

Biosocial Perspectives on the Family

COURTSHIP AND MATE SELECTION

Among the most fascinating—but also puzzling—recent findings are those that suggest an association between a basic feature of the immune system and the process of selecting a mate. Immunologists long ago identified basic features of our cells that enable the immune system to recognize self versus other and subsequently eliminate potentially damaging molecules it determines as other. The basic feature of this part of the immune system is proteins found on cell surfaces called human leukocyte antigens (HLA) or the major histocompatibility complex (MHC). Put simply, the MHC defines for each person a unique “immunological fingerprint.” Recent findings suggest that interpersonal cues signal information about individual differences in MHC. Humans can detect individual differences in odors (sweat) associated with MHC, which influence decisions regarding mate selection and perceived attractiveness (Wedekind,

Seebeck, Bettens, & Paepke, 1995). In other words, mate selection might be influenced by olfactory or other cues that signal immunological differences. The greater the immunological differences, the greater the chances of producing a viable infant. Inbreeding avoidance may be the most important function of MHC-associated mating preferences (Potts, Manning, & Wakeland, 1994). Studies of mice suggest that MHC preferences come about through imprinting (Yamazaki et al., 1988). Infants learn how their own MHC type smells, and evolutionary forces have evolved a preference for dissimilar types.

It is of interest that scores of studies find behavioral and social similarity important to understanding mate selection. Winch, Ktsanes, and Ktsanes's (1954) theory of complementary needs never received much support (e.g., Udry, 1964). The MHC studies draw family scholars back to exploring complementarity, albeit in a different form, as an explanatory variable.

This preference for immunological differences would certainly help to explain mate selection studies of Kibbutz marriages and Chinese arranged marriages. Shepher (1971) studied mate selection in Israel Kibbutz where from the time of birth, children were raised in child-care facilities. Parents saw them a few hours a day, but most of the time they were with the care providers and other children. Shepher observed that, upon reaching adulthood, individuals never married someone from the same facility. Wolf (1995) studied arranged marriages in China that took place in the early part of this century. Marriages were often arranged when children were very young. In some communities, the female child would go to live in the male's home where she was treated as one of the children. In other communities, the female remained with the birth parents until mature, whereupon she moved to the male's family. Compared with those who did not reside together until maturity, the couples who lived together as children had unsuccessful marriages. Many were never consummated, and few had children. Men were consistently unfaithful and had children with mistresses. For MHC preferences to be the explanatory mechanism in these studies, we would need evidence of imprinting (akin to the mouse studies) to explain the rejection of kibbutz-mates and sons of foster families.

Family researchers should find this work of interest not only because of its relation to mate preferences and incest avoidance, but also because of its relation to birth outcomes. For example, HLA

similarity has been associated with repeated spontaneous abortions (Thomas, Harger, Wagener, Rabin, & Gill, 1985), and lower birth weight (Ober et al., 1987).

Students of contraceptive use also will find the HLA studies of interest. Estradiol reduces women's ability to discriminate immunological differences among potential mates. High estradiol may be found among pregnant women and women on "the pill." A modern contraceptive method may be resulting in poor mate selection from the standpoint of producing children who are less likely to survive. The inability of these women to detect appropriate mates may affect the stability of courtship relationships. Cohabiting pill users have significantly higher rates of union dissolution (controlling for a wide assortment of suspected covariates) than other nonhormonal-based contraceptors (Carver, 1998).

Developments in another line of research bear watching because of their relevance to mate selection. Faces judged to have above average symmetry are regarded as more attractive. Facial symmetry may be associated with greater immunological competence and increased gene variation, which means that mating with such individuals would increase the chances of infant survival (Gangestad & Buss, 1993; Gangestad & Thornhill, 1998; Grammar & Thornhill, 1994; Mitton, 1993; Thornhill & Gangestad, 1993). Preference for masculine facial features has been observed to vary during the phase of the menstrual cycle. When conception is most likely, women prefer less masculine faces than during the rest of the menstrual cycle (Penton-Voak et al., 1999). The masculine faces may signal immunological competence, whereas the less masculine faces may indicate paternal interest and investment in offspring. Gangestad and Simpson (in press) integrate these findings into a theory that suggests women vary their reproductive strategy according to the harshness of the environment. When the environment is difficult, women place more weight on indications of genetic fitness than they do when the environment is less demanding. How these findings, if borne out by subsequent studies, would play out in mate selection or extra-pair sexual relationships is deserving of study.

The integration of measures of basic features of the immune system into mate selection and courtship research serves to increase understanding of incest avoidance, contraceptive use, and unstable courtship relations as they relate to the evolutionary need to produce viable offspring.

RELATIONSHIP QUALITY AND STABILITY

Testosterone's links to marrying and divorcing are considered first, followed by reports of research on the relationship between marital quality and testosterone. Genetic influences on divorce are considered, as is the association between marital conflict and immunity.

Marital Status

In the preceding section, several biological mechanisms were suggested that may define marital relationship quality and stability. Insight is obtained from evidence that testosterone levels in men drop after they marry. In a 10-year longitudinal study of Air Force officers who underwent four physical exams over that period of time, Mazur and Michalek (1998) were able to compare changes in testosterone with changes in marital status. Unmarried men's testosterone levels were high, but following marriage, they decreased. One scenario is that single men are mostly in the company of other men, and everyday competition (some of which may be over women) keeps testosterone levels elevated (e.g., Booth, Shelly, Mazur, Tharp, & Kittok, 1989). Once married, exposure to other men declined, and the need to compete for women disappeared. Another scenario is that the marriage itself lowered testosterone—similar to what was observed after the birth of an infant. Wives expect men to behave in supportive and nurturing ways, and lowering testosterone may be crucial to successfully enacting the caring spousal and parent roles. Alternatively, biological messages (e.g., pheromones) having to do with sex or reproduction may cause testosterone to decrease.

Relationship Quality

Even though marriage is accompanied by a drop in testosterone, hormones may still be related to marital quality. An analysis of men from a representative sample of 4,462 former military servicemen between the ages of 33 and 42 showed that men with higher testosterone production were less likely to marry in the first place; once married, they were more likely to divorce (Booth & Dabbs, 1993). The likelihood of never marrying was 50% higher for men whose testosterone levels were one standard deviation above the mean compared with those whose testosterone levels were one standard deviation below the mean. Similarly, men at the higher level were 43% more likely to

divorce than were those at the lower level. Once married, men with higher testosterone levels were 31% more likely to leave home because of a troubled relationship with their wife, 38% more likely to have extra-marital sex, and 13% more likely to report hitting or throwing things at their spouse. In addition, high-testosterone men were more likely to report low-quality marital interaction, a finding supported by Julian and McKenry (1989). These findings were net of other social variables such as low socioeconomic status or deviant behavior in other arenas. It is important to note, however, that substantial numbers of men with high testosterone had excellent marriages. The mechanism that explains this differential marital success is unknown. There is also the caveat that cross-sectional studies do not clarify whether conflictual marriages raise testosterone.

On the other hand, marriage does play a protective role with respect to the link between testosterone and antisocial behavior and depression. Men with high testosterone levels are at risk of committing a crime and being depressed. Marriage, along with steady employment, reduces the likelihood of both (Booth, Johnson, & Granger, 1999; Booth & Osgood, 1993). Because these studies are based on cross-sectional data, it is not possible to estimate the causal ordering of the variables. The work of Mazur and Michalek (1998) and Gubernick, Worthman, and Stallings (1991) has suggested that marriage may reduce the likelihood that high-testosterone men commit crimes and get depressed. The nature of the mechanism is unclear, however.

We know little about hormones and women's marriages. Having low levels of testosterone may be important to relationship quality, or quality may be associated with hormones associated with reproduction, such as estradiol or oxytocin. Equally important is dyadic research on marital partners to see how hormone-behavior links in one individual are related to hormone-behavior links in the spouse.

Genetics and Divorce

Given that divorce rates are so consistent from society to society (Goode, 1993), it is not surprising that a number of studies have shown genes to influence divorce. Estimates of the heritability of divorce have ranged from .26 (Turkheimer, Lovett, Robinette, & Gottesman, 1992) to .53 (Jockin, McGue, & Lykken, 1996; McGue & Lykken, 1992). Jockin et al. (1996) hypothesized that per-

sonality traits play a key role. They demonstrated that between 30% and 42% of the heritability of divorce risk comes from genetic factors affecting personality. This finding is supported by a study of the association between parent and offspring divorce indicating that behavior problems mediate a significant share of the link (Amato, 1996). Analysis is needed that combines methods used by family researchers (survival analysis) with behavior genetics methods to explain the genetic mediation of divorce (e.g., Meyer, Eaves, Heath, & Martin, 1991).

The consequences of divorce for children may also have genetic origins. In a large-scale study of divorce, Block, Block, and Gjerde (1986) and Cherlin and colleagues (1991) both demonstrated that boys' elevated risk for behavior problems observed after divorce disappeared when behavior problems many years before divorce were controlled. Although Cherlin, Chase-Lansdale, and McRae (1998) demonstrated in a later study that the gap between children from divorced and non-divorced families widened as children moved into young adulthood, there remains a significant amount of unexplained variance. It is possible that the behavior problems of the boys before and after divorce are related because of underlying enduring personality characteristics and not because a high-conflict marital relationship generates the problems. This is an example of a finding that could be greatly informed by including a genetic component in the study.

Marital Conflict, Immunity, and Health

Data from large epidemiological studies suggest that poor personal relationships are a major risk factor for morbidity and mortality (House, Landis, & Umberson, 1988). The search for mechanisms has revealed substantial evidence regarding the role of immune function. Kiecolt-Glaser, Glaser, Cacioppo, and Malarkey (1998) demonstrated that abrasive marital interactions have important endocrine and immunological correlates. In general, marital separation or divorce, higher marital conflict, and lower marital satisfaction are associated with lower immune function. Such stress-related immunological changes may be a pathway through which close personal relationships influence health (e.g., infectious diseases, cancer, wound healing).

Testosterone is related to poor union quality and stability, as are genetic influences. In contrast, evidence that environmental factors influence hor-

mone levels involves the finding that testosterone declines when men marry. Marital conflict and instability may compromise the immune system, which in turn affects health.

**Evolutionary Foundations of Cultural Variation:
Evoked Culture and Mate Preferences**

Steven W. Gangestad¹, Martie G. Haselton², and David M. Buss³

¹Department of Psychology, University of New Mexico, ²Communication Studies and Department of Psychology, University of California at Los Angeles, and ³Department of Psychology, University of Texas at Austin. E-mail correspondence: sgangest@unm.edu

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

Running Head: EVOLUTIONARY PSYCHOLOGY AND CULTURE

7/11/2005

Abstract

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.

Environmental Contingency in Mating Strategies

The heuristic value of the evolutionary approach is illustrated by work on non-human 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, (1) females whose social mates have relatively small forehead patches are particularly likely to engage in extra-pair copulations (Sheldon et al., 1999), (2) females tend to seek extra-pair matings when they are most fertile (Michl et al., 2002); (3) 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 et al., 1997); (4) the offspring of males with large forehead patches tend to be male, the sex that most benefits from having such a sire (Ellegren et al., 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, Gangestad, Miller, Scheyd, McCollough, & Franklin, 2003), more masculine faces (Johnston et al., 2001; Penton-Voak et al., 1999, Penton-Voak & Perrett, 2000), and male behavioral displays of social presence and intrasexual competitiveness (Gangestad, Simpson, Cousins, Garver, & 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: (1) 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 non-fertile phases (Gangestad et al., 2002; Haselton & Gangestad, 2005); (2) 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); (3) When women particularly value investment in a relationship from a man, they may prefer less masculine faces (Penton-Voak, 2001); (4) when women pursue a short-term mating strategy,

they show an elevated preferences 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 socio-ecological circumstances in which women should

particularly value male relationship investment, they may prefer less masculine faces; where investment is not especially valued, or where 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 have 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) have 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 adult male 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 9 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).

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

¹ Broader samples of cultures (such as the widely used 186 culture Standard Cross-Cultural Sample [SCSS]) include societies with more developed forms of agriculture, which may be less relevant to an understanding of human societies prior to the last 10,000 years. Nonetheless, estimates based on them are similar: 65% in the SCSS (Schlegel & Barry, 1986); 65% in a broader sample of 499 societies (Sanday, 1973). Wood and Eagly (2002) cite 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 (1975), which reports a grouped relative frequency distribution of female contribution to subsistence across all 862 societies, implies a *possible* range of 33–42% 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; 2001) have 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) argue that these male activities have been shaped by selection to partly function as parenting effort. As Hawkes et al. (2001) acknowledge, 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 male 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.

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 (1986) 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 relationships between indices 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 analysis is also consistent with Eagly and Wood's recent findings that the sex difference in mate preferences for resource control varies with women's relative empowerment (Eagly & Wood, 1999; also see Kasser & Sharma, 1999). The United Nations publishes two indices used by Eagly and Wood (1999) 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/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, where 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; also see Buss & Barnes, 1986) explained these findings largely in terms of social roles. In a subsequent paper, 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 propose 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, p. 702). 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, p. 702; see also Eagly & Wood, 1999, pp. 412-413). 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 hypothesis and Wood and Eagly's 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 suggests that different cultural practices will be evoked by different ecologies: Means of economic production affect sexual division of labor, which thereby affect cultural practices. Low's hypothesis is that humans possess domain-specific adaptations that adjust mating behaviors depending on environmental cues linked with differential fitness payoffs in ancestral environments.

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

² One difference between these indices 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.

Mate Preferences and Parasite Prevalence

Parasite threat. Pathogens pose threats to the health of any long-lived organism. While 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 30-50% 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, etc.) 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

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 male is more desirable than becoming the first mate of the most attractive available unmated male (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

³ Rhodes, Zebrowitz, Clark, Kalick, Hightower, & McKay (2001) examined the association between components of physical attractiveness (averageness and symmetry) and actual health records and found few relationships. 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.

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 cultures study may be associated with mate value.

These predictions are as follows:

1) *Current health.* Signs of current health may indicate low current parasite load and high parasite resistance; hence health should be preferred more in parasite-prevalent environments.

2) *Good heredity and robustness.* Likewise, signs of physical robustness or a family history thereof may indicate low current load and high resistance; hence they should be preferred more in parasite-prevalent environments.

3) *Intelligence and intrasexual competitive abilities.* Low (1990a) argued that sexual selection increases in pathogen-prevalent environments; male reproductive success in particular should vary more in such environments. Increases in sexual selection may increase male attempts to display good condition through successful intrasexual competition. Work using fluctuating asymmetry as a marker of developmental health (asymmetry due to imprecision of development due to perturbations caused by disease, mutations, and toxins) has shown that male social dominance and intelligence are associated with good developmental health (see Gangestad & Thornhill, 1997). In parasite-prevalent environments, intellectual abilities may be compromised by parasites (e.g., Watkins & Pollitt, 1997) and, hence, male intelligence and intrasexual competitive abilities may be particularly valued in pathogen-prevalent environments (see Miller,

2000, for additional arguments for the importance of intelligence as an indicator of pathogen-resistance).

4) *Paternal investment*. Mate selection often, if not always, requires tradeoffs. If men are valued for their health because it signals heritable ability to resist pathogens (e.g., as revealed through intrasexual competitive abilities and intelligence), women may compromise their desire to have a mate who is highly investing in offspring for access to a higher value mate (Gangestad & Simpson, 2000). (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).