis of the complexity of ontogeny (West-Eberhard, 2003), have apparent relevance to this question of culture and its variants (e.g., Heyes, 2003).

Culture may be viewed as a highly dynamic information pool that coevolved with the extensive information-processing abilities associated with our flexible communicative and sociocognitive competencies (Alexander, 1979). With the increasing importance and power of information in hominin social interaction, culture and tradition may have become an arena of social cooperation and competition (Coe, 2003; Flinn, 2004; see also Sternberg & Grigorenko, 2004).

The key issue is novelty. One of the most difficult challenges to understanding human cognitive evolution, and its handmaiden culture, is the unique informational arms race that underlies human behavior. The reaction norms posited by evolutionary psychology to guide evoked culture within specific domains may be necessary but insufficient (Chiape & MacDonald, 2005). The mind does not appear limited to a predetermined Pleistocene set of options—such as choosing mate A if in environment X but choosing mate B if in environment Y—analogous to examples of simple phenotypic plasticity (MacDonald & Hersherberger, 2005). The human jukebox does not just keep the same

old selection of tunes; the Beatles displaced Elvis, and so forth.

Keeping up in the hominin social chess game required imitation. Getting ahead favored creativity to produce new solutions to beat the current winning strategies. Random changes, however, are risky and ineffective. Hence the importance of cognitive abilities to hone choices among imagined innovations in ever more complex social scenarios. The theater of the mind that allows humans to “understand other persons as intentional agents” (Tomasello, 1999, p. 526) provides the basis for the evaluation and refinement of creative solutions to the never-ending novelty of the social arms race. This process of filtering the riot of novel information generated by the creative mind favored the cognitive mechanisms for recursive pattern recognition in the open domains of both language (Deacon, 1997; Nowak, Komarova, & Niyogi, 2001; Pinker, 1994) and social dynamics (Geary, 2005). The evolutionary basis for these psychological mechanisms underlying culture appears rooted in a process of “runaway social selection” (Alexander, 2005; Flinn, Alexander, & Coe, 2006).

Runaway Social Selection

Darwin (1871) recognized that there could be important differences between (a) selection occurring as a consequence of interaction with ecological factors such as predators, climate, and food, and (b) selection occurring as a consequence of interactions among conspecifics (i.e., members of the same species competing with each other over resources such as nest sites, food, and mates). The former is termed *natural selection* and the latter *social selection*, of which sexual selection may be considered a special subtype (West-Eberhard, 1983). The pace and directions of evolutionary changes in behavior and morphology produced by these two types of selection—natural and social—can be significantly different (Alexander, 1974, 2005; R. A. Fisher, 1930; West-Eberhard, 2003).

Selection that occurs as a consequence of interactions between species can be intense and unending, for example with parasite–host red queen evolution (Hamilton, Axelrod, & Tanese, 1990). Intraspecific social competition may generate selective pressures that cause even more rapid and dramatic evolutionary changes. Decreasing constraints from natural selection, combined with increasing social competition, can generate a potent runaway process. Human evolution appears characterized by such circumstances (Alexander, 2005; Flinn, Geary, & Ward, 2005). Humans, more so than any other species, appear to have become their own most potent selective pressure via social competition involving coalitions (Alexander, 1989; Geary & Flinn, 2002; Wrangham, 1999; e.g., Chagnon, 1988) and dominance of their ecologies involving niche con-

struction (Deacon, 1997; Laland, Odling-Smee, & Feldman, 2000). The primary functions of the most extraordinary human mental abilities—language, imagination, self-awareness, ToM, foresight, and consciousness—involve the negotiation of social relationships (Adolphs, 2003; Geary, 2005; Siegal & Varley, 2003; Tulving, 2002). The multiple-party reciprocity and shifting nested subcoalitions characteristic of human sociality generate especially difficult information-processing demands for these cognitive facilities that underlie social competency. Hominin social competition involved increasing amounts of novel information and creative strategies. Culture emerged as a new selective pressure on the evolving brain.

Evolution of the Cultural Brain

The human brain is a big evolutionary paradox. It has high metabolic costs, it takes a long time to develop, it evolved rapidly, it enables behavior to change quickly, and it generates unusual levels of informational novelty. As noted earlier, its primary functions include dealing with other human brains (Adolphs, 2003; Gallagher & Frith, 2003; Siegal & Varley, 2002; Tulving, 2002). The currency is not foot-speed or antibody production but the generation and processing of data in the social worlds of the human brains’ own collective and historical information pools. Some of the standout features of the human brain that distinguish us from our primate relatives are asymmetrically localized in the prefrontal cortex, including especially the dorsolateral prefrontal cortex and frontal pole (Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001; Semendeferi et al., 2001; Zilles et al., 1996; for a review, see Geary, 2005). These areas appear to be involved with “social scenario building” or the ability to “see ourselves as others see us so that we may cause competitive others to see us as we wish them to” (Alexander, 1990, p. 7; cf. Bekoff & Sherman, 2004) and are linked to specific social abilities such as understanding sarcasm (Shamay-Tsoory, Tomer, & Aharon-Peretz, 2005) and morality (Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005). An extended childhood seems to enable the development of these necessary social skills (Joffe, 1997). Learning, practice, and experience are imperative for social success. The information-processing capacity used in human social competition is considerable and perhaps significantly greater than that involved with foraging skills (Roth & Dicke, 2005).

Evolution of the Cultural Child

The altricial (helpless) infant is indicative of a protective environment provided by intense parental and

alloparental care in the context of kin groups (Chisholm, 1999). The human baby does not need to be physically precocial. Rather than investing in the development of locomotion, defense, and food acquisition systems that function early in ontogeny, the infant can work instead toward building a more effective adult phenotype. The brain continues rapid growth, and the corresponding cognitive competencies largely direct attention toward the social environment. Plastic neural systems adapt to the nuances of the local community, such as its language (Alexander, 1990; Bjorklund & Pellegrini, 2002; Bloom, 2000; Geary & Bjorklund, 2000; Geary & Huffman, 2002; Small, 1998, 2001). In contrast to the slow development of ecological skills of movement, fighting, and feeding, the human child rapidly acquires skill with the complex communication system of human language (Pinker, 1999). The extraordinary information-transfer abilities enabled by linguistic competency provide a conduit to the knowledge available in other human minds. This emergent capability for intensive and extensive communication potentiates the social dynamics characteristic of human groups (Deacon, 1997; Dunbar, 1997) and provides a new mechanism for social learning and culture. The recursive pattern recognition and abstract symbolic representation central to linguistic competencies enable the open-ended, creative, and flexible information-processing characteristic of humans, especially of children.

Reconciling Domain-Specific Modularity With Informational Novelty

Humans are unique in the extraordinary levels of novelty that are generated by the cognitive processing of abstract mental representations. Human culture is cumulative; human cognition produces new ideas built on the old. To a degree that far surpasses that of any other species, human mental processes must contend with a constantly changing information environment of their own creation.

Cultural information may be especially dynamic because it is a fundamental aspect of human social coalitions. Apparently arbitrary changes in cultural traits, such as clothing styles, music, art, perceptions of beauty, food, dialects, and mate choice decisions, may reflect information "arms races" among and within coalitions. The remarkable developmental plasticity and cross-domain integration of some cognitive mechanisms may be products of selection for special sensitivity to variable social context (e.g., Boyer, 1998; Carruthers, 2002; Sperber & Hirschfeld, 2004). Human culture is not just a pool or source of information; it is an arena and theater of social manipulation and

competition via cooperation. Culture is contested because it is a contest.

The effects of coalition conformity and imitation of success may drive culture in directions difficult to predict solely on the basis of simple functional concerns or evolved psychological mechanisms. This social dynamic would explain the apparent lack of a simple biological utilitarianism of so much of culture and the great importance of historical context and social power (e.g., Wolf, 2001). Deconstruction is a complicated but necessary enterprise, for we are all players in the social arena. The twist is that we are evolved participants.

This perspective may reconcile important gaps between the evolutionary psychological paradigm and the more history-oriented anthropological approaches (e.g., Richerson & Boyd, 2005) because it suggests an evolved human psychology that is creative, dynamic, and responsive to cultural context (e.g., Kenrick, Li, & Butner, 2003), rather than being more rigidly constrained by domain-specific modules.

Culture and Mate Choice: Context-Specific and Context-General Conditional Responses

Beauty appears to have some cross-culturally universal components (Jones, 1996; Kenrick & Keefe, 1992). Health, youth, fertility, and status have near-ubiquitous appeal. Romantic attachment involves the same hormones and neurotransmitters and the same locations in the brain (Bartels & Zeki, 2004; H. Fisher et al., 2002). The devil is in the details. Evolutionary psychology has tended to focus on a limited set of mate choice criteria, largely based on research among industrialized global cultures. Analyses of variation in mating systems from human behavioral ecology have tended to focus on associations between subsistence practices, control of material resources, and male–female reproductive strategies (e.g., Borgerhoff Mulder, 1991; Geary & Flinn, 2001; Hill & Hurtado, 1996; Smith, Borgerhoff Mulder, & Hill, 2001). For example, mating relationships tend to be less stable and less exclusive in societies with subsistence ecologies that lack important resources individual men can monopolize (Flinn, 1981). Moreover, individual variability of mating relationships within a society also tracks resource control (e.g., Flinn, 1986, 1988, 1992). Gangestad et al (this issue) reiterate the importance of this type of flexible evoked culture response to the material world.

The importance of kin-based coalitions for the control of social and material resources, and the resultant nuances of human mating systems in traditional societies (Chagnon, 1997; Flinn & Low 1986; Irons, 1983), however, have not yet been incorporated into a comprehensive theoretical framework in evolutionary psychology. The awareness of these shortcomings, and the interest in a broader cross-cultural database advocated by Gangestad et al. (this issue), are potential great strengths that will go far to advance our understanding

of the nature of human psychology and its adaptive variations. This synthesis also portends renewed interdisciplinary efforts among anthropology, biology, and psychology across a broad range of research questions that may help resolve concerns that “many psychologists have not been studying human nature—they have been studying the nature of educated, middle-class, young adult Westerners (or the children of such people)” (Norenzayan & Heine, 2005, p. 765).

Note

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Evolution and Transmitted Culture

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It is a truism that cultures, or widely distributed clusters of ideas, practices, and their material effects, exist in all human populations, vary markedly from one group to another, and shape human lives in profound ways. Linguistic dialects, cooking methods, technology, calendars, time-keeping devices, writing, formal schooling, folktales, religious beliefs, agricultural practices, and, as recent evidence indicates, even basic psychological processes such as selfways and cognitive tendencies vary across groups and form the bulk of human activity in all societies in the world.

Culture is an evolutionary puzzle for two reasons: (a) No other unitary species in the world shows the extent of intergroup variation in behavior that is seen in humans, and (b) this intergroup variation is largely independent of reproductive events. What accounts for this variation? It cannot be genetic differences. Although there is considerable evidence from behavioral genetics that some individual differences in behavior within any given group are partly genetic (e.g., Plomin, Owen, & McGuffin, 1994), genetic differences between human groups are too small and behavioral variation between groups too large for genetic evolution to explain most human intergroup variation. Moreover, two groups of genetically similar individuals who live in different environments end up with radically different beliefs and behaviors. Nongenetic explanations are needed. Gangestad, Haselton, and Buss (this issue), are right that evolutionary processes that do not invoke genetic differences can shed light on why and how cultural variation emerges.

Cultural Variation in Psychology

In most of psychology as well as anthropology, culture is treated as a given. Psychologists interested in culture have tended to focus on the extent to which cultures vary and how this variation affects not just the superficial content of beliefs and behaviors but the very nature of basic domain general psychological processes, including the self (Markus & Kitayama, 1991;

Triandis, 1989), cognition (Medin & Atran, 2004; Nisbett, Peng, Choi, & Norenzayan, 2001), attention and perception (Nisbett & Miyamoto, 2005), motivation (Heine, Lehman, Kitayama, & Markus, 1999), and emotion (Mesquita, 2001; Nisbett & Cohen, 1996).

This is understandable. For most of its modern history, psychology has faced a daunting cultural challenge. The vast bulk of empirical research in psychology, with some notable exceptions, many originating from evolutionary psychology (e.g., Buss, 1989; Daly & Wilson, 1988), has been conducted with an astonishingly narrow subset of the world's population: Western, middle-class, industrialized, secular people (and their children). Needless to say, this subgroup is a culturally unrepresentative sample of the world and comprises a small percentage of the world's population. As a result, until recently the invariance of psychological processes was assumed as a given, and little was known about the extent to which psychological theories and findings would generalize to the rest of the world's population, and in fact many of the central theories and findings of psychology do not travel well (see Norenzayan & Heine, 2005, for a discussion of universals and cultural differences). This picture has been changing slowly. Growing cross-cultural research promises to expand the psychological database to encompass the world's cultural diversity, and, as a result, theories about human behavior can gain greater accuracy and generality, placing psychological science on firmer empirical foundations.

But culture is not just the *explanans* but also the *explanandum* of social science. It is a thing that must be explained. Why does culture exist at all? Are there phylogenetic homologies of culture in other species? How does culture emerge, and what are the psychological mechanisms by which beliefs and behaviors achieve cultural stability in a population of minds? Why are some distributions of beliefs and behaviors more culturally prevalent than others? How do culturally acquired beliefs interact with innate tendencies? These are important questions about culture that invite psychologists to treat culture as an emerging process as

well as a causal force in human psychology (Kameda, Takezawa, & Hastie, 2003; Lehman, Chiu, & Schaller, 2004; Norenzayan, Schaller, & Heine, *in press*; Schaller & Crandall, 2004).

Evoked and Transmitted Cultural Variation

As Tooby and Cosmides (1992) have proposed, from an evolutionary perspective, there are two known processes that offer a naturalistic account of how culture emerges: (a) Culture can be evoked by local environmental triggers acting on the same underlying psychology (evoked culture); (b) culture can travel from mind to mind by processes of transmission, analogous, but not identical, to Darwinian genetic evolution (transmitted or epidemiological culture, e.g., Sperber, 1996). To illustrate how evoked culture operates, Tooby and Cosmides discussed how the same food-sharing mechanism can lead to different cultural norms depending on the degree of variability in foraging success. Egalitarian norms for food sharing and sanctions against hoarding are strong where foraging or hunting success is highly variable across time, but not when the supply of food is relatively stable. In their article, Gangestad et al. (this issue) admirably elaborate on the notion of evoked culture to explain cultural variation in mate preferences. In this case, the authors argue that the same underlying mate preference for indicators of health interacts with an ecological cue to produce cultural variation—where parasite prevalence is high, features signaling health are more important and diagnostic of underlying health, and as a result attractive mates are preferred more strongly than in regions with low parasite prevalence.

Transmitted or epidemiological culture, in contrast, is prototypically what most social scientists consider culture (Nisbett, 2003; Richerson & Boyd, 2005; Sperber 1996). This refers to the fact that genetically similar people living in similar environments may possess strikingly different beliefs and practices that they acquire from others in their group. Culture emerges when information is transmitted not genetically but socially through social learning mechanisms such as mimicry, imitation, and instruction (Tomasello, Kruger, & Ratner, 1993), as well as a byproduct of communicative processes such as gossip, conversations, and telling of stories (Schaller, 2001). With significant assistance from other human beings, people acquire and transmit substantial amounts of information that subsequently alters their behavior in profound ways. Growing research points to some rudimentary forms of cultural transmission in other species, particularly chimpanzees, who exhibit culturally variable traditions in some 39 behaviors (Whiten, 2005). However, cultural transmission in humans is so massive and

rapidly cumulative that many evolutionary scientists consider it a species-specific second system of inheritance in humans, distinct from, but interacting with, genetic inheritance (Richerson & Boyd, 2005; Tomasello, 1999). Richerson and Boyd went so far as to argue that transmitted culture is an adaptation and that babies are born biologically prepared to rapidly learn the beliefs and practices of their social group. A learning bias that adopts the most common behaviors of the ingroup may have been selected in the ecologically fluctuating ancestral environment in which human psychology evolved. Whether or not transmitted culture can best be considered a naturally selected adaptation, psychological research grounded in evolutionary science can shed light on this powerful but poorly understood engine that drives culture.

Although Gangestad et al. (this issue) are careful to note that cultural variation is likely to be the result of both evocation and transmission, like Tooby and Cosmides (1992) and many evolutionary psychologists, they privilege the notion of evoked culture as the central evolutionary framework to explain cultural variation. Of course, evoked culture is a welcome development that promises to engage evolutionary psychology with cultural psychology and may encourage fruitful new avenues to explain not just psychological universals but cultural variation as well. But why have evolutionary psychologists been wary of the concept of transmitted culture? Is transmitted culture a Trojan horse that, once invited in, would unleash conceptual anarchy and unravel the project of anchoring psychology in an evolutionary framework? On first thought, it might seem so. Many of the cultural elements that spread in a population are, at best, arbitrary conventions such as dress code, whether to eat horse meat or dog meat, or whether to serve the said meat as a sizzling steak or boil it into a goopy goulash. At worst, they are Darwinian nightmares, competing with genetic interests and even undermining them, such as when the idea of celibacy, suicide, the practice of using contraceptives, eating rotten foods, or writing scientific articles instead of having children succeed in colonizing a large number of minds.

But no need to worry about transmitted culture! Even if a significant part of the content of culture may be fitness-neutral or in some cases may even compete with genetic fitness, evolutionary thinking is essential for our understanding of (a) the evolved psychological capacities that power cultural transmission and (b) whether cultural elements themselves are subject to a secondary evolutionary process—variation, selection, and retention analogous to natural selection. Evolutionary thinking is also essential to understand how genetic and cultural evolution influence each other. In the rest of this article, then, I aim to give transmitted culture its due, with two goals in mind. With evolutionary psychologists in mind, I argue for the centrality of

transmitted culture in accounting for a significant, if not overwhelming, bulk of human variation on the planet. With cultural psychologists in mind, I argue for the importance of evolutionary science in explaining cultural transmission as one of the central mechanisms of human cultural variation.

Evolved Capacities for Transmitted Culture

The set of psychological capacities that allowed humans to learn from others and calibrate their behavior to the cultural group in which they live are rooted in evolutionary processes. There is already a great deal of good theoretical work, mostly from anthropology, about such capacities (Boyd & Richerson, 1985; Richerson & Boyd, 2005; in psychology, see Tomasello et al., 1993). Several independent mechanisms that may contribute to transmitted cultural differences have been proposed and examined. The simplest of those is social learning, which allows humans to imitate other humans without any particular bias as to who gets to be the model of imitation. This mechanism could have been selected for, because individuals in a group live in more or less the same environment and are likely to face similar survival challenges. By allowing individuals to imitate the behavior of others, social learning can evolve by freeing individuals from the costs of trial and error learning, as long as the alternative cost of imitating maladaptive behaviors are not too high.

Another mechanism identified by Henrich and Boyd (1998) is “conformist transmission,” which, unlike simple social learning, is biased toward adopting the most common behaviors in a group. Such conformist transmission is robust in environments that fluctuate within space and over time and may have been selected for in the human ancestral environment that seems to have been quite unstable, for example in weather and in availability of food supply (see Richerson & Boyd, 2005). Finally, a form of biased transmission may have evolved that is sensitive to the success or prestige markers of individuals, such that successful individuals in a group are more likely to be imitated (Henrich & Gil-White, 2001). Although social psychologists have examined similar social influence processes, there has been insufficient effort to ground this research in an evolutionary framework. Most likely, there are several, psychologically distinct, flexible transmission mechanisms that optimally operate in different social contexts. It is up to evolutionary social psychology to generate hypotheses regarding the behavior of these mechanisms, examine their boundary conditions, and link them to known culturally acquired beliefs and behaviors. Such work is mutually relevant to both evolutionary psychology and cultural psychology and prom-

ises to enrich both fields as well as psychology more broadly.

Cultural Evolution

Clarifying the psychological mechanisms of transmitted culture is only part of the evolutionary story of culture. Once transmission mechanisms give rise to cultural forms of learning, they open the floodgates to cultural evolution. Cultural elements then enter into what is probably a secondary evolutionary process in humans that is distinct from genetic evolution but interacts with it in complex ways. This is because evolution is substrate-neutral (Dennett, 1995). Any entity—be it DNA, computer viruses, or mental representations—capable of replication, selection, and retention is likely to undergo Darwinian processes. Cultural evolution is a hotly debated topic, and several theoretical issues still remain open. One issue that has received attention is the accuracy of cultural transmission. Unlike genetic transmission, cultural transmission has low fidelity (Atran, 2001). Whereas genetic transmission is largely a process of faithful replication, cultural transmission is more akin to transformation or inference (Sperber, 1996; see also Boyer, 1994). At every instance of cultural transmission from one individual to another, cognitive and emotional biases transform the mental representations. For example, a folktale or an urban legend that is told and retold is not preserved in identical form across minds the same way DNA replicates from parent to offspring. Rather, each act of transmission is a systematic reconstruction, and several versions of the same folktale or urban legend emerge in oral traditions. Nevertheless, quasi-stable cultural traditions do emerge over time, either because these psychological biases or what Sperber called “attractors” systematically push beliefs into certain regions, or because, as Henrich and Boyd (2002) argued, stable cultural beliefs at the population level can plausibly emerge even if transmission is low-fidelity at the individual level.

Either way, these cognitive and emotional biases render psychology central to the study of cultural evolution (see, e.g., Boyer & Ramble, 2001; Heath, Bell, & Sternberg, 2001; Norenzayan, Atran, Faulkner, & Schaller, in press). Here again, psychology informed by evolutionary thinking can contribute to our understanding of how ideas achieve cultural success. The cultural prevalence of supernatural beliefs such as ghosts and Gods, for instance, can be understood as by-products of cognitive and emotional programs that were designed for other purposes, such as agency detection, memory, and existential fears (e.g., Atran & Norenzayan, 2004; Barrett, 2001; Boyer, 1994; Guthrie, 1993).

Furthermore, cultural evolution is essential for our understanding of human nature because it sheds light on many (culturally altered) behaviors that are otherwise quite puzzling from the standpoint of genetic evolution or evoked culture. Evolutionary psychologists correctly point out that human mental adaptations were selected for in the ancestral environment, not in the modern cultural environment, and therefore they could be maladaptive today. But why did the modern cultural environment become so astonishingly different from the ancestral environment in less than 10,000 years? The answer is cultural evolution. For example, populations exposed to higher education are less likely to have offspring, which means that the practice of higher education can spread in populations even though it has the net effect of reducing genetic fitness (Richerson & Boyd, 2005). The most compelling naturalistic explanation for such effects is cultural evolution.

Back to Evoked Culture

Although evoked and transmitted culture are theoretically distinct processes, it is notoriously difficult to disentangle the two. In their framework, Gangestad et al. (this issue) tested variation in parasite prevalence against variation in gender inequality to explain mate preferences. Although parasite prevalence clearly is an evoked variable (characteristic of the environment), it is unclear whether gender inequality is best construed as the product of evocation or transmission. As Gangestad et al. discuss in some detail, there are various competing explanations for gender inequality across cultures in the first place. When men produce more surplus calories (usually by hunting) than women, gender roles diverge. Men and women may engage in different activities because of evocation (ecological factors) or transmission (how boys and girls are socialized and trained in the society). Most likely it is both. Therefore, Gangestad et al. provide evidence that evocation does account for cultural variation in mate preferences, but their design does not allow for a clear test of whether transmission contributes to this variation.

Indeed, Gangestad et al. (this issue) point to the issue of the inseparability of evoked and transmitted culture when they discuss Nisbett and Cohen's (1996) work on the culture of honor. The southern United States, as well as the Mediterranean region, has a tradition of honor, in which toughness and aggressive response to insults is prized in a way that it is not in the northern United States or in most of northern Europe. The origin story of this difference is in fact evoked culture: Where wealth is easily stolen, as in ecologies supporting herding economies, men are more deeply preoccupied with maintaining their honor or reputation for toughness. The U.S. South was settled by Scotch

Irish herders, whereas the U.S. North was settled mostly by European farmers, and as a result a tradition of honor is prevalent in the South but not in the North. But cultural differences persist even when the original economic conditions disappear. Culture of honor continues to flourish in industrialized Houston, even though herding is a thing of the past. The best explanation for the persistence of honor cultures is social transmission, and indeed a variety of evidence supports this view (Nisbett & Cohen, 1996; see also Cohen, Vandello, Puente, & Rantilla, 1999). Perhaps a common scenario across cultures is that ecological differences evoke an initial cultural response that adaptively varies but then is picked up by processes of transmitted culture, amplified, and perpetuated even when the initial conditions are no longer present.

How, then, can we disentangle the relative contributions of evoked and transmitted culture? Richerson and Boyd (2005) proposed the ideal "common garden experiment": Take two groups of individuals with very different cultures, say, Inuit fishermen and Ache foragers, and switch them around—some Inuit move into the rainforests of Paraguay and some Ache move into the icy fringes of Greenland. Would the Ache foragers in Greenland begin to resemble the Inuit more than they would resemble their Ache compatriots in Paraguay, as the evoked culture explanation would predict? Or would they remain more like their Ache compatriots and, without the cultural repertoire of arctic survival, quickly perish in the harsh climate, as the transmitted culture explanation would maintain?

In the absence of such a naturalistic experiment, what can researchers do? One approach is to hold one variable constant while examining the effect of the other variable. Comparing groups living in similar environments but with different beliefs and practices allows researchers to isolate the effects of transmitted culture. The Amish of the U.S. Midwest, for example, live in the same ecological environment as neighboring German-ancestry farmers but to this day have maintained beliefs and practices that are markedly different. The complementary strategy would be to measure the effects of a novel ecological variable on a group that shares the same culture (e.g., by examining how farmers in the U.S. North living in a farming community differ from farmers who have migrated to a new environment in which they adopt herding). Psychologists interested in cultural variation have been slow in adopting such research questions that are ultimately important in isolating the mechanisms of cultural variation. These questions can be fruitfully examined by studying immigrant populations who move to an ecologically different setting and conversely by tracking cultural evolution in several groups who live in similar ecological circumstances.

For example, one interesting study (Rice & Steele, 2005) compared the average subjective well being

(SWB) of European countries with various European ethnic groups in the United States whose ancestry is derived from these countries. Cultures across countries differ markedly in their average SWB, and it was found that the relative differences in SWB among these American ethnic groups, although smaller, were nevertheless preserved even after generations of living in the same country, under similar ecological conditions of American middle-class life. Because group differences in SWB in these samples are likely not genetic, such a finding supports the idea that an important psychological variable such as SWB is transmitted socially across generations and can persist for a long time even in a different environment.

Conclusion

In the past two decades, both cultural psychology and evolutionary psychology have enjoyed marked growth. Cultural psychologists have been documenting the extent of cultural variation in psychological functioning. Evolutionary psychologists have been documenting the species-specific mental architecture that evolved to solve adaptive problems in the ancestral environment. Yet evolutionary explanations for how culture emerges in the first place, as well as for cultural differences, have been relatively neglected in cultural psychology and are beginning to be addressed only recently. Conversely, empirical work on cultural variation has been relatively neglected in evolutionary psychology. Greater interest in the scope and nature of cultural variation among evolutionary psychologists, and greater interest in evolutionary explanations in cultural psychology, are a welcome development that stands to strengthen psychology as a science. Evolutionary considerations that underlie processes of both evoked and transmitted cultural variation are an exciting point of convergence between these two fields and are an important scientific advance for a psychology that encompasses the world's cultural diversity.

Notes

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Evoked Culture and Evoked Nature: Coevolution and the Emergence of Cultural Animals

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Arguments about whether behavior is best explained by invoking nature or culture have been a staple of social sciences for decades. Declaring them over and resolved, especially in the form of both sides' repeated claims to have won, has not brought them to an end. In work such as the target article by Gangestad, Haselton, and Buss (this issue), however, one can begin to get a glimpse of how a conceptual integration might occur. As they suggest, cultural variation is not a prime-mover sort of autonomous explanation for behavior but rather a well-documented phenomenon that itself calls for explanation. The authors propose that evolutionary theories can potentially offer a powerful basis for explaining cultural variation.

Our enthusiastic support for the target article's line of argument is accompanied by a sense that the nature–nurture debates are not likely to be ended even if conceptual integration continues apace. The practical issues concerning proximal causation, for example, likely will continue to revive debates as to how much a change in cultural conditions or socialization practices can alter problem behaviors. Can murderers and sex offenders be rehabilitated to become model citizens? Can race differences in intellectual performance be eliminated? Do women inevitably make better parents, lovers, and leaders than men?

Our purpose in this brief comment is not to dispute or criticize the thoughtful arguments made by

Gangestad et al. (this issue) so much as to offer complementary ideas that can possibly advance the project of integrating nature and culture within the same theory. We suspect that researchers sympathetic to culture will regard the target article—and similar efforts to explain culture by invoking nature—as a sort of hostile takeover. It might be easy for cultural sympathizers to read this work as saying that evolution can explain everything, including culture. Perceptions of hostile takeover can perhaps be softened, however, by suggesting that culture has also influenced nature, thus augmenting “evoked culture” with “evoked nature.”

In a model of human nature based on a survey of psychological research findings, Baumeister (2005) concluded that the most apt integrative formula would treat the human psyche as exceptionally well designed for culture. Humans have the same basic wants and needs as most other animals, but the ability for humans to live in culture changes the strategies by which they set out to satisfy these basic goals. That is, moving beyond the long-standing notion that humans are simply social animals, the most all-encompassing explanation of what is distinctive about humans would depict them as cultural animals.

To argue that culture influenced (evoked) nature, several conceptual refinements are necessary. First, the importance of culture is not limited to cultural differences. In practice, the vast majority of theorizing about

culture emphasizes differences, and whenever one sees the word *culture* in the title of a psychology talk or article, one can bet with confidence that cultural differences will be the theme. But, of course, cultural differences come and go too rapidly to become encoded in genes—hence the conventional wisdom that culture could not have influenced nature. If we look at culture per se instead of cultural differences, however, then it does become plausible that culture may have influenced human nature. The fact of living in culture has been part of human life all over the world and throughout its history (and prehistory).

Is it possible that culture evoked nature in some aspects of human psychology? That question brings up the second conceptual refinement. Baumeister (2005) speculated that culture may have been a selection factor in human evolution. There are several indications that culture has played a crucial role in shaping human evolutionary processes. One indication is the accumulating evidence that the beginnings of culture can be found in nonhuman species (e.g., De Waal, 2001). To be sure, these fall far short of the sophistication of human culture. Nevertheless, if nonhuman primates have rudimentary culture, then culture may have provided some of selection factors in the development of *Homo sapiens*. Another indication is that, although cultural differences often take scientific center-stage over cultural similarities, there are also a great many important similarities across cultures. At least some of these similarities may reflect important universals in human group psychology, universals that have played a role in shaping the evolution of individual human minds.

Culture would have changed the selection pressures on human evolution—that is, culture changed what traits were important for reproductive success among humans. Humans who were best able to navigate the challenges and opportunities of culture would have been most successful at passing on their genes. For example, once hominid groups engaged in social exchange, then individuals who were more capable at social exchange may have reproduced more effectively. By fundamentally changing the nature of group-level interpersonal dynamics, the advent of culture modified the rules of the natural selection game. What emerges, then, is a picture of gene-culture coevolution, in which biological evolution selects for cultural beings whereas culture shapes the fitness landscape on which evolution operates (cf. Lumsden & Wilson, 1982). Put another way, once culture began to emerge, evolution likely selected for traits that helped individuals reap the novel benefits and avoid the novel dangers of cultural life. Individual humans, in turn, would have possessed stronger and stronger cultural capacities over time, which would have reinforced the further development of culture. Thus, the biological evolution of the human mind and the evolution of human culture are very likely to have reinforced one another throughout history.

Several universal aspects of culture may have changed the fitness landscape in which humans evolved. Language and symbolic thought, for example, are apparently universal features of human culture, and moreover they are rather distinctively human (Pinker, 1994). Some nonhuman animals do communicate with each other, typically with simple grunts or barks, but most linguists balk at stretching the term *language* to cover such communication. The cultural animal style of argument is that small, incipient patterns found in prehuman creatures opened up styles of interactive behavior that proved so adaptive that natural selection cultivated them into major, central, distinctively human traits. Applied to language, the argument would be that the beginnings of oral and auditory communication in other animals opened up the possibility for richer and more effective social life, and so improvements in the ability to communicate in that way conferred important adaptive benefits.

Hence it is likely that language shaped the manner in which human biological evolution occurred. We doubt that the adaptations for human speech—the vocal apparatus capable of producing thousands of distinct sounds, the ear capable of hearing subtle differences, and the brain capable of grammar and vast vocabulary—occurred all at once. Rather, once hominids began to talk, then individuals who were biologically better suited to language use survived, flourished, and reproduced better than their linguistically inept peers. In this way, what is undeniably a cultural and learned reality—language—could have guided the selection of biological traits.

An alternative view is that biological adaptation fully preceded the development of culture and simply made possible its development. Applied to language, this view entails that humans evolved their marvelous vocal apparatus, fine-resolution hearing, and grammatical brain first, and only after these were fully ready did people invent language. This strikes us as postulating a stroke of luck so extraordinary as to suggest intelligent design. (One would have hoped, however, that an intelligent designer would have given all humans the same language, thereby sparing us endless misunderstandings, hassles, and translation costs!) But it seems much more plausible that language and its biological underpinnings evolved in concert.

The view of culture as a biological strategy can also be used to explain the eventual success of our own species over its rivals. Human evolution was hardly a straight path, and in fact most evidence now points to various versions of human beings evolving in different parts of the globe. In single hand-to-hand combat, our Cro-Magnon ancestors might have found Neanderthals to be formidable opponents (indeed, the Neanderthals are believed to have had both larger brains and greater physical strength than *Homo sapiens*), but Neanderthal culture was no match for ours. The Neanderthal inca-

capacity for role differentiation and division of labor would have crippled their ability to create an economic culture, and this alone could explain why they went extinct when competing against the economically competent *Homo sapiens* (Horan, Bulte, & Shogren, 2005).

The importance of role differentiation (for economic life in culture) suggests one small refinement of the argument by Gangestad et al. (this issue). They say that what scientists call culture is a matter of “within-group similarity and between-group difference.” Similarity is undoubtedly an important aspect of culture, especially with regard to shared practices, beliefs, values, and the like, but a full understanding of culture most likely has to recognize within-group differences—even to the extent of proposing that culture promotes within-group differentiation. Culture is a system, and a system consisting of identical parts is not going to produce the kinds of system gain that a system of highly specialized, differentiated parts can have. (That’s apparently what doomed the Neanderthals.) As evidence, it is probably sufficient to look at one of the biggest themes of cultural change across the centuries, namely the relentless movement toward ever greater specialization inside of ever larger systems. Culture makes us all increasingly different from each other, at least in terms of our increasingly narrowly specialized roles within the larger community.

A great strength of the Gangestad et al. (this issue) article is in pointing the way to how cultural differences could have emerged in response to local conditions. Baumeister (2005) rather vaguely suggested that cultural differences represented different solutions to the same problems, but without much basis for explaining why one solution might prevail in one place and another elsewhere. As Gangestad et al. (this issue) indicate, differences in food availability, sex ratios, and other environmental conditions can make different approaches and solutions more effective in some places than others, thereby contributing to the immense variation in human culture.

The view that humans evolved for culture depends on the gradual construction of what Gangestad et al. call “an intricately designed, environmentally sensitive psychological architecture.” That remarkable architecture is what makes humans special. Most plausibly,

that architecture came into being under evolutionary selection pressures that included the emergence of a new kind of social system, such that whoever was most capable of taking part in that system and contributing to it was most likely to pass on his or her genes.

Four biological advantages of culture were suggested by Baumeister (2005): language and the resultant improvement in capacity for both communication and thought; intergenerational progress based on the accumulation of knowledge; division of labor and its resultant gains in efficiency; and economic exchange, which increases material wealth and hence well-being. Those are perhaps the universal benefits of culture, which all cultures manage to confer. Local environmental contingencies can then evoke important differences in how cultures provide those benefits and capitalize on those advantages. But also, those benefits of culture may have been decisive in evoking the further development of human nature so as to capitalize on them. In this way, we can follow Gangestad et al. (this issue) toward explanations of both the universal and the culturally relative aspects of the human experience.

Note

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Three Ways That Data Can Misinform: Inappropriate Partialling, Small Samples, and Anyway, They're Not Playing Our Song

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Gangestad, Haselton, and Buss (this issue) have contributed a provocative analysis of cultural variation in mate preferences. We applaud their advocacy of an interactionist perspective on mate selection that takes nature and nurture into account simultaneously. We, like they, reject artificial dichotomies between evolved dispositions and environmental influences. As they acknowledge, our debates with them center on the details of our respective interactionist theories, especially the ways in which evolutionary processes calibrated the human psychological dispositions that are manifest in mate preferences among modern humans. To advance this debate, we begin by briefly reviewing our theory and critiquing Gangestad et al.'s evolutionary psychology theory.

Our comment then addresses three flaws in Gangestad et al.'s (this issue) empirical demonstrations that lead them to conclude support for their own evolutionary psychology theory over a biosocial account (Wood & Eagly, 2002). The first is the partialling fallacy, whereby Gangestad et al. control the status of women for its socioeconomic and ecological determinants in their attempt to show that this variable is not relevant to mate choice. The second is the small sample shortcoming, whereby their analyses are compromised by too many variables given the small number of cases. The third is their use of obsolete predictors, whereby they represent pathogen prevalence with old data in their attempt to show the relevance of this variable to mate choice.

Social Structural Origins of Sex Differences in Mating Preferences

Behavior Patterns as Emergent

The human capacity to benefit from a fairly wide range of mating opportunities optimizes possibilities for reproduction and survival, just as the human capacity to thrive on many different types of foods favors survival in widely differing environments. The study of human food preferences details the way that these preferences emerge from the interaction between biological predispositions and properties of the environment (e.g., Rozin, 2000; Striker, 1990). Specifically, human food practices appear to depend on the options inherent in local conditions, within the limits set by spe-

cies-wide evolved preferences (e.g., sweet foods) and aversions (e.g., rotting food). Humans thus learn what foods are available and healthful in their environments, and this learning is culturally shared. Food preferences are an emergent product of evolved dispositions and other influences rather than preprogrammed through evolution and merely contingently emitted in response to environmental conditions.

Mating preferences follow a similar logic. They are an emergent product of the evolved characteristics of the human species, individuals' developmental experiences, and their situated activity in society. Beliefs about the costs and benefits of mating are socially transmitted and shared within cultures. Not only humans, but other vertebrate species, including birds and fish, have mating preferences that reflect learning from observing others' sexual behavior and mate choices along with other forms of social transmission of these preferences to conspecifics and across generations (Freeberg, 2000). For example, female quail apparently acquire a preference for an experimentally altered male wearing a feather headdress after observing another female's apparent choice to mate with such a male (White, 2004). The learning mechanisms that allow for socially transmitted assessments of the costs and benefits of mating not only alter selection pressures and subsequent evolution but themselves represent a kind of evolutionary process (Freeberg, 2000).

Roles as Channeling the Costs and Benefits of Behaviors

Among humans, much of the learning of the costs and benefits of behavior is channeled through men's and women's social roles, which divide labor between the sexes. Roles are especially relevant to understanding sex differences in mating and other behaviors. Differing role obligations and opportunities cause men and women to experience differing costs and benefits of mating choices and consequently to value different types of relationship partners (Eagly & Wood, 1999; Wood & Eagly, 2002).

Several processes mediate between the division of labor and typical male and female behaviors. The differing roles of men and women foster the formation of distinctive gender roles, by which people are expected to have characteristics that equip them for activities

typical of their sex. For example, to facilitate caring for young children, women are expected to be nurturing and kind, and to facilitate participation in warfare, men are expected to be aggressive and brave. Gender roles, along with specific roles (e.g., occupational, family) then guide behaviors, including sexual behavior. The effects of roles on behavior are in turn mediated by developmental and socialization processes as well as by processes involved in social interaction and self-regulation. In addition, biological processes such as hormonal changes orient men and women toward certain roles and facilitate role performance.

The social roles of men and women are themselves powerfully influenced by the evolved physical attributes of the sexes and related behaviors, especially women's childbearing and nursing of infants and men's greater size, speed, and upper-body strength (Wood & Eagly, 2002). These evolved sex differences interact with the prevailing social, economic, technological, and ecological forces to yield a division of labor that reflects the ease and efficiency with which each sex performs life tasks.

To illustrate this theory's power, Wood and Eagly (2002) discussed the tendency across many societies for men and not women to hunt large game. The crux of their argument is that women's gestation, nursing, and care of infants limit their ability to perform tasks such as hunting that require speed, uninterrupted periods of activity, or long-distance travel away from home. This account is compatible with the small percentage of known foraging societies in which women regularly hunted large game. In one of the most extensively investigated examples, women of the Agta in the Philippines hunted, assisted by dogs, wild pigs and deer (Estioko-Griffin & Griffin, 1981). Because the Agta lived in a relatively resource-rich environment with game available in close proximity to home, hunting and child care were not incompatible. Women took infants along with them and left weaned children at home until they were old enough to join the hunt.¹

Comparison With Gangestad et al.'s Evolutionary Psychology Theory

In Gangestad et al.'s (this issue) theory, evolution has designed the human mind to have domain-specific dispositions that are contingent on environmental input. They offer the analogy of the jukebox based on humans' capacity to deliver a selection of preprogrammed responses, depending on the directions from environmental inputs. In contrast, our evolutionary theory assumes far more flexible emergent responses

that reflect learning from environmental input, developmental experiences, and evolved dispositions.

We assume that human psychology has evolved to favor the emergence of new preferences with changing circumstances. As Foley (1995–1996) explained, even humans' early ancestral environments were characterized by a diversity of habitats and associated challenges of reproduction and survival. If evolution endowed humans with prepackaged contingent preferences that maximized outcomes tailored to past evolutionary pressures, they would be ill-equipped to generate innovative solutions to changing environments. A human mind preprogrammed with many domain-specific adaptations would be too rigid to respond effectively to the novel conditions that humans have encountered as their environment has shifted in response to ecological changes, population growth, and the development of complex economies and technology. Less flexible species than humans are more vulnerable to extinction in novel environments.

Our emphasis on humans' behavioral plasticity and the wide range of environments in which they can thrive does not suggest a blank slate so much as evolved dispositions that depend on social and environmental input for the form in which they are expressed in behavior. A more compelling account of human mating preferences than a mechanistic jukebox model of environmentally evoked dispositions maintains that such responses emerge flexibly from multiple influences, given humans' unique adaptation for culture. This evolutionary reasoning recognizes that human cultural traditions, unlike the cultures of other primates, accumulate contemporaneously and over historical time (i.e., the ratchet effect). As an example of this reasoning, Tomasello (1999) proposed that the distinctly human forms of social learning that yield pooling of cultural knowledge emerged largely from a single evolutionary event, which he described as the evolution of humans' ability to understand others as intentional agents like the self. Given this capacity, humans' genetic heritage does not carry the burden of specifying the detailed outcomes evident in contemporary human behavior. Instead, mating preferences, like many other aspects of human behavior, can be understood as emergent from uniquely human forms of social learning in interaction with evolved dispositions and particular developmental and societal contexts.

Relevance of Cross-Cultural Patterning of Human Mate Preferences

Our dynamic framework draws attention to the division of labor within a society as an influence on mating preferences (Eagly & Wood, 1999). The criteria that women and men use to select mates reflect the divergent responsibilities and obligations inherent in their

¹Gangestad et al.'s (this issue) claim that "it is not at all clear how Wood and Eagly explain men's hunting" reflects their lack of familiarity with what Wood and Eagly (2002) have written on this subject.

social roles. In societies with a strong division between male providers and female homemakers, women should seek a mate who is a good provider because they are reliant on men to garner resources for them and their children. Men should seek a mate who is a skilled homemaker and child caretaker because their children's ability to thrive and to some extent their own ability to do so depend on women's mastery of domestic tasks. The provider-homemaker marital system should also favor sex differences in age preferences. These preferences emerge because older men are likely to have acquired resources, and younger women, because they are likely to lack resources, value marriage and older partners with resources. However, all of these sex differences in mate preferences would lessen to the extent that the provider-homemaker division of labor erodes and women and men are similarly placed in the social structure.

In a test of these predictions (Eagly & Wood, 1999), we reanalyzed the same data that have once more been reanalyzed by Gangestad et al. (this issue). The data are from Buss's (1989) study of the mate preferences of young adults from 37 diverse, primarily urbanized, cash-economy cultures, with 54% from Europe and North America. In our reanalysis, we represented the social position of women and men by two nation-level indexes available from the United Nations (United Nations Development Programme, 1995). The more relevant of these two indexes, the Gender Empowerment Measure (GEM), represents the extent to which women participated equally with men in economic, political, and public decision-making roles. The second index, the Gender-Related Developmental Index (GDI), reflects the equality of the sexes in basic access to health care, education and knowledge, and income. Although these indexes are useful, neither is fully adequate to represent the male-female division of labor.²

Consistent with the prediction that mate preferences reflect each sex's attempts to maximize outcomes within their environments, women's preferences for older mates and mates with resources and men's preferences for younger mates and mates with housekeeping and cooking skills were more pronounced in societies with less gender equality, as represented by the GEM and GDI. Providing additional evidence that the preferences of men and women were a common response to a sex-typed division of labor, the sex differences in mate preferences tended to coexist within societies: In societies in which women expressed

especially strong preferences for mates with resources and older mates, men also expressed especially strong preferences for mates with domestic skills and younger mates. Nonetheless, because a gender-equal division of labor had not been attained in any of the societies in Buss's (1989) data set, the sex differences in mate preferences were present to some degree in all of the sampled societies.

In contrast to our biosocial analysis, Gangestad et al. (this issue) propose that mate preferences are pre-programmed, evolved dispositions that are evoked by attributes of the current environment that were associated with fitness in our ancestral past. Their reanalysis of Buss's (1989) cross-cultural data to address this idea suffers from three serious errors that compromise their conclusions. These involve the misspecification of predictors through inappropriate partialling, the overly small samples given the number of predictors in their models, and the use of obsolete pathogen data.

The Partialling Fallacy

The partialling fallacy is a form of specification error that occurs when predictors in regression are not meaningfully distinct (Gordon, 1968). If regression models include controls that themselves capture the meaning of key predictors, then the equation retains too little of the predictors to allow for interpretation. On a statistical level, such inappropriate partialling inflates the standard errors of the regression coefficients and thereby compromises replicability of the analyses (Gordon, 1968). Gangestad et al. (this issue) fell prey to this error when they imposed statistical controls for income, latitude, and region in their regression analyses, ostensibly to remove confounds and thereby obtain purer measures of Eagly and Wood's (1999) key predictor, the division of labor between the sexes. With these controls, the remaining predictor is uninterpretable and assumes undesirable statistical properties.

Before probing this critique of Gangestad's (this issue) analyses, let us illustrate this point by examining an even more obvious example of the partialling fallacy (Ezekiel & Fox, 1959). A study conducted to determine the size standards for children's clothing predicted these standards from various body measurements as well as age and sex (see data in O'Brien & Girshick, 1939). The key statistical predictors turned out to be height and girth at the hips. Once these variables were controlled, age contributed no net effect. A researcher following Gangestad et al.'s simplistic regression logic (see footnote 6) would conclude that age is irrelevant to the sizing of children's clothes. Given that age, height, and girth at the hips are intrinsically and causally linked, even a moment's thought reveals the causal relevance of children's age

²The GDI, indexing the relative access of women and men to societal resources, provides only an indirect measure of gender equality. Even the GEM measure is inexact because it indexes the extent to which women hold seats in parliaments and have technical and managerial occupations, without taking into account the authority associated with these roles. Women and men are counted if they hold managerial or technical roles, regardless of the placement of these roles in organizational hierarchies.

to their clothing sizes, saving even the least sophisticated interpreter of data from such a conclusion.

Now, concerning status of women, the male–female division of labor and patriarchal social structure are intrinsically tied to economic development in world societies because societal modernization produces systematic changes in the social position of the sexes. As Inglehart and Norris (2003; see also Inglehart, 1997) explained, modernization has proceeded in two phases as societies have moved from agrarian economies to more modern forms. In the first, or industrialization, phase, women enter the paid workforce, and fertility rates fall dramatically. Although women gain basic political rights such as the vote, their power and status remain relatively low, and most aspects of the division of labor continue unchanged. In the second, or postindustrial, phase of modernization, women gain access to management and the professions and increase in political influence. Equality of the sexes increases with the weakening of the division of labor in the home, family, and workplace and the replacement of the traditional breadwinner–homemaker family by a wide variety of adult living patterns.

This postindustrial stage prevails only in the more advanced industrialized societies, which are characterized by the greatest wealth and the highest levels of human capital. Wealth varies dramatically depending on whether societies are in the postindustrial, industrial, or agrarian phase of development. In 1998 in a sample of 191 nations whose modernization was defined by the composite Human Development Index (United Nations Development Programme, 1995), the gross domestic product per capita was \$29,585 in postindustrial nations, \$6,314 in industrial nations, and \$1,098 in agrarian nations (Inglehart & Norris, 2003). The close association that exists between economic development and gender equality is consistent with Inglehart and Norris's prediction of attitudinal support for gender equality across 55 nations assessed between 1995 and 2001 from nations' income. Per capita gross domestic product was correlated .61 with support for gender equality, which was in turn correlated .84 with the GEM. Thus, societal income is closely and meaningfully related to gender equality.

What does geographic location have to do with the division of labor? Region and latitude are correlated with the division of labor because some nations are more favorably situated for modernization due to their geography and ecology. The arguments for the importance of geography and ecology, interacting with technological developments, have been set forth by many scientists, most popularly by Diamond (1997). Certain societies possessed the natural resources that contributed to economic development, along with the geography that facilitated trade and the communication of innovations. As historians and social scientists have extensively documented, such advantages have pro-

pelled some societies, especially those of North America and Europe, into the industrial and then the postindustrial stage. It is thus understandable that gender equality is related to region and latitude.

Our reasoning about the intrinsic linkages of gender equality to nations' wealth, region, and latitude is consistent with the correlations of these variables with the GEM and GDI United Nations indexes of equality shown in Appendix A of Gangestad et al. (this issue). Nations' income and latitude are highly correlated with gender equality (r s range from .63 to .75), and the various geographic regions show more modest associations. With this pattern, specification errors occur when the gender equality indexes are partialled for income, latitude, or region in predicting mate preferences. Because Gangestad et al.'s regression models are subject to specification errors that arise from controlling gender equality for its determinants, it is understandable that few significant results remain for the GEM and GDI indexes in Tables 1, 2, and 3, in which the authors report the findings predicting preferences from these indexes.

Additional complexities arise because it is impossible to discern exactly what controls Gangestad et al. (this issue) instituted for each analysis reported in Tables 1, 2, and 3. The authors evidently instituted differing controls across the analyses (see footnote 5), making the various analyses noncomparable. They report that their first-stage analyses were regressions that "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." In the second-stage analyses, aspects of which are reported, some regressions might have controlled, for example, for one or more of the dummy-coded region variables and other regressions for latitude or income. Although the details of these analyses remain unreported, Gangestad et al.'s description of their method implies that analyses on each dependent variable included a distinct set of control variables and that these variables changed across the analyses. Because interpretation of the effects of the gender equality and pathogen prevalence predictors depends on the specific controls included, it is unclear how to interpret the effects reported by Gangestad et al.

In their unusual analysis strategy of including multiple and varying controls for national wealth and geographic location, Gangestad et al. (this issue) deviate from earlier research. Low's (1990) analysis linking pathogen stress and the prevalence of polygynous marital systems reported some analyses controlling for geographic region and other analyses controlling for latitude but did not include multiple controls and did not control on national income.

In sum, given that gender equality is but one component of a set of intrinsically linked societal factors, it is inappropriate to partial out the influence of these other

factors when interpreting the effects of this variable. Nations' gender equality, as one aspect of social structure, is embedded in a complex of linked features of the economy, polity, and family.

The Small Sample Shortcoming

The small samples available for Gangestad et al. (this issue) to test their regression models provide additional reason to question the reliability of the findings reported in Tables 1, 2, and 3. Regression analyses are made unstable by inadequate sample size in relation to the number of predictors included in the analysis. Although Gangestad et al.'s report obscures the details of their analyses, the first-stage analyses apparently entered seven predictors (income, latitude, regional contrasts 1 through 5). The second-stage analyses had fewer predictors, evidently just over three on the average (control variable, GEM, and pathogen prevalence), but the range of the number of predictors is unreported.

Although the aggregated data represented in Buss's (1989) 37 cultures study possess particular statistical properties, the models used in Gangestad et al.'s (this issue) analyses are presumably subject to the standard requirements of regression procedures. In a classic analysis of the sample sizes necessary for adequate power in regression models, Green (1991) evaluated numerous rules of thumb that have been used by researchers over the years. He concluded that detection of a medium-sized effect with power equal to .80 in multiple regression requires a sample size greater than $50 + 8p$, where p is the number of predictors. With a sample size of 37, the analyses were inappropriate even in the second stage of the regressions and more so in the first stage. In recognition of the small sample size and relatively low power, the authors report that they used a liberal alpha equal to .10 to determine statistical significance. However, this decision rule is inadequate to address the problem of instability of findings given samples too small for the number of predictors.

Anyway, They're Not Playing Our Song

Gangestad et al. (this issue) based their analysis of parasite prevalence on old parasite data contained in books by Craig and Faust (1943), Rodenwaldt (1952), and Simmons et al. (1944–1954). The jukebox analogy implies that contemporaneous local conditions elicit the preprogrammed preferences that control mating. The data that Gangestad et al. used from "the first half of the 20th century" have uncertain relevance to the mate preferences of late 20th century humans. These outdated eliciting conditions can't play the right song.

One reason for using older estimates of parasite prevalence might be that sexual behavior changes only with considerable lag as the environment changes. Therefore, earlier parasite data might be preferable to parasite data more contemporaneous with the 1982–1986 dates when mate preferences were assessed (see Gangestad & Buss, 1993). However, this lag appears to be relatively small. Typical mating practices can change quite rapidly along with other social changes that bring an increase in the status of women. Illustrative of such change in the 20th century in the United States, a meta-analysis of data from 1943 through 1999 showed extremely large shifts toward more sexual activity beginning at earlier ages, especially among girls, and considerably greater approval of premarital intercourse (Wells & Twenge, 2005). By 1999, the once quite different sexual behavior and attitudes of young men and women appeared to have become virtually identical.

If more modern data on parasite prevalence were not available, Gangestad et al. (this issue) might be justified in relying on old data. However, prevalence indicators contemporaneous with the dates of the mate preference assessments are widely available. In fact, Low (1994) included sources from the 1980s (e.g., Markel & Voge, 1981) in her cross-cultural analyses of pathogen prevalence, and she attempted to match the date of each culture's parasite data to the time period of the other data in her analysis.

The importance of coordinating the dates of the parasite estimates and the mate preference assessments is highlighted by evidence of the volatility of parasite distributions across the 20th century. Part of this instability comes from inexact assessments, given that early estimates of the prevalence of parasites often were based on informal assessments rather than on reports from national health agencies and other reliable sources.³ More important, the actual prevalence has shifted as the parasites have evolved and as events have transpired to increase or decrease their incidence. In recognition of the speed of adaptation of parasites and hosts, evolutionary theorists have posited the red queen hypothesis, suggesting that, like the red queen in Lewis Carroll's book, *Through the Looking Glass*, interacting species must evolve continuously to keep up, even in a constant physical environment (see Ridley, 1994).

³Several developments have increased the precision of estimates of parasite prevalence across world geographic regions. The accuracy of data has benefited from "sentinel" practices whereby general practitioners in many nations report the diseases that they have diagnosed, international agreements mandate the reporting of some diseases, and the World Health Organization (2004) systematically records the distributions of diseases (Cliff et al., 2004). Taking advantage of these improvements, the Global Infectious Diseases and Epidemiology Network database indexes 337 human parasitic and infectious diseases in 224 nations and updates these estimates weekly based on a range of sources.

Additional impetus for increased or decreased incidence comes from the changes in humans' and parasites' environment during the period from the early to the late 20th century. Reduction of parasites has been achieved during some periods in particular regions due to pesticides, population shifts, environmental manipulations, increased health infrastructure, and accessibility of drug treatments. In other regions at other points in time, parasite incidence has increased due to reduced financial support for eradication, loss of public health infrastructure, overpopulation, climate change, and evolution of parasite resistance to insecticides and drugs. For reviews of the multiple effects of human activity and climatic change on the epidemiology of parasitic zoonoses affecting humans, see Cliff, Hagggett, and Smallman-Raynor (2004), Gramiccia and Gradoni (2005), and Macpherson (2005).

The volatility of parasite data is evident in Cliff et al.'s (2004) comparative mapping of the incidence of malaria at the middle and end of the 20th century, especially in the considerable retreat of malaria from areas such as coastal South America and China. In addition, Gubler (1998) noted that four of the diseases in Gangestad et al.'s (this issue) analysis (i.e., filariasis, trypanosomiasis, leishmaniasis, and malaria) that are transmitted through blood-sucking anthropods such as mosquitoes were effectively controlled outside of Africa by the 1960s, largely due to insecticides. However, he also indicated that for a number of reasons these diseases reemerged in the next 20 years and reached epidemic levels in particular world regions. As another example of change, researchers in the Zhejiang Province of China reported a 72% reduction in the prevalence of 26 species of human parasites between 1987 and 1989 and 1998 and 1999 (Wu et al., 2001). This shift consisted of a decrease from an 80% infection rate to 23%, based on biological measurements of multiple samples of individuals. Given this considerable volatility of parasite infections, a valid test of the possibility that mate preferences are contingent on pathogens requires careful documentation of the prevalence in each world region contemporaneous with the timing of the assessment of mate preferences.

It is additionally interesting to note that Gangestad et al.'s (this issue) interpretation of pathogen effects may itself suffer from specification error because pathogen distribution and diversity are moderately strongly associated with latitude (Guernier, Hochberg, & Guégan, 2004). In Gangestad et al.'s data, these relations are represented by the correlations of pathogen prevalence with geographic region and latitude (see Appendix A). In general, parasitic and infectious diseases become more common and diverse at lower latitudes. The power of latitude as a predictor is due to various covarying bioclimatic factors. Investigation of a number of such variables within the database of the Global Infectious Diseases and Epidemiology Net-

work (2005) found that the best predictor of pathogen species distribution is the annual variation of precipitation around the mean (Guernier et al., 2004). Many pathogens appear to be adapted to climatic patterns of strongly contrasting wet and dry seasons, which are more common nearer to the equator. In addition, mean annual temperature predicted some groupings of pathogens, as did mean annual precipitation.

Given that climate is important to the diversity and occurrence of human pathogens and that the relevant climatic variables are correlated with latitude, we wonder how to interpret pathogen prevalence data controlled for region or latitude—the key proxy variables that represent the bioclimatic factors causally related to pathogens. Adding controls for latitude or region in the analyses in Tables 1, 2, and 3 does not make the pathogen predictor easier to interpret. Instead, the resulting pathogen variable represents the variability in early 20th century pathogen distributions that is not predictable from latitude. This analysis thus provides a classic demonstration of the partialling fallacy, and the results do not yield clear interpretation.

Conclusion

The analyses provided by Gangestad et al. (this issue) do not contribute meaningfully to the debate about the causes of mating preferences. The jukebox theory and ideas about contingently expressed dispositions, although advancing evolutionary psychology toward the recognition of cultural variation, fail to acknowledge the emergent quality of these preferences. These preferences reflect evolved physical attributes and psychological dispositions, including the uniquely human abilities that have fostered behavioral flexibility and enabled complex societies. Humans' evolved characteristics, together with their developmental experiences and situated activity in society, shape their mating preferences, including sex differences in these preferences.

Notes

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AUTHORS' RESPONSE

Toward an Integrative Understanding of Evoked and Transmitted Culture: The Importance of Specialized Psychological Design

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Nearly all commentators agree on several fundamental arguments of our target article: (a) Cultural and evolutionary views of behavior are complementary and integratable, not necessarily opposing, explanations; (b) cultural phenomena are produced by psychological adaptations; and (c) cultural variation results from an evolved psychology interacting with environments that humans both encounter and actively create. Our response strives toward a comprehensive, integrative, evolutionary perspective on cultural phenomena and emphasizes several themes also noted by commentators: (a) Psychological adaptations that underlie culture must be rigorously specified; (b) theories about these adaptations must be consistent with the fundamental tenets of modern evolutionary theory; (c) adaptations underlying culture will be many in number; (d) adaptations should be explored at multiple levels of analysis; (e) contemporaneous transmission processes are crucial for a complete understanding of culture; and (f) progress in understanding both evoked and transmitted culture, as well as the ways in which they interact, will hinge on increasingly specific scientific descriptions of "culture."

We are thankful for the eight thought-provoking commentaries on our target article and its topic, the evolutionary foundations of cultural variation. They are remarkable in many ways. The authors are highly accomplished within their respective fields and, indeed, have importantly contributed to the field's understanding of culture and cultural variation. Their disciplinary training and specializations span a broad spectrum—from mainstream social psychology to cultural psychology, from biocultural anthropology to core evolutionary psychology.

Yet nearly all agree on a few fundamental issues and themes. Most endorse the idea that cultural and evolutionary views of behavior are complementary and integratable, not necessarily opposing, explanations. Most believe that cultural phenomena have foundations in the evolutionary selection for human psycho-

logical adaptations. Most endorse the view that cultural variation results from evolved developmental and psychological outcomes interacting with environments that humans encounter and actively construct. The heartening level of consensus with these broad themes of our target article is remarkable given the historical resistance to evolutionary approaches. Indeed, the consensus among the commentators may signal a sort of culturally emergent, evolution-based leading theoretical edge in psychology and the social sciences.

The purpose of our target article was twofold. First, we argued for the broad thesis that evolutionary and cultural perspectives are not opposing explanations; an integrative approach is not only possible but required. Second, we argued for one important class of ways in which evolved adaptations lead to patterned, systematic variations in beliefs and practices across cul-

tures—the processes and products of evoked culture. We illustrated this approach by presenting theory and cross-cultural data on mate preferences.

Although most commentators agree that evoked culture is both important and worthy of further study, most commentators did not dwell on that topic (exceptions are Lieberman [this issue] and Schmitt [this issue]). Instead, most address the evolutionary foundations of cultural phenomena we fully acknowledged but did not address at length—transmitted culture and related phenomena (see the conclusion section of the target article). Norenzayan (this issue) argues that the evolutionary foundations of transmitted culture must be explained. Schaller (this issue) poses questions about links between evoked and transmitted culture. Kenrick (this issue) argues that evolved adaptations constrain the form of, but may not determine the precise shape of, cultural practices. Flinn (this issue) emphasizes that culture is an arena for social competition among individuals and coalitions, which generates novel cultural phenomena. Baumeister, Maner, and DeWall (this issue) consider the view that people not only create culture through adaptations but also have adaptations for culture (see also Schmitt, this issue).

In general, commentators challenge workers in the field to strive toward a comprehensive, integrative, evolutionary perspective on cultural phenomena—a level of consensus that augers well for future work in this field. Eagly and Wood's (this issue) commentary, by contrast, rejects the conceptual integration involving evoked culture.

Our response focuses on building an integrative view of the evolutionary foundations of culture. As most commentators argue, both the transmission and generation of novel cultural information have evolutionary foundations. We outline possible evolutionary origins of these phenomena. We further argue that these phenomena by no means exclude evoked culture. Empirically, phenomena of evoked culture clearly coexist with, and interact with, transmitted culture. More fundamentally, there are good theoretical reasons why specialized adaptations underlying transmitted culture do not override or replace the functions of specialized adaptations responsible for evoked culture. Only through understanding the evolved functions of the adaptations that underlie different cultural phenomena can we better predict the domains in which these phenomena will be found and how they interact with each other. Our arguments draw liberally on insights offered by commentators. We do not claim to present a fully developed, integrative view of the evolutionary foundations of culture. It is our hope, however, that our response meaningfully contributes toward that end.

The bulk of our response focuses on the interesting conceptual issues raised by the commentators. These include arguments that (a) psychological design underlying evoked culture must be rigorously specified, (b)

culture is not a unitary entity or phenomenon, (c) evolutionary foundations of transmitted culture are important for a comprehensive understanding of culture, and (d) evoked and transmitted culture are likely to be intertwined and ultimately must be examined within a unified theoretical framework.

To illustrate the concept of evoked culture, we presented data on cross-cultural variation in mate preferences as a function of pathogen prevalence and gender equality. The focus of our target article was, however, largely conceptual, not empirical. Arguments for how cultural variants may be evoked did not rest on this illustration, and, indeed, we discussed other examples in our target article and provide more in this response. Most commentators also focus on conceptual issues and say little about our illustration. The exception is that of Eagly and Wood (this issue), who dedicate much of their commentary to critiquing our statistical analyses. Near the end of our response, we address these criticisms.

Conceptual Issues in the Study of Evolution and Culture

Psychological Design Underlying Evoked Culture Must Be Rigorously Specified

Cultural variability reflects behavioral flexibility: Humans respond differentially as a function of their developmental and current environments. As Schaller (this issue) notes, however, merely stating this is “almost boring.” The interesting question is not whether people evidence contingent responsiveness but rather when, how, why, and in what particular ways they do (see Kenrick, this issue; Lieberman, this issue; Schaller, this issue; Schmitt, this issue). Addressing these issues comprehensively will ultimately require understanding the specific proximate mechanisms—genetic, developmental, neurophysiological, psychological—through which contingent responsiveness occurs. Many evolutionary processes can create adaptations that produce current behavioral flexibility. The psychological design of such adaptations can take many forms. It is not sufficient to say merely that human behavior is flexible, emergent, or “plastic,” a term we find misleading because of its connotations of infinite malleability. These claims are observations, not explanations. The science requires a specific account of the precise ways in which environmentally contingent responsiveness occurs. Our target article explicitly stressed this key point.¹

¹Though we stress adaptation here, some psychological features are byproducts of adaptation, not directly selected for themselves (e.g., Buss et al., 1998). Understanding of these too, however, requires an evolutionary perspective (e.g., Andrews, Gangestad, & Matthews, 2002).

Lieberman (this issue) reinforces and extends this theme. An adequate explanation of any organism's responsiveness to environmental contingencies, she states, demands "rigorous description of the kinds of cognitive programs and information-processing procedures involved in the production of behavior." "Learning," "socialization," and "neural plasticity" are not rigorous descriptions; they are mere "placeholders" that severely underspecify how inputs translate into behavior. She furthermore argues, as did we, that information-processing procedures that, theoretically, could effectively guide adaptive decision making and, empirically, account for adaptive behavior require systems specialized for particular domains of inputs and decisions. Evolution through natural selection is the only causal force known to lead to complex functional mechanisms. Cultural variants are products of functional psychological processes in interaction with environments.

One goal of evolutionary psychology, then, is to elucidate these psychological procedures through evolutionary functional analysis. Lieberman (this issue) discusses at length a particular research program—one examining the foundations of incest aversion—that nicely illustrates this approach. As she shows, after specifying a plausible psychological design that uses length of coresidence and witnessing maternal care as cues to siblingship, researchers were able to discover the association of these cues with sexual aversions and kin-directed altruism (e.g., Lieberman, Tooby, & Cosmides, 2003). A hypothesis stating merely that siblingship is learned is unlikely to have led researchers to these novel findings.

Lieberman (this issue) and Kenrick (this issue) specifically criticize social role theories, such as that of Eagly and Wood (this issue), for not rigorously specifying the processes underlying behavioral variation. In their commentary, Eagly and Wood argue that their "emphasis on humans' behavioral plasticity and the wide range of environments in which they can thrive does not suggest a blank slate so much as evolved dispositions that depend on social and environmental input for the form in which they are expressed in behavior." That is, they suggest, the procedures that individuals use to solve problems are not selected from a preset menu but rather "emerge flexibly from multiple influences, given humans' unique adaptation for culture," reasoning that "recognizes that human cultural traditions, unlike the cultures of other primates, accumulate contemporaneously and over historical time."

We are encouraged by Eagly and Wood's (this issue) increasing acknowledgement of the role of evolution and "evolved dispositions" in their explanations; they specifically appeal to notions that such evolved dispositions underlie transmitted culture (see Norenzayan, this issue). Nonetheless, their commen-

tary argues for a conception of culture and the processes that give rise to it that other commentators view as overly narrow, underspecified, and incompatible with modern evolutionary theory. Thus, Lieberman (this issue) states that

for bodily specializations (e.g., female specializations for childbearing and men's greater size and strength) to impact behavior in specific ways as Wood and Eagly (2002) suggest, there have to be information-processing procedures that use this information (e.g., time and energy costs associated with childbearing), integrate it with specific information from the environment ... and motivate certain behaviors over others (e.g., motivations for seeking a mate with resources). ... Oddly, social learning theorists that have voiced strong opposition to this perspective (e.g., Wood & Eagly, 2002) privilege differences in bodily specializations as direct causal forces in shaping mating behavior yet deny the causal role of parental investment theory.

Similarly, Kenrick (this issue) notes

Eagly and Wood resist considering how animals' brains and bodies tend to coevolve, so that where there is a structure, there is usually some programming to run it. They also resist considering the many parallel sex differences found in other species. ... they find it somehow preferable to yield as little ground as possible to a brain that does not operate like a Blank Slate ... male and female nervous systems are presumed [by Eagly and Wood] to operate in virtually identical ways as people absorb the culturally assigned roles their particular societies create around the external morphological differences.

See also Buss (1996).

Within the context of our target article's theme, evoked culture, a key way in which Eagly and Wood's (this issue) commentary is overly narrow is that it perpetuates mistaken either-or thinking by implying that the capacity for transmitted culture leaves no place for evoked culture. It was precisely our purpose to purge false dichotomies from thinking about culture. We—along with most commentators—disagree that evidence of one weighs against the existence of the other (see also Richerson & Boyd, 2005). Consider, for example, the effects of local selective pressures on birth weights. Through evolutionary analysis, Thomas et al. (2004) showed that, as mortality due to parasitic infections increases, optimal birth weight increases. As mortality due to poor nutritive conditions increases, however, optimal birth weight does not similarly increase. A comparative analysis across countries showed that birth weights in countries with relatively common parasitic infections are greater than expected based on nutrition and maternal size alone. This variation may be explained in terms of precisely

the kind of process captured by the concept of evoked culture: adaptive responses to local conditions. We cannot see how it is helpful or informative to explain these adaptively contingent responses (and their downstream effects on behavior) with statements that they “emerge flexibly from multiple influences, given humans’ unique adaptation for culture” (Eagly & Wood, this issue).

We can also consider an example of Eagly and Wood’s (this issue) own choosing, namely, food preferences. Eagly and Wood argue, “Humans ... learn what foods are available and healthful in their environments, and this learning is culturally shared. Food preferences are an emergent product of evolved dispositions and other influences *rather than* preprogrammed through evolution and merely contingently emitted in response to environmental conditions” (emphasis added to highlight the explicit either-or nature of their argument). Interestingly, Lieberman (this issue) uses this same domain—food preferences—to illustrate evoked culture. Billing and Sherman (1998) found that human groups living in hotter climates (where risk of ingesting pathogen-infected meat is more likely) also use more spices (plant products with strong flavors, e.g., those containing capsaicin), especially those effective at combating food-borne pathogens. They ruled out a variety of alternative explanations, including the possibility that spices are simply more available in hot climates. Spice use is not solely determined by availability. As some nonhuman species appear to “self-medicate” by ingesting pungent plant products with antimicrobial properties when ill (e.g., Clayton & Wolfe, 1993), adaptations affecting spice use in humans may phylogenetically predate the hominid line (e.g., Huffman, 1997), though the precise mechanisms underlying variation in preference for spicy foods remain unknown. Fessler (2003) discussed another example in this domain, that is, variation in salt appetite in offspring as a function of maternal condition, for which there is very good evidence that highly specialized mechanisms are involved (e.g., Morimoto, Cassell, & Sigmund, 2002).

Of course, these examples do not deny that diets are also affected by learning of taste aversions and the food preferences of others (e.g., through cultural transmission). Contrary to Eagly and Wood’s (this issue) either-or dichotomy, we need not and should not be forced to choose between these alternatives (see also Flinn, this issue; Schaller, this issue). Similarly, in our view, Eagly and Wood mistakenly ask us to choose between the alternatives that mate preferences are influenced by specific inputs to specialized systems (e.g., cues of parasite prevalence, factors affecting male and female productive activities) and the view that mate preferences are affected by broader social consequences (see also Schmitt, this issue).

Evoked Culture Is Not a Complete Explanation

Schaller (this issue) correctly notes that the need to specify evolved procedures that underlie evoked culture applies equally to phenomena that is purportedly the outcome of more general forms of learning. Patterned covariation between ecological conditions and cultural practices or beliefs is an observation. It must be explained. For the explanation to argue for evoked culture, the responsible mechanism should be specialized for particular inputs varying across relevant ecological conditions.

A mechanism need not be specified at the physiological level for one to offer a compelling argument for adaptive specialization. We concur with Lieberman (this issue) that procedures can be specified at multiple levels, and an important one from a functional standpoint is the algorithmic level—a specification of relevant inputs to the mechanism and decisions (outputs). The learning of food aversions involves procedures specialized for food aversions. Based on observations that conditioning to nausea is limited to particular kinds of stimulus features and temporal separations between stimulus presentation (food intake) and nausea, the evidence for specialization is overwhelming (e.g., Garcia & Koelling, 1966). Similarly, very specific patterning of inputs (e.g., coresidence with kin) and sexual aversion strongly suggests that incest avoidance is the outcome of a system of kin recognition and a system that regulates sexual aversion in response to those recognized as kin (Lieberman, this issue).

Although physiological evidence is not required to identify specialized psychological adaptations, evidence of specialized physiology can compellingly rule out some classes of explanations. Findings now powerfully demonstrate that female mate preferences, sexual fantasies, and patterns of attraction are affected by fertility as it varies across the ovulatory cycle (e.g., Gangestad & Thornhill, 1998; Gangestad, Thornhill, & Garver, 2002; Haselton & Gangestad, in press; Penton-Voak et al., 1999). These findings cannot be explained by learning of social roles, societal expectations, or forms of transmitted culture. Another fascinating example concerns men’s testosterone, which decreases predictably when they become fathers (e.g., Berg & Wynne-Edwards, 2001; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002; Storey, Walsh, Quinton, & Wynne-Edwards, 2000), a response that appears to facilitate prosocial responsivity to infants (Fleming, Corter, Stallings, & Steiner, 2002). These physiological findings provide powerful evidence of specialized psychological adaptation.

The data we presented on covariation between parasite prevalence and mate preferences constitutes *prima facie* evidence for evoked culture mediated by specialized procedures, as an alternative explanation is not ob-

vious. But what is the nature of such specialized procedures? What cues function as input? How are they operated on? These questions await future research, as do many questions concerning the specialized mechanisms that underlie evoked culture in other domains. We concur with Schaller (this issue) that inquiry into the roots of evoked culture “opens the door to an enormous world of scientific exploration.”

Evolutionary Foundations of Transmitted Culture

Although our target article fully acknowledged the importance of transmitted culture, and indeed provided an example of it and its potential interaction with evoked culture in the conclusion section, we focused primarily on evoked culture. We did so not because we privilege evoked culture as an explanation of cultural variation (cf. Norenzayan, this issue). The primary audience to whom we wrote our article is social scientists, who almost universally acknowledge important roles for transmitted culture. Most may also have little problem accepting the idea that psychological processes permitting transmitted culture are themselves evolved. We suspected that far fewer would be familiar with the arguments we presented—that cultural variation can originate through specialized adaptations designed for conditional outcomes—and hence we emphasized evoked culture.

We concur with Norenzayan (this issue) and several other commentators that forms of transmitted culture are important for evolution-minded theorists to explain. Although forms of transmitted culture exist in limited ways in other species (Perry et al., 2003), they pale in comparison to the tremendous human capacity for cultural transmission. People obviously learn vast amounts of knowledge, skills, and beliefs from talking to and observing others, whether through formal training or informal social interactions. Although some take these phenomena for granted, as scientists we should not. They no doubt occur only because humans have evolved psychological adaptations through which they can occur (Norenzayan, this issue). In this sense, there can be little doubt that humans possess specialized adaptations for culture, as proposed by Baumeister and Maner (this issue), Flinn (this issue), and Schmitt (this issue).

Just as other psychological adaptations demand precise specification and functional understanding, so too do adaptations for cultural transmission (Lieberman, this issue). It is not sufficient to say simply that people learn from other people. Evolutionary psychologists and anthropologists have dedicated much effort to specifying the nature of psychological adaptations for culture (e.g., Boyer, 1998, 2000; Henrich & Gil-White, 2001; Richerson & Boyd, 2005; Sperber, 1996). This area is far too expansive for us to summarize here.

Instead, we raise several key issues posed from an evolutionary perspective and sketch out possible theoretical avenues for exploration, with particular emphasis on the specialized psychological design underlying transmitted culture. We also argue that, from an evolutionary perspective, many psychological processes should be relatively immune to influence through transmitted culture. That is, in addition to adaptations for creating, transmitting, and receiving culture, humans also have adaptations for filtering, distorting, and sometimes entirely resisting certain forms of cultural transmission. The theme uniting our illustrations is that a complete understanding of transmitted culture requires an understanding of specialized, content-rich psychological adaptations.

Adaptation for sociality and social selection. Humans learn remarkably well through listening to and observing others. A key question to understanding human evolution concerns the selection pressures that led to these capacities. One possibility is that, as people increasingly occupied a “cognitive niche” (Tooby & DeVore, 1987)—relying on acquired information about local ecologies to hunt and forage a wide variety of foods across large ranges—the advantages to information transfer to kin increased, selecting for co-evolved capacities for language and social learning. Once these capacities began to evolve, information became an important commodity that individuals could exchange with others. Unlike many other commodities, individuals did not have to part with the commodity itself, hence limiting the cost of transferring benefits to others. These capacities may have thereby fueled the evolution of extensive forms of reciprocal altruism and mutually beneficial cooperation (e.g., friendship and “deep engagement”; Tooby & Cosmides, 1996).

At the same time, information transfer often carries costs for the giver. For example, information transfer can lessen competitive advantages over competitors and indeed render the transmitter vulnerable to certain forms of exploitation or attack by competitors. Conflicts of interests between information providers and recipients exist, and, therefore, the exchange and extraction of information should be governed by complex adaptations for nonkin social relations’—such as discrimination between friends and nonfriends, mind-reading of others’ knowledge states, and attempts to withhold information—sensitivity to level of reciprocal exchange. Once information became highly useful (e.g., because it facilitated foraging success), then adaptations for sociality also emerged and became increasingly complex, and transfer of information about other people became as common as transfer of nonsocial information. Flinn’s (this issue) commentary masterfully illuminates the process of social selection and the antagonistic coevolutionary procession of strategy, counterstrategy, counter-counterstrategy, and

so on, fueled by social selection. Cognitive capacities for acquiring and formulating useful ecological information and those for negotiating social relations need not be competing explanations for brain expansion in hominids; they should have coevolved.

Information exchange and niche picking.

Through social exchange, individuals with valued information accrue material advantages. Hence, once information became a useful commodity to be exchanged, selection favored individual capacities to originate it. One way that individuals could originate information was to create novel solutions to problems, such as more effective ways to catch local prey or attract a mate. Hence, selection favored innovation and technological development, which reinforced human occupation of the cognitive niche and further elaborated human social relations (see also Flinn, this issue). In nonhuman primates, social status is largely a function of dominance, the ability to get what one wants through use or threat of force. In humans, social status is also based on the ability to acquire and dispense informational resources—prestige (Henrich & Gil-White, 2001). Prestige, in turn, can for many people in many ecologies be maximized through specialization of task performance, not a “jack of all trades” strategy, leading individuals in many ecological settings to niche-pick and roles to be specialized, a theme emphasized by Baumeister and Maner (this issue). In sum, many aspects of human social systems can be understood as downstream, evolved outcomes that followed once humans occupied a cognitive niche.

Selective adaptive immunity to transmission processes. Despite the value of information acquisition through transmitted culture, we argue that humans have evolved adaptations in many domains of human contingent responsiveness that are designed to be relatively immune to learning through language-based transmitted culture. Not all human adaptive problems are most proficiently solved through innovation or acquired knowledge of novel solutions. Although it is ultimately an empirical issue, there are compelling theoretical reasons to believe that only a fraction of recurrent adaptive problems are solved through acquired knowledge of novel solutions. Many adaptive problems are solved by attention to particular cues that ancestrally recurred and served as reliable guides to adaptive decision making (e.g., Tooby & Cosmides, 1992).

In many of these cases, solutions based on transmitted information are, on average, poorer, not better, decisions. A very short list of likely candidates include who is my mother, my father, and my sibling? How can I avoid the maladaptive effects of close inbreeding? Which food is rotting? Which potential reproductive partners am I genetically compatible with? Which

women are fertile? Which individuals display cues correlated with being good coalitional allies, dyadic friends, or mates? Which potential reproductive partners might deliver “good genes”? Who are likely candidates of being infected with a contagious disease? Is my partner having sex with someone else? (e.g., Kenrick, this issue; Lieberman, this issue; Schaller, this issue). Selection should have shaped psychological systems evolved to solve these problems to be sensitive to problem-relevant privileged information only. Hence, some adaptations should be designed to be relatively closed to the outputs of processes involved in transmitted culture that have the potential for disrupting successful solutions to these adaptive problems.

In other cases, adaptations designed to receive and process culturally transmitted information should be highly selective, imposing frames and filters that accept some information and reject others. Consider information transmitted from parent to child. Because parents and children partially diverge in their reproductive interests (Trivers, 1974), it would be surprising if selection created adaptations in children to passively receive and accept all parental transmittals. Just as parents may have adaptations designed to manipulate a child to invest in his or her siblings in a manner maximally aligned with parental interests, children should have evolved adaptations to resist these forms of parental manipulation. (See Baumeister and Maner [this issue] and Schmitt [this issue] on such adaptations in response to culture.)

In an influential article, Zajonc (1980) argued that “preferences need no inferences.” People are often moved by gut-level feelings impervious to verbal, rational argument (e.g., a gut feeling that someone cannot be trusted may not be changed by arguments to the contrary). In this way, they are much like perceptions (e.g., perceptual illusions) that are not changed by rational reasoning (the moon really cannot be bigger when close to the horizon). Many of these gut-level feelings derive from specialized systems responding to information with privileged access to them, encapsulated from other systems. Indeed, Zajonc proposed that affective systems are phylogenetically older than and hence separate from language-based cognitive systems and even anticipated evolutionary psychologists’ arguments for instances of cognitive isolation in noting, “It was a wise designer who provided separately for each of these processes instead of presenting us with a multiple-purpose appliance that, like the rotisserie-broiler-oven-toaster, performs none of its functions well” (p. 170). Evolutionary psychologists go further in arguing that there are not two systems here (cognitive and affective) but rather many (on multiple emotional systems, see Tooby & Cosmides, 1990).

In sum, transmitted culture is undoubtedly important to an understanding of human cultural variability. As Norenzayan (this issue) argues, the existence of

transmitted culture demands evolutionary explanation. Though some important work has been done, the evolutionary foundations of cultural transmission remains an important area for further work—specifying precisely what selection pressures led to these cultural capacities, as well as precisely what information-processing adaptations these capacities entail. Some important discoveries, we suggest, will be made by discovering adaptations that selectively accept, reject, filter, or immunize other adaptations from the multiplicity of information to which humans are exposed from socially transmitted sources. An evolutionary perspective is required to address these questions.

Evoked Culture and Transmitted Culture Are Intertwined

Toward the end of our target article, we discussed ways in which transmitted culture and evoked culture may work in concert, using the example of explaining cultural differences in homicide rates by a combination of transmitted culture (values of honor transmitted from parents to children) that change thresholds for activating evolved psychological circuits for violence, thereby inducing evoked culture. Both Schaller (this issue) and Norenzayan (this issue) substantially develop this theme, suggesting other ways in which transmitted and evoked culture interact.

Because people live in communities in which information flows between individuals, evoked responses may nearly always affect information transmission. Hence, if people have a particular appetite for spices, spices get incorporated into diets and recipes, and these recipes get shared through cookbooks. Schaller's (this issue) point, however, is more profound than this. He suggests that people may have specialized adaptations for transmitting and receiving information pertinent to specific ecological features important to fitness. When infectious disease is present, it is adaptive not only to pay particular attention to cues of infection in others and minimize contact with individuals who are perceived to possibly be infected; it is also adaptive to communicate this information to offspring or friends and to receive it from them. These interesting ideas are consistent with a more general theme elaborated by Baumeister and Maner (this issue) and mentioned by Schmitt (this issue): People not only create culture; because they have been creating culture for a long time, people have specific adaptations to culture—that is, adaptations that function to receive and transmit cultural information in specialized ways (see also Richerson & Boyd, 2005).

Some of the processes Schaller (this issue) refers to require no elaborate forms of culture. Infant rhesus monkeys can readily learn to fear snakes (though not evolutionary novel dangers) based on single-trial exposures to fear reactions of their mothers to snakes (Cook

& Mineka, 1990). Similarly, adaptations leading individuals to pay attention to disgust reactions of others may function to glean important reliable information about social targets, particularly in pathogen-relevant environments (Schaller, this issue). Relatedly, Eagly and Wood (this issue) note that people's mate preferences can be influenced by the preferences of others. "Mate-choice copying" adaptations have evolved in many species, including ones with limited sociality, and can be selected whenever the reliability of information about others' mate qualities can be bolstered by information independently acquired by same-sex others (e.g., Gibson & Hoglund, 1992). The extent to which information expressed by others is useful may vary across domains, however, partly because emotional communication can be deceptive as well as informative. Schaller's commentary points to interesting avenues of research. Can the patterning of attunement to social information across domains and contexts be understood adaptively—that is, do the acts of others particularly inform individuals' own decisions when, ancestrally, those acts added fitness-relevant information?

Norenzayan (this issue) too notes the interdependent nature of evoked and transmitted culture. He asks whether we can possibly separate their effects. If spice-loving people move from one ecology to another, will their food preferences change in response to local conditions and they throw away their cookbooks? Or will they adhere to old recipes through processes of cultural transmission despite new ecological inputs? Norenzayan offers evidence that, at least in some instances, transmission processes maintain practices despite ecological change. In other instances, however, cultural change occurs remarkably rapidly. For instance, the Ache of Paraguay are highly renowned for their generous food-sharing patterns. Shares of meat acquired from kill of large game are distributed throughout the community. Yet when the Ache were put on reservations and established horticultural commons, free-riding problems and distrust of the communal system emerged almost immediately (Hillard Kaplan, personal communication, MONTH DAY, YEAR). More generally, if cultures were highly and reliably conserved through transmission processes, rapid cultural change, such as that witnessed in the U. S. over the past century, simply wouldn't occur (see Flinn, this issue; Norenzayan, this issue). As we discuss below, evolutionary perspectives may shed light on the impact of factors that enhance stability on the one hand and change on the other.

Culture is More Than Just Evoked or Transmitted: Dynamical Approaches to Understanding Cultural Phenomena

Flinn (this issue), Kenrick (this issue), and Baumeister and Maner (this issue) remind us that cul-

tural phenomena cannot be understood solely in terms of evoked reactions and exchange of information between individuals. Cultures consist of groups of individual agents interacting with one another. Individuals have both shared and conflicting interests. Individuals are evolved for group living and, hence, have psychological adaptations for furthering their own interests within group structures. Cultural phenomena must partly be understood as outcomes of dynamical interactions of individuals each acting in accord with these adaptations. Evolutionary dynamical approaches (Kenrick, this issue) use simulations to explore how group level outcomes emerge when individual agents with adaptive strategies are placed together with each other and allowed to interact. Kenrick, Li, and Butner (2003) provide several illustrations.

Consider a cultural phenomenon that appears to be universal—groups establish rules and customs of conduct and sanctions for not obeying these rules and customs; cultural practices become institutionalized. Rules often concern behavior central to fitness: who one can marry; who one can have sex with; who decides who will be marital partners; permitted and forbidden forms of violence and revenge; rules of inheritance; patterns of food sharing. Unlike transmission of technological culture, which occurs in forms in some other species, no other species has any element of institutionalized human culture (or rituals that reinforce these customs; Hill, in press). There is debate about the reasons people establish rules of this sort and have adaptations to be motivated by norms (e.g., Sripada & Stich, in press). One view states that inter-group conflict was important in human history (e.g., Alexander, 1987). Rule-making that solved coordination problems that arise when individuals with conflicting interests interact may have allowed some groups to succeed over others (e.g., Gintis, 2003).

There are many ways in which rules can solve coordination problems, however. A key question concerns the means by which rules get established. Individuals have unequal power to exert social influence (e.g., have differing amounts of prestige, dominance, and status, which lead them to have less ability to attract coalition partners). Some individuals' interests are shared with more group members than others. In theory, weighted effects of individuals exerting influence over rules and customs affect their outcomes. Despots who acquire enormous amounts of power, for example, establish rules unilaterally. Establishment of rules itself, then, must be seen as a dynamical outcome of individuals strategically acting in self-interest. Flinn (this issue) provides an interesting example. Kin (e.g., parents) have interests in individuals' (e.g., sons' and daughters') mating and hence may attempt to exert control over those decisions, particularly in arenas in which interests of "ego" and kin conflict. Kin can win out and establish rules not in ego's interests. For instance, in

matrilineal systems of inheritance, men pass material wealth to sisters' offspring rather than wife's offspring. This system virtually never benefits fathers' fitness. Under conditions of low paternity certainty, however, it may benefit paternal kin (e.g., men's parents and sisters; Hartung, 1985), whose influence may outweigh that of fathers. Indeed, Malinowski (1929) observed that male Trobriand islanders, who practice matrilineal inheritance, disliked having to pass on their belongings to their sister's sons; they preferred to give them to their own putative children.

Low paternity certainty and matrilineal inheritance tends to occur in particular ecologies (specifically, where fishing and horticulture are important sources of food, purportedly because foraging activities interfere with men's ability to guard mates; Hartung, 1985; see also Flinn, 1981). Here, then, may be a case in which aspects of evoked culture reverberate through the dynamical system that affects customs, leading to covariation between ecological factors and institutionalized components of culture.²

Culture Is an Arena for Competition and "Generated" Culture

In a fascinating essay, Flinn (this issue) argues that seeing culture as an arena for competition between individuals yields even more profound consequences. We argue above that selection operated on humans to innovate—to create ever better solutions to problems; effective innovators gained fitness advantages in an evolved, human social-cultural context (see also Baumeister & Maner, this issue). Flinn sees the most important informational arms races to be in the social arena. People apply their creative abilities not merely to solve technological problems; first and foremost, they do so to compete with others within a cultural context of minds interacting with other minds. Cultures accumulate novelty within their shared informational pools as people jockey to exert their influence over social contexts in their own favor. Cultural information is not merely transmitted, copied, or replicated in this

²Wood and Eagly (2002) noted that, whereas paternity uncertainty is associated with matrilineal inheritance of material wealth, associations with men's direct care of own vs. sister's offspring have not been detected (Gaulin & Schlegel, 1980). They claimed that paternity became important in human history only when inheritance of accumulated material wealth became an issue. That is, they argued that, contrary to the claims of evolutionary psychologists, men do not have long-standing adaptation to care about paternity (or, relatedly, sexual control of women). Eagly and Wood did not rigorously specify procedures whereby men, lacking any concern about paternity prior to introduction of accumulated wealth, learn to care about it once accumulated wealth gets passed down through inheritance. The reasoning above, we think, provides a more satisfying explanation. Inheritance rules can be dictated and controlled by kin against the interests of fathers. It's much more difficult, however, for kin to dictate which children fathers can spend time with.

process. It is creatively generated. Unlike traditional models of cultural transmission, which conserve and stabilize cultures through time (see Norenzayan, this issue), then, “generated” cultural processes can potentially fuel rapid social change.

We already discussed one arena in which coalitions of individuals may attempt to exert influence over social contexts—the establishment of rules, customs, and sanctions. Flinn’s (this issue) essay implies many others. Consider, for instance, an analogy to marketing strategies. Companies can sell products by fulfilling consumers’ needs. But they can also do so by manipulating the minds of others to create needs that they can fulfill. In a similar fashion, individuals can gain prestige by developing skills valued by others. But they can also do so by exerting their influence over what skills are to be valued, thereby creating social contexts in which their own skills give them a competitive advantage.

When coalitions jockey for influence in this way, the dynamics of the system can produce relative stability (e.g., when dominant coalitions have strategies that trump all potential counter-strategies of competing coalitions) or rapid change. Another way in which culture may be evoked is that system dynamics may depend on ecological circumstances (e.g., the means of production and individuals’ abilities to monopolize them; Flinn, this issue). Future modeling (e.g., Kenrick, this issue; Kenrick et al., 2003) and research may lead to better understandings of these dynamics.

Earlier, we argued that, despite novelty of information generated through innovation and cultural transmission, many adaptive problems should be solved through evolved psychological adaptations sensitive to privileged information, such that, at fundamental levels, information processing is not affected by the generation of novel culture. We reiterate that claim here. Though the precise ways by which individuals attain status, prestige, and influence may vary across cultures and dynamically change over time within populations, the effects of status and prestige on outcomes should nonetheless be at least partly a function of evolved psychological adaptations that respond to other individuals’ status and prestige.

Issues Pertaining to Statistical Analysis of Cross-Cultural Data

Eagly and Wood (this issue) claim that three flaws compromise our analyses and conclusions: the partialling fallacy, a small sample shortcoming, and use of an obsolete predictor. In all cases, their claims are mistaken or do not change our basic conclusions.

The Original Analyses Do Not Commit the Partialling Fallacy

The *partialling fallacy* (Gordon, 1968, 1987) can occur when one enters correlated variables into a regression analysis. The error is not a problem of inappropriate statistical procedures *per se*; it pertains to the *substantive interpretation* of results in the context of proper causal theory. Statistical results are not self-interpreting; their meaning is always embedded within, and requires proper specification of, theory.

The partialling fallacy can arise when an outcome is regressed on redundant measures of the same conceptual variable. Suppose a researcher interested in effects of socioeconomic status (SES) regresses an outcome on parental education and parental occupational status. As the effect of each measure holds constant another measure of the same conceptual variable (SES), neither effect can be interpreted as an effect of SES. A measure of SES with some aspect of SES held constant is not a good measure of SES.

Eagly and Wood (this issue) discuss a related problem. Suppose a theory says that A leads to C through an effect on B (e.g., $A \rightarrow B \rightarrow C$). Both A and B should covary with C. Because A affects C *only* through its effects on B, however, when B is partialled out, A should *not* predict C (e.g., Baron & Kenny, 1986). If one concludes that the theory is wrong because “A has no effect on C,” the results are improperly interpreted. A *does* affect C, though (as expected by theory) *only* indirectly through B. In the example from Gordon’s article Eagly and Wood discuss, age obviously affects sizing standards of clothing, but only through its mean effects on body size. When body dimensions are partialled out, age naturally has no independent effect on sizing standards.

The partialling fallacy does *not* arise automatically whenever predictors are correlated. Researchers have examined associations across species (or phylogenetic contrasts) between brain size and other features with body size controlled (e.g., Barton, 1999), despite a correlation between brain size and body size close to .9. If one’s interest is the effects of brain size *independent* of the effects of body size, controlling for brain size is called for, *and there is no partialling fallacy*. Indeed, *not* partialling out body size could lead to very misleading answers to the questions posed (see below).

We controlled for income, geographical region, and latitude in our analyses. We stated theoretical reasons for doing so. Eagly and Wood (this issue) nonetheless claim that we committed partialling fallacies by discussing at length reasons why income and region might affect and hence covary with gender equality. But these associations (which our data confirm; see fn 6) do not forbid control of these variables from analyses, just as the strong association between body size and brain size doesn’t forbid partialling out body size when examin-

ing effects of brain size. (Indeed, controlling for confounds is often a *good* idea.) Partialling fallacies involve misinterpretation of results due to improper theory. Did we “[fall] prey to” partialling fallacies (Eagly and Wood, this issue)? In fact, we did not.

Figure 1, panels a-d, presents 4 causal models of relations involving gender equality, region, and a sex difference.

In model a, gender equality and region tap the same conceptual variable, which affects the sex difference. The model is analogous to the situation with SES we describe above (Gordon, 1968). In model b, region mediates the association between gender equality and the sex difference. It is analogous to Eagly and Wood's (this issue) example in which body size is partialled out to examine the effect of age on sizing. If either model applied to our data, we may have committed partialling fallacies. But neither model does. Region is not merely another measure of the conceptual variable “gender equality” (model a) and gender equality cannot affect region (model b).

In models c and d, region affects gender equality, which affects the sex difference. They *are* appropriate to our data and capture precisely Eagly and Wood's (this issue) claim that we controlled “gender equality *for its determinants*” (emphasis added). But if model c holds, controlling for region is an error of minor consequence, not a partialling fallacy (see the following). And if model d holds, *not* partialling out region constitutes a serious error.³

The Multiple Ways to Commit a Specification Error

Eagly and Wood (this issue) repeatedly claim that we committed specification errors but do not define for readers what constitutes one. In econometrics, a specification error is committed when a researcher has not properly specified causal relations in a model and hence interprets results inappropriately (e.g., Kennedy, 2003). The partialling fallacy reflects just one kind. In multiple regression, two major kinds occur. One is *including an irrelevant variable*, one with no direct effect independent of other variables. If model c in Fig-

³If region were to predict gender equality near-perfectly, gender equality may have little opportunity to show effects, even if model c is right. For that reason, we examined overlap between measures. Region accounts for 48% of the variance in the GEM (see fn 5, 6) and, therefore, GEM varies considerably within region. Moreover, if model c is correct, associations between gender equality and sex differences should be stronger than those between region and sex differences (Baron & Kenny, 1986). As stated in footnote 6, however, on key sex differences we found the *opposite* pattern; region had stronger effects. Eagly and Wood (this issue) point to this footnote as evidence of our “simplistic regression logic,” which misses its theoretical analysis relevant to evaluating the nature of pertinent causal relations.

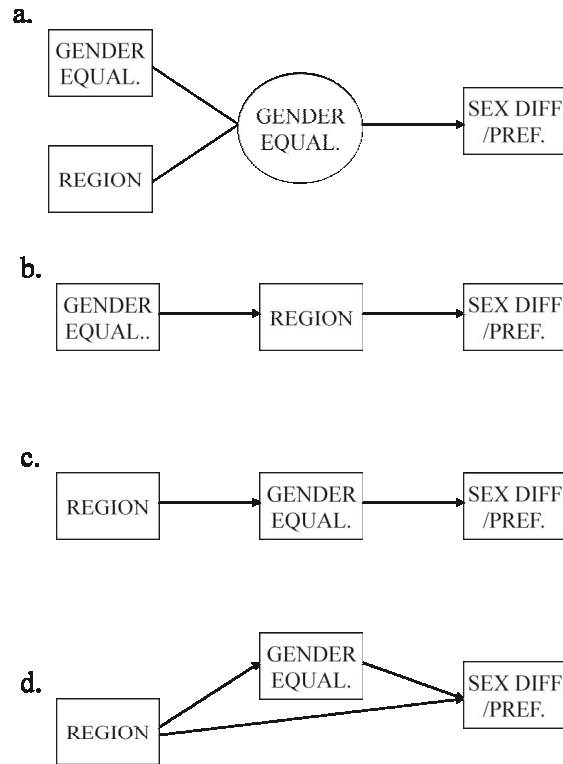


Figure 1. Four models of the associations between gender equality, region, and a sex difference in mate preferences (or a mate preference in general). (a) Gender equality and region tap the same conceptual variable affecting the sex difference. (b) The effect of gender equality on the sex difference is mediated by region. (c) The effect of region on the sex difference is mediated by gender equality. (d) An indirect effect of region on the sex difference is mediated by gender equality, but region has its own direct effect on the sex difference as well.

ure 1 is correct, region is an irrelevant variable. Regressing the sex difference on gender equality as well as region commits a specification error. Its cost, however, is not typically serious. Power to detect other effects is reduced somewhat. *But all effects are estimated without bias* (i.e., on average across samples, effect estimates are neither too high nor too low; e.g., Kennedy, 2003). In model c, therefore, *inclusion of region as a predictor does not bias the estimate of the effect of gender equality on the sex difference*.

Still, if there's a cost in power (even if no distortion in estimated effects and hence no partialling fallacy), why not drop region as a predictor and examine simple bivariate relations between gender equality and sex differences (e.g., Eagly & Wood, 1999)? The reason is that model d may be right. Here, region affects sex differences *independently* of gender equality. If model d is correct and region is ignored, another specification error is committed: *omitting a relevant variable* (one with effects independent of other predictors). *This error is much more serious than including an irrelevant variable*. Effects of other variables can be estimated very inaccurately and be badly misinterpreted. When not knowing whether a confound has an independent

effect, researchers often control for it, choosing to err by including an irrelevant variable rather than omit a relevant one, precisely because of the asymmetric costs of these errors.

We did not adopt this very conservative approach. Instead, we performed analyses in two stages. We first identified control variables with significant effects (on average, just one). We then ran analyses that included as predictors the main variables of interest, gender equality and parasite prevalence, as well as these control variables. As we included control variables *only* when it appeared they might have their own effects, we tried to avoid the serious specification error of omitting relevant variables while also minimizing retention of irrelevant variables. Though Eagly and Wood (this issue) claim our analyses (which control for different variables in different analyses) leave interpretation unclear, we do not see why. Their logic is straightforward (e.g., Neter, Kutner, Nachtsheim, & Wasserman, 1996). And, as variables that predict one mate preference may not predict others, controlling for different variables in different analyses makes logical and data-analytic sense. If readers prefer analyses that control for a fixed set of variables, however, the conservative strategy of controlling for all variables, whether significant or not, yielded nearly identical results (not surprisingly, as we included control variables only when they appeared to make a difference; see footnote 5).

In any case, which model is right, model c or d? As we noted, region had effects *independent* of other variables (including gender equality) on sex differences in preferences for financial resources, domestic skills, and status and striving. In broad strokes, Asians exhibited more traditionally sex-typed mate preferences. For *these* sex differences (the *only* ones we controlled for region), model *d* clearly fit. Ironically, while Eagly and Wood (this issue) argue that we committed specification errors by *including* region, in fact, *omitting* region as a control variable in these analyses entails specification errors.⁴

A deeper irony lurks here as well. In claiming we committed partialling fallacies, Eagly and Wood (this issue) effectively argue for model a—that region and income are measures of gender equality, with no interesting effects on sex differences or mate preferences independent of gender equality. Yet cultural psychologists have documented a variety of variations in the way peo-

ple in different cultures think and relate to one another (e.g., Eastern vs. Western cultures; Choi, Nisbett, & Norenzayan, 1999; Heine, 2001; Heine, Lehman, Markus, & Kitayama, 1999; Markus & Kitayama, 1991). These variations seem to be as important as variations in gender equality. Again, the main predictor of sex differences in mate preferences was not gender equality but, rather, a contrast between Asian and non-Asian cultures, a finding worthy of further exploration. A view of cultural variation that ignores these effects is simultaneously narrow and misleading.

The Estimated Effects of Pathogen Prevalence are Not Due to Specification Error

Eagly and Wood (this issue) also argue that partialling fallacies bias our estimated effects of parasite prevalence. Parasite prevalence varies by latitude and region (the amount of variance in parasite prevalence and gender equality shared with control variables being nearly identical; fn 5). Eagly and Wood wonder how controlling for these factors affect estimated effects of parasite prevalence. But there is no mystery here: No matter which model in Figure 1—b, c, or d—is correct (parasite prevalence replacing gender equality), the direct effects of pathogen prevalence are estimated without bias (Kennedy, 2003).

Small Sample Limitations

Eagly and Wood (this issue) draw attention to our small sample size—37 countries. Small sample size obviously compromises power. Our inclusion of control variables lowered power as well. By a formula they present, we lacked 80% power to detect moderate associations between predictors in a multiple regression and outcomes. This formula is actually wrong; it pertains to the *multiple correlation* for all predictors, which we did *not* test, rather than to the *partial correlation* for a single one (Green, 1991). The correct formula shows that, to retain equivalent power, one must add just one case for each variable partialled out. Eagly and Wood (1999) analyzed the data we analyzed. We sacrificed some power by partialling out control variables but compensated by using a liberal alpha (.10). Whereas Eagly and Wood (1999) had 80% power to detect a correlation of .45, on average we had 80% power to detect a partial correlation of .43. If we included irrelevant variables, partial correlations would have been slightly lower than zero-order correlations, leading to somewhat lower power—but, as we just argued, our procedures were unlikely to retain irrelevant variables. We see no reason to favor slightly more powerful but misleading simple bivariate analyses over our analyses.

Our target article recognized that undetected effects of the GEM and GDI on sex differences could be due to

⁴Of 16 total analyses (8 for overall preferences, 8 for sex differences) region was controlled in 8, income was controlled in 5, and latitude was controlled in 4. Details available upon request.

Income was retained in just two analyses on sex differences, preferences for Interest in Children and Physical Attractiveness. When it was excluded, GEM's effect on sex differences in preference for Physical Attractiveness became significant (at $p < .10$; b rose to .52), with increased GEM predicting *greater* sex differences. Excluding income does not lead to results more favorable to Eagly and Wood's (this issue) theory.

low power. Nonetheless, theories about gender equality should expect effects to generally be in predicted directions. They were not. Across 4 predicted sex differences (financial prospects, domestic skills, physical attractiveness, and age [keyed so that theory expects positive effects]), the GEM and GDI had mean effects of .13 and -.15, respectively, with a grand mean of -.01. The mean effect on principal components of sex differences was -.15 (Table 3, target article). As we discussed, perhaps theories about the effects of women's productive activity will fare better when tested on data from foraging societies (e.g., Marlowe, 2003; see also Flinn, this issue).

Purported Problems With Our Measure of Parasite Prevalence

Lastly, Eagly and Wood (this issue) question our reliance on parasite prevalence estimates from the mid-20th century rather than current estimates. Though raising interesting points (see below), this criticism does not explain away our findings.

Gangestad and Buss (1993) used past parasite prevalence estimates because (a) parasite prevalence may affect people's mate preferences concurrently or over a course of development; participants in the 37-culture study were run in the mid-1980s but born in the 1960s; (b) evoked and transmitted culture are not independent (Norenzayan, this issue; Schaller, this issue); cultural change may lag change in parasite infestation. Parasite prevalence *did* predict various mate preferences, which could reflect early developmental effects or cultural lag. But another explanation is possible. Our parasite prevalence measure would no doubt covary strongly with current prevalences. As Eagly and Wood (this issue) note, the parasites we considered are found in wet, tropical regions. That was true in 1950—and in 1980. Either past or concurrent parasite prevalence could drive the effects we reported.

Future research may address whether past or current parasite stress better predicts mate preferences. Given rising interest in the effects of mortality risks on human development and psychology (e.g., Thomas et al., 2004), researchers may develop measures of parasite prevalence better than our own. Experiments that manipulate effects of perceived threat of contagion (e.g., Schaller) may augment cross-cultural studies.

In sum, Eagly and Wood's (this issue) methodological criticisms are misaimed. First, we did not commit partialling fallacies. Second, low power cannot explain the pattern of effects of gender equality on sex differences in mate preferences. Third, the question of whether past or current parasite stress better predicts mate preferences is interesting, but Eagly and Wood's criticisms of our measure do not explain away our findings. We appreciate their commentary and the continued discussion about the evolution of mating psychol-

ogy, but the basic conclusions drawn from the analyses in the target article remain unchanged.

Conclusion

We are impressed by, and grateful for, the many insights provided by the diverse collection of commentators. Taken together, we believe that the target article, the commentaries, and this response to the commentaries help to provide scaffolding for understanding the evolutionary foundations of culture. This scaffolding includes evoked culture, transmitted culture, and the specialized evolved psychological mechanisms involved in these critical processes. It's an exciting time in science to be working at the interface of evolutionary psychology and culture.

We believe future progress in this area will depend critically on several avenues. First, theoreticians must rigorously specify the evolved psychological adaptations that underlie both evoked and transmitted culture, as several of the commentators point out. Nebulous concepts such as "learning," "socialization," and "plasticity" fail to provide that rigorous specification.

Second, theories about the nature of psychological adaptations that underlie evoked and transmitted culture must be consistent with the fundamental tenets of modern evolutionary theory. They cannot assume that individuals are passive receptacles of social or cultural information. They cannot assume unity of interests of individuals within cultures. And they cannot assume that male and female minds are essentially identical in domains in which they have recurrently confronted different adaptive problems over deep time.

Third, we anticipate that the discovery of the psychological adaptations underlying evoked and transmitted culture are likely to be many in number, and at least some (we believe many) will be specific in nature. Contrary to some views, the existence of specialized adaptations does not imply "rigidity." Nor is "constraint" the best metaphor. A bird's wings "enable" it to do something it could not otherwise do without these adaptive specializations—to fly. Similarly, multiple specialized psychological adaptations *enable* humans to respond flexibly and contingently to varying cultural input in functional ways that would not be possible without those adaptations. We envision in the future the discovery of many psychological adaptations dedicated to processing and responding to the tremendous volume of cultural information found in our intensely social species.

Fourth, we anticipate that scientists working in this area will increasingly explore psychological adaptations at multiple levels of analysis. These include an information-processing description (see Lieberman), as well as genetic, neuron-physiological, and developmental descriptions. They will also include increasingly precise descriptions of the statistical structure of

social and ecological information. Single investigators, of course, cannot be expected to perform all of these tasks. We envision that different investigators or teams of investigators, working at different levels of analysis, will contribute in a cumulative fashion.

Fifth, although we focused primarily on evoked culture in the target article, we concur with many of the commentators that transmitted culture is extremely important. In this context, we anticipate discovering that some domains will yield rich repositories of transmitted culture. We also anticipate that other domains will show adaptive immunity to transmission processes. Where the statistical structure of ancestral cues created reliable guides over the long expanse of human evolutionary history for the successful solution to adaptive problems, openness to socially transmitted information could be adaptively disruptive. In other cases, we anticipate that adaptations designed to receive, process, and transmit cultural information will be highly selective. Psychological adaptations will impose frames and filters that preferentially accept some information, reject other information, and distort in a systematic manner yet other information. Some adaptations will show design for adaptively biased social transmission. The field is merely at the beginning stage of discovering the psychological adaptations involved in transmitted culture, and we look forward with excitement to discoveries in this area.

Sixth, we propose that progress in understanding both evoked and transmitted culture, as well as the ways in which they interact, will hinge on increasingly specific scientific descriptions of "culture." Some theoreticians use the term "culture" as though it were a unitary entity, and we may have been guilty of this at times as well. Culture, however, is not a "thing" with singularity; it's an umbrella concept subsuming a collection of extraordinarily varied phenomena, each of which requires scientific analysis. A novel method of tool making, for example, is a different sort of cultural phenomenon than social gossip about the sex lives of leaders or religious beliefs about the nature of deities. Progress in understanding evoked and transmitted culture will require specifying the precise cultural phenomena requiring explanation, rather than treating culture as a unitary entity. We believe that this movement toward a finer-grained analysis of cultural phenomena will aid the discovery of the psychological adaptations underlying their evocation and transmission.

Note

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