Context-specific mate choice criteria: Women's trade-offs in the contexts of long-term and extra-pair mateships

JOANNA E. SCHEIB University of California, Davis

Abstract

Women's mate choice criteria were examined experimentally in the contexts of long-term and extra-pair mateship scenarios. In long-term mateships, women may benefit by pairing with males who provide material resources and assistance in child rearing. In contrast, in extra-pair mateships, women may benefit in other ways, with such benefits outweighing the potential costs imposed by a primary mate who discovers the relationship. One benefit, or evolutionary function, of extra-pair mateships may be to replace a primary mate, in which case mate preferences should look similar across long-term and extra-pair contexts. However, another function of extra-pair mateships may be to obtain high quality gametes (i.e., "good genes"), in which case women should be differentially attracted to cues of heritable phenotypic quality, such as physical attractiveness. By using detailed verbal and pictorial descriptions of men and requiring participants to trade off physical attractiveness for good character (i.e., being a good cooperator and parent), it was possible to determine whether women's criteria for partners varied across experimental contexts. Findings suggest that extra-pair mateships may have served the evolutionary function of obtaining "good genes," because attractiveness was more important in extra-pair mateships to the detriment of good character. This effect was maintained even when characteristics of the female participants (age, parity, marital experience) were covaried. In addition, the preference for physical attractiveness was specific to the sexual context; it did not generalize, in a second experiment, to choices among short-term male coworkers.

An analysis of mate choice in humans must include not only how and why humans choose long-term mates, but also how and why they choose extra-pair partners. Evolutionary research on mate choice initially focused on general preferences for and choices of a mate, with many studies investigating the differences between women and

Address correspondence to Joanne E. Scheib, Department of Psychology, University of California, Davis, CA 95616. E-mail: jescheib@ucdavis.edu.

men (see reviews in Batten, 1992; Betzig, 1997; Buss, 1994; Cashdan, 1996; Cunningham, Druen, & Barbee, 1997; Ellis, 1992; Gangestad & Simpson, 2000; Miller & Todd, 1998; Thornhill & Gangestad, 1996). Later work called attention to variation in mate preferences due to additional factors, such as the duration of the relationship. In these cases, researchers contrasted preferences for short-term mates (e.g., dates, one-night stands) to those for long-term mates (e.g., spouse) (e.g., Buss & Schmitt, 1993; Kenrick, Sadalla, Groth, & Trost, 1990, 1993; Landolt, Lalumière, & Quinsey, 1995). One assumption underlying all of this work was that the individuals did not already have a relationship partner and thus were making decisions about in-pair mates. Most recently, a number of studies have focused on choices for extra-pair mates, where one or

This work was supported by the CIBA Foundation and the Social Sciences and Humanities Research Council of Canada. The author thanks K. Weimer for assistance with data collection, K. Eva for assistance with data entry, and M. Wilson, S. Gangestad, M. Daly, P. Shaver, and K. Widaman for discussion of the ideas and helpful comments on an earlier version of this article. The author is also grateful to J. Simpson and three anonymous reviewers whose comments also helped improve the article.

both of the participants already have longterm mates. In this article, I examine women's preferences for extra-pair mates in light of two hypotheses about the evolutionary function of extra-pair relationships: mate replacement and the acquisition of high quality gametes.

An evolutionary or functional analysis of adaptive problems, such as choosing the "optimal" mate, entails the characterization of contingent responsiveness of the female to attributes of males and to other factors such as the female's alternative reproductive options. For example, a female who preferred good health in a potential mate would out-reproduce females who did not have this preference, if healthiness conferred a survival advantage to offspring. If the preference for signs of good health had a heritable basis (e.g., a perceptual-visual and olfactory-preference for clear skin over infected sores), then over many generations a greater proportion of individuals would have this preference, and it would become part of the psychological decision-making machinery involved in choosing mates.

What mate preferences would benefit a woman in the sense of increasing her reproductive success? When viewed *functionally*,¹ the goal of a mateship is to produce and rear offspring to independence, a task that requires substantial parental invest-

ment (Lancaster, 1991; Lancaster & Lancaster, 1983). Thus, a woman should prefer attributes in a mate that will contribute to this goal (Trivers, 1972). A man can make at least two kinds of contributions to a mateship, in addition to providing genetic material. First, he can contribute material and energetic assistance to offspring, such as providing them with food and other resources, as well as carrying, caring for, teaching, and protecting them. Second, he can provide assistance to and cooperate with the woman herself, which will influence her well-being and ability to rear offspring. (Although these kinds of assistance are closely related, it is worth distinguishing between them, especially when considering how mateships or pair-bonds are maintained. See the work of Hazan and Zeifman (1999) for an elaboration of this idea with respect to attachment systems.) It is reasonable, then, to predict that a woman will prefer men with attributes indicative of willingness and ability to provide assistance. It is important to add the caveat that this does not imply that all men are expected to provide all types of assistance, or that the direct assistance provided to offspring is necessarily parental in nature. Such assistance is sometimes better characterized as mating effort (Blurton Jones, Marlowe, Hawkes, & O'Connell, 2000; Hawkes, 1991; but see Marlowe, 1999). Also, sisters, kin, and others in a woman's support network may provide valuable assistance in addition to or in the place of a mate, depending on the woman's social environment and ecology (e.g., Hrdy, 1997, 1999; Lancaster, 1991). But under the common circumstances in which long-term mateships occur and where a woman and her offspring can benefit from a mate's contributions, she is expected to have preferences for attributes indicative of a man's willingness and ability to provide assistance (Symons, 1979; Trivers, 1972).

Previous Research: Women's Long-Term Mate Preferences

Research findings from traditional societies, as well as from North America, provide

^{1.} The focus of this article is on functional or evolutionary explanations. Explanations at other levels, in combination with an evolutionary one, can provide more complete understandings of behavior (see Holekamp & Sherman, 1989, and Tinbergen, 1963, for discussions of levels of explanation). A proximate-level explanation, which is the most common level of explanation in traditional social psychology, provides an understanding of the mechanisms of a behavior, such as how it occurs. For example, Rusbult and colleagues' work on the interdependence of individuals provides a proximate explanation of how romantic relationships can be maintained (e.g., Rusbult & Buunk, 1993). An evolutionary explanation of romantic relationships provides an explanation of why such relationships would have ever occurred in the first place. Thus, the two levels combined can give a better understanding of the behavior by providing both its underlying motivation (proximate level) and function (ultimate level).

support for the idea that women prefer, and children benefit from, men who have resources and are willing to share them (for a review of traditional societies, see Betzig, 1988). For example, among the horticulturalist Kipsigis of Kenya, men who offered more acres of land per wife were preferred as husbands by women (and their parents, as the Kipsigis practice "arranged" marriages) (Borgerhoff Mulder, 1990). In North American societies, women also appear to value cues of material and social success in potential husbands (e.g., Landolt et al., 1995; Sadalla, Kenrick, & Vershure, 1987; Townsend & Wasserman, 1998), as revealed in data on income, job status, and women's preferences. Women prefer that their spouses be ambitious and career-oriented and have a good earning capacity (Buss & Barnes, 1986; but see also Eagly & Wood, 1999), and men who meet these criteria tend to have greater mating success than men who do not (Pérusse, 1993).

Although women appear to value good material prospects in a mate, results from these studies also suggest that women prefer attributes in men that indicate that they would make good cooperators in a longterm mateship, both in terms of devoting time to offspring (i.e., showing an energetic investment directly in offspring) and in direct dealings with their mate. This is especially evident in findings by Buss and colleagues, in which both men and women value characteristics, such as kindness, dependability, fondness for children, and intelligence, that are likely to be indicative of a good coparent and companion (review in Buss, 1994; see also Buss, 1989; Hazan & Zeifman, 1999; Kenrick et al., 1990, 1993; Miller & Fishkin, 1997; Scheib, 1994). In addition, women consistently rate these attributes as some of the most important in potential mates, often more so than resource-related items. Similarly, Jensen-Campbell, Graziano, and West (1995) found that women considered men attractive when they exhibited prosocial behavior, and that such behavior was required for dominance to be rated as attractive. For example, a dominant man who was low in prosocial

behavior was not deemed attractive. Although less information is available from traditional societies, some comes from the Ache of Paraguay who, until recently, were hunter-gatherers. Hill and Hurtado (1996) asked Ache women what made a good marriage partner. Women reported that the man be "handsome" and "kind." Men provided further elaboration, reporting that those who could easily get a wife had to be both good hunters and "strong," where strong meant having great endurance, "work[ing] hard when everyone was tired . . . or who would carry his children" (p. 228). Interestingly, the emphasis that a man be both a good hunter and "strong" is similar to findings by Jensen-Campbell et al., in that the attractiveness of being a good hunter was influenced by prosocial behavior.

Physical attractiveness

Finally, even though women value physical attractiveness less in potential mates than do men, attractiveness is nonetheless still important (e.g., Buss, 1994; Regan, 1998). The utility of physical attractiveness in a mate has not always been clear, although the strong and consistent preference for it within and across cultures (e.g., Jones, 1996) suggests that attractiveness may serve to signal information about the bearer's phenotypic quality. In the past, however, it has been argued that selection removes heritable variation in traits related to fitness, such that all potential mates have essentially the same genes for these traits (e.g., Charlesworth, 1987; Kirkpatrick, 1986). But recently, it has been found that mutations and the co-evolution of pathogens with their hosts (e.g., human hosts) are sufficient to maintain genetic variation in fitness traits (e.g., Charlesworth, 1990; Charlesworth & Hughes, 2000; Hamilton, 1982), including sexually selected traits, thus allowing these traits to evolve as honest signals of overall phenotypic quality (Kirkpatrick, 1996; Rowe & Houle, 1996). Subsequent selection on the basis of traits signaling heritable phenotypic quality, in the context of mate choice, is called "good genes" sexual selection. Recent research findings suggest that physical attractiveness is one such sexually selected trait (review in Thornhill & Gangestad, 1999a).

Darwinian analyses of physical attractiveness with respect to "fluctuating asymmetry" (FA) have provided such insight. In a number of studies, physical attractiveness is related to measures of a male's body or facial symmetry (e.g., reviews in Gangestad & Simpson, 2000; Gangestad & Thornhill, 1997b; Hume & Montgomerie, 2000; Perrett, Burt, Penton-Voak, Lee, Rowland, & Edwards, 1999; Thornhill & Gangestad, 1999a). Bilateral symmetry in body morphology is thought to be a marker of phenotypic quality as evidenced through developmental stability and pathogen/parasite resistance (i.e., immunocompetence; Møller, 1990; Parsons, 1992). The lack of symmetry on morphological traits that are symmetrical at a population level (FA) is partly a result of a lower ability to resist the harmful effects of perturbations during development, caused by mutations, pathogens, and toxins (Van Valen, 1962; Møller & Swaddle, 1997). Susceptibility to FA is also partly heritable, suggesting that morphological symmetry is associated with genetic determinants of phenotypic condition (review in Møller & Thornhill, 1997). Thus, phenotypic quality in a male mate is likely to influence offspring viability and, if the male stays around, may also affect his ability to invest in offspring (Gangestad, 1993; Gangestad & Thornhill, 1997b). For these reasons women are expected to value phenotypic quality in potential mates. Consistent with this, physical attractiveness, which is related to symmetry, is used in women's choices of mates. This explanation for why women value attractiveness for the heritable benefits it signals is a good genes hypothesis (Gangestad, 1993; see also Hamilton & Zuk, 1982; Zahavi, 1975 for related viability-based good genes hypotheses).2

Further insights into the information that attractiveness signals is provided by the consistent but environmentally-contingent importance attributed to attractiveness in long-term mates. In a cross-cultural study, Gangestad and Buss (1993) found that physical attractiveness was more highly valued in environments where the prevalence of pathogens was greater, suggesting that attractiveness signals health status and disease resistance.

Other research on physical attractiveness suggests additional links to traits that signal quality. For example, one component of attractiveness in male faces is masculinity, such as prominent chins and cheekbones (e.g., Bullock & Montgomerie, 2000; Cunningham, Barbee, & Pike, 1990; Franklin & Johnston, 2000; Grammer & Thornhill, 1994; Scheib, Gangestad, & Thornhill, 1999). These features become sexually differentiated at puberty with the increase of circulating androgens (Enlow & Hans, 1996). Masculinity may provide signals of quality for two reasons: (1) In a recent study, Scheib et al. (1999) found that masculinity was correlated with symmetry, a marker of quality as discussed above; and (2) greater masculinity is thought to reflect a greater ability to deal with the immunosuppressive effects of testosterone, thus reflecting an individual's immunocompetence (Grafen, 1990; Folstad & Carter, 1992; Thornhill & Gangestad, 1993). This latter reason is based on the handicap principle of sexually selected traits (Zahavi, 1975), in which the size of the trait reflects the extent to which an individual is able to support the costs associated with it. Basically, only those who can afford the energetic costs of the trait can afford to have it. Although the relationship between adult levels of testosterone and facial masculinity is unknown, one study measured levels in adolescent boys (age 13 and 15) and found strong positive relationships with ratings of facial dominance and testosterone (Mazur, Halpern, & Urdy, 1994). Taken together, these results suggest that masculinity, a component of attractiveness, provides another marker of quality that women use in their mate choices.

^{2.} The related "sexy son" hypothesis (Fisher, 1930) also posits benefits from choosing an attractive mate, but is not based on viability arguments. Offspring benefit only insofar as inheriting the traits that made their fathers attractive.

Mate choice in other contexts

In research to date, the major focus has been on women's preferences for mateships in general, with emphasis on long-term relationships. But evolutionary-minded researchers have also examined women's preferences for mateships of shorter duration, such as dates and one-night stands (Buss & Schmitt, 1993; Kenrick et al., 1990, 1993; Landolt et al., 1995; Wiederman & Dubois, 1998). Relative to men's preferences, women's preferences for short-term mates are similar to those for long-term mates (e.g., Buss, 1994, p. 88), with the exception that women emphasize the greater importance of physical attractiveness in their short-term mates (Regan, 1998; Wiederman & Dubois, 1998).

Extra-pair mateships

Women might also show specific mate preferences in response to the potentially unique characteristics of extra-pair mateships. Extra-pair mateships differ from short-term mateships in substantial ways. First, extra-pair mateships imply that the individual has a primary mate, whereas shortterm mateships do not. For a woman's primary mate, extra-pair mateships often represent the selective problem of misdirecting one's limited paternal care toward another's offspring, when greater benefits could be obtained by investing in one's own offspring [for exceptions, see cases of secondary or multiple fathers in the Ache (Hill & Hurtado, 1996), Bari (Beckerman, Lizarralde, Ballew, Schroeder, Fingelton, Garrison, & Smith, 1998), and Tibetans (Haddix, 2001)]. Thus, a second difference between short-term and extra-pair mateships is that the latter carry intrinsic risks to the woman, the most significant of which is being discovered by one's primary mate. Upon suspecting or discovering an extra-pair mateship, the primary mate can impose costs, including reducing his parental care to offspring (e.g., Anderson, Kaplan, & Lancaster, 1999; see Owens, 1993, for a theoretical review; Davies, 1992, for an example of facultative adjustment according to cues of extra-pair copulations and paternity in dunnocks, abandoning the relationship, or inflicting mental and physical harm on the woman (e.g., Daly & Wilson, 1998; Wilson & Daly, 1992, 1993). Yet despite these risks, it is possible that in evolutionary history women benefited from extra-pair mateships. Indeed, anatomical, physiological, and psychological traits in males suggest that polyandrous matings have been a persistent practice of women in the past. For example, human males have moderately large testes (relative to body size) compared with primates with single-male mating systems, suggesting that sperm competition and the need for high volumes of sperm were selective forces in human evolution (Harcourt, Harvey, Larson, & Short, 1981; see Kenagy & Trombulak, 1986, for comparative evidence in mammals; Møller, 1988, for evidence in birds; but see also Brown, Shumaker, & Downhower, 1995). Wyckoff, Wang, and Wu (2000) provide additional support for this idea with comparative data indicating that several genes related to sperm function have been evolving at a relatively faster rate in humans and chimpanzees (female chimps mate polyandrously) than in gorillas for whom the frequency of sperm competition is very low. In humans, through the use of the galvanic skin response and subjective report, Buss, Larsen, Westen, and Semmelroth (1992) found sex differences in the type of stimuli that elicit jealousy: Men were more upset by their mate's sexual infidelity, whereas women's responses were greater to emotional infidelity. The authors argued that the sex difference in the physiological and psychological responses reflects adaptations to different selective problems faced by men and women: A mate's sexual, as opposed to emotional, infidelity represents a greater problem for men because it can lead to caring for unrelated offspring, whereas a mate's emotional, as opposed to sexual, infidelity represents a greater problem for women because it can result in losing paternal investment to another woman (but see also DeSteno & Salovey, 1996). Further evidence comes from an experimental manipulation. Pound, Javed, Ruberto, Shaikh, and del Valle (1999) provided sperm donors with sexually explicit videos that varied in the extent to which they contained visual cues of sperm competition. They found that semen parameters improved with the presence of cues of sperm competition during specimen production. Specifically, sperm concentration and total sperm number were greater for specimens produced by males on exposure to a video containing cues of sperm competition than on exposure to a video in which these cues were absent. Taken together, these findings suggest that polyandrous matings and sperm competition have been a part of human evolutionary history and that a number of responses in males reflect adaptations to the problem of directing limited paternal care toward one's own, rather than another male's, offspring.

Extra-pair mateships: Functional benefits

How might women benefit from extra-pair mateships? Based on insight from the disciplines of animal behavior and primatology, Smith (1984) and Symons (1979) proposed a number of possible functional benefits to humans (see also Benshoof & Thornhill, 1979). An immediate benefit of extra-pair mateships would be the acquisition of material resources, which could reduce a woman's time needed for foraging and/or supplement her and her offspring-especially useful in times of scarcity. Additionally, an extra-pair mate might also be less dangerous to or even more protective of the woman and her offspring, especially if he may have fathered these offspring (see also Hrdy, 1997). In some circumstances, such as being dissatisfied with one's current mate, extra-pair mateships might also provide a woman with the opportunity to assess men as potential long-term mates---the mate replacement hypothesis. More indirect benefits a woman might gain include the following: high quality gametes ("good genes") that would increase offspring quality, "sexy son" genes that would increase

a son's chance of reproductive success through the same genes that made his father attractive, genetic diversity as an "evolutionary hedge" against an unpredictable environment, and fertility backup.

Extra-pair mateships: Evidence

Several studies have focused on behavior in extra-pair mateships, providing preliminary support for three of Symons's and Smith's hypotheses: acquisition of high quality gametes, acquisition of resources (material resources and protection), and mate replacement. Early studies first focused on extra-pair mateships as a way to acquire gametes (the quality of the gametes was not addressed). Bellis and Baker (1990) compared the timing of in-pair and extra-pair sex in a sample of over 2,000 women and found that women had sex with extra-pair partners more often during times in the ovulatory cycle when they were likely to conceive. Baker and Bellis (1993) then suggested that the timing of a woman's orgasm could influence sperm retention patterns and possibly the outcome of sperm competition. Using data from their earlier study, they suggested that when women were polyandrous, their patterns of orgasms favored the retention of sperm from extrapair, over in-pair, partners.³ Later, Gangestad and Thornhill (1997a) specifically tested the hypothesis that women might gain high quality gametes from extra-pair mateships, by using reports from men. They investigated the type of male attributes that would predict women's choices of extrapair partners. In addition to age and measures of present and future income, FA and facial attractiveness were included as measures of heritable phenotypic quality. Of the five attributes, only men's FA and facial attractiveness were related to their reports of

^{3.} Although male adaptations to sperm competition could have been driven by extra-pair sexual coercion, the findings that women are more likely to have extra-pair sex when they can conceive and have high retention orgasms with these men suggest that a significant proportion of polyandrous matings were voluntary in evolutionary history.

being chosen as an extra-pair partner: More symmetrical men reported being chosen more often than less symmetrical men, and men's physical attractiveness (independently) predicted how often they had been chosen as a woman's extra-pair partner. Findings from other studies support the idea that extra-pair mateships function as a way to acquire resources. Hill and colleagues have found that women obtain resources (meat) from men who are also likely to be their (extra-pair) lovers and that children benefit not only from these extra resources but also from protection provided by these "secondary" fathers that significantly impacts their rates of survival to adulthood (Hill & Hurtado, 1996; Hill & Kaplan, 1988; see also Beckerman et al., 1998). In addition, Greiling and Buss (2000) found that women rated resources-related attributes as likely benefits from extra-pair mateships. Preliminary evidence also suggests that extra-pair mateships might function as a way to replace a primary mate. For example, when women rated the importance of different attributes in long-term and short-term mates, Buss and Schmitt (1993) found that relative to men, women's preferences across the two contexts were quite similar. Thus, short-term relationships, which share some characteristics with extra-pair mateships, might serve as a way to assess potential long-term, primary mates (Buss, 1994, p. 87). Further support for this idea comes from Greiling and Buss (2000) who found that women rated having someone who might replace one's current mate (e.g., the extra-pair partner was interested in a commitment) as a likely benefit of extra-pair mateships.

Researchers have examined possible benefits that could be obtained from an extra-pair mateship, as well as suggesting that women sometimes behave differently in this context (i.e., timing of extra-pair sex and orgasms, Bellis & Baker, 1990; Baker & Bellis, 1993). A question arising from these studies is whether women's preferences for extra-pair partners ever differ from those for long-term mates. For example, it may be that women prefer extra-pair partners who have the *overall* best attributes, relative to other possible mates, regardless of the type of mateship (long-term or extra-pair). In one study that examined women's preferences for long-term and extra-pair partners no differences were found (Scheib, 1994). These results must be interpreted cautiously, however, because the stimuli were designed primarily to evaluate women's preferences for sperm donors rather than identify differences between preferences for long-term and extra-pair mates.

What attributes might women be expected to value in extra-pair mateships? Given the potential costs associated with extra-pair mateships, women might be expected to be attracted only to those males with attributes providing the highest payoffs. If these pay-offs were in the form of replacing one's primary mate, then similar preferences would be expected for extrapair and long-term mates. Alternatively, given that extra-pair mateships may be short-lived and/or covert, male attributes that would be beneficial in a long-term mateship, such as being a good cooperator and parent, might decrease in importance, whereas attributes that increased the chance of producing high quality offspring (such as good genes) or that helped those offspring (such as acquiring immediate resources and/or protection) would figure more prominently.

Current Research

In the current research, I examine the importance of a potential mate's good character and physical attractiveness in long-term and extra-pair mateships while controlling for the effects of his material resources. Following previous research, a man's good character is expected to be highly valued in a long-term mate because it signals a potentially good cooperator—both as a coparent and companion. Physical attractiveness, which is thought to be one cue of heritable phenotypic quality, is also expected to be one of the more important attributes in a long-term mate but should be less important than a mate's good character. Women's preferences for extra-pair mates can then be compared with those for long-term mates. If extra-pair mateships function to replace a primary mate, then women would be expected to show similar preferences across the two contexts. However, if extrapair mateships function as a way to obtain high quality gametes, as signaled by physical attractiveness, then the relative importance of physical attractiveness should increase in extra-pair mates. This should be most evident when high quality gametes are obtained without concurrent mate replacement, and, thus, women would be expected to trade off, or give up, good character for physical attractiveness when forced to choose between these attributes in an extrapair mate. Thus, this research focuses on two hypotheses about extra-pair mateshipsmate replacement and the acquisition of high quality gametes-and tests whether women ever prefer men who provide high quality gametes but who would not make good replacements for a primary mate.

A trade-off methodology was used to test these ideas in which women had to choose between men with attributes signaling a good mate replacement and men with attributes signaling high quality gametes. Participants were presented with information in the form of descriptions (vignettes) and photos of pairs of men, which had been pre-rated for good character and physical attractiveness. Each pair included one man who had a better character but was less physically attractive, and one man who was more physically attractive but had a less desirable character. These stimuli forced women to trade off character for looks, or vice-versa, and hence tested the relative importance of these attributes in long-term and extra-pair mateships. These stimuli also prevented women from making choices that allowed them to get everything-good character and good looks-a possibility not excluded in more commonly used stimuli, such as lists of attributes that subjects rate (see also Li, Bailey, & Kenrick, 2001, who use a "necessity vs. luxury" method to study mate preferences). Thus, with this trade-off method, choosing a physically attractive man (i.e., signaling high quality gametes) meant giving up a man with a good character (i.e., signaling a possible mate replacement). In addition, the stimuli provided participants with information in a form more similar to what people would normally use in decision making (i.e., visual information and summary descriptions about a person), at least initially, than if they were presented with a list of attributes to rate. Finally, women between ages 25 and 40 years were preferentially targeted as participants to include participants who had more experience with, or at least a better understanding of, the costs and benefits of extra-pair mateships.

Experiment 1

Method

Participants. One hundred thirty-one female undergraduate students participated in the study for experimental course credit. To increase the number of older participants, most of the experimental sign-up sheets invited only women between ages 25 and 40 to participate. In addition, 29 female graduate students and other women who were employed on or off campus volunteered to participate in the study, bringing the total to 160. The volunteers were noted to test whether their responses were related to their volunteer status. Eight additional undergraduates participated but were not included in the sample because they were older than the cut-off of 40 years or did not identify themselves as heterosexual.

Participant age ranged from 18 to 40 years, with a mean of 26.0 (SD = 7.0). Fifty-four (33.8%) participants were married or in marriage-like unions. A slightly greater proportion (37.5%) had marital experience, which included those who were now separated, divorced, or widowed. Thirty-seven (23.1%) had children.

Materials. In a method similar to that used in Simpson and Gangestad's (1992) second study, stimuli were pairs of men, each one



Physically attractive



Each pair of pictures satisfied the following rules:



Each pair of descriptions satisfied the following rule:

HEIGHT: 2 inches taller than you SEXUAL ORIENTATION: heterosexual PERSONAL: Works in the region. Likes carpentry. usually to build things for the house. Listening to live music in a pub with a close group of friends is also a favorite. Summer weekends are great for romantic walks on nearby trails and winter ones for downhill skiing. Character >> (dependable, faithful & loyal, good companion, good parent, good provider, kind & understanding, likes children, mature, patient)

> Height <<

HEIGHT: 5 inches taller than you SEXUAL ORIENTATION: heterosexual PERSONAL: Works in the region. Rainy weekends are great for reading up on pieces in his weapon collection. Sunny ones are best for playing rugby or rock climbing. Any time's great for jamming on guttars with the guys.

Figure 1. Example of a stimulus pair of men.

described by a vignette that included his interests, sexual orientation (all men were heterosexual), and height.⁴ Five stimulus pairs were used, and a photograph was provided with each vignette (see Figure 1). Twenty-three female judges between ages of 19 and 53 (Mdn = 27) provided the ratings of the vignettes and pictures but did not participate in the main study. Sevenpoint scales ("not at all" to "extremely") were used for all ratings. Vignettes were rated on nine attributes describing a person's character, focusing on cues of a good cooperator and parent, and included some attributes used by Simpson and Gangestad (i.e., kind and understanding, faithful and loyal, good parent), as well as others selected specifically for this study (i.e., dependable, good companion, good provider, likes children, mature, patient). A vignette's overall character rating was the average of the nine attribute ratings. Vignettes were also rated on how financially well-off the person sounded. Finally, the vignettes were paired, so that each pair had one vignette with a significantly better character rating than the other (all ps < .0001), including being relatively less tall (i.e., "2 inches taller than you [the participant]," whereas the man with the less desirable character was "5 inches taller than you"). The vignettes, however, did not differ on ratings of being financially well-off (all ps > .01).⁵ Stimulus pictures were obtained from bulk-mail advertisement catalogs; they were then rated for physical attractiveness and for being financially well-off, and their ages were

^{4.} Moderately greater height (relative to the woman) contributes to ratings of physical attractiveness in romantic relationships (review in Pierce, 1996), and, thus, was included to differentially increase the attractiveness of the target men.

Level of significance was adjusted for multiple comparisons.

estimated. Pictures were then paired, so that each pair contained one picture that was significantly more physically attractive than the other (all ps < .0001) but that did not differ from the other on ratings of being financially well-off (ps > .01). Estimated mean ages of the pictures ranged from 26.4 to 33.2 years. When the men's ages differed within a pair (2 out of 5 pairs), the less attractive men were always slightly older.6 Final stimuli included five pairs of men, with each pair containing one man with a vignette describing a better character but with a less physically attractive picture (man with good character), and another man with a vignette describing a less desirable character but with a more physically attractive picture (physically attractive man). Given these stimuli, participants had to weigh the benefits of having a physically attractive mate against the benefits of having a mate with good character and choose between them. In this way, the importance of physical attractiveness relative to good character could be identified in an extrapair mate and compared with its importance in a long-term mate.

Procedure. Participants completed individual, anonymous questionnaires in groups of about 20, with empty seats between them to assure privacy. Participants were presented with the five pairs of stimulus men, in random order, and asked to choose one man from each pair. Using a between-subjects design, 78 women were asked to imagine that they were single and were choosing the man in each pair that they would prefer as a husband (long-term condition). In the extrapair condition, 82 women were asked to imagine that they were married and were choosing the man in each pair that they would prefer for a brief sexual affair. In an

6. This was done to be consistent with the picture's associated vignette: The less attractive man was rated as having a better character, which included being more mature (and hence had the picture that was rated as older), whereas the more attractive man was rated as having a worse character, which included being less mature (and hence had the picture that was rated as younger).

earlier study (Scheib, 1994), subjects were told that they were not likely to see this extra-pair partner again. In the present research, however, this wording was not included to increase the possibility that subjects would consider the target man as a possible mate replacement. The instructions in the present research were also very similar to those used by Greiling and Buss (2000) in which subjects were to "Think of a woman [man] who is in a committed relationship but who chose to have a short-term sexual relationship with another person."7 Their results most strongly supported a mate replacement hypothesis for extra-pair mateships, suggesting that the instructions in the present experiment would not preclude the possibility of subjects choosing the target man as a possible mate replacement. Finally, in addition to the experimental task (i.e., longterm or extra-pair mate), women were asked to provide their marital status, age, and parity (i.e., whether or not they had children).

Results and discussion

Measuring preferences for good character versus physical attractiveness. A participant's choices were scored from 0 to 5 to indicate the number of times she chose the man with good character over the physically attractive man. A score of 0 indicated that no men with good character had been chosen; that is, all the participant's choices had been for physically attractive men. A score of 5 meant that all choices had been for men with good character and that no physically attractive men had been chosen.

Relationships among the measures. Pearson correlation coefficients were computed between all of the variables in the study: experimental condition (extra-pair vs. longterm mates), participant status (volunteer vs. experimental credit), a woman's marital status (single vs. married/marital-like), marital experience (single vs. ever married), age, and parity (children vs. none),

^{7.} Women completed the task for both female and male targets.

Variables	1	2	3	4	5	6	7
1. Number of men with good character chosen		.41**	.26**	.30**	.27**	27**	.08
 Experimental condition Marital status 		_	.02	.02 .92**	.00 .56** .65**	03 58** 65**	.04 .03 .00
4. Marital experience 5. Age 6. Children						64** —	.00 .23** 10
7. Participant status							

n = 160; ** correlation is significant at the 0.01 level (two-tailed).

and the dependent variable (number of men with good character chosen). (See Table 1.)

Notice first that a participant's status (i.e., volunteer vs. experimental credit) was related only to her age, which is not surprising because older women were specifically sought to increase the age of the participant pool. Participant status was not related to choice of stimulus men and so was not included in subsequent analyses. Second, notice that choice of stimulus men was related to all the other measures: Women tended to choose more men with good character for the long-term condition than for the extrapair condition (r = .41); as did women who were married (r = .26) or had marital experience (r = .30), as well as older women (r = .30).27), and women with children (r = -.27). Because marital status and experience were conceptually and empirically similar (they were correlated .92), only marital experience was included in the subsequent analyses. Experience, rather than current marital status, might be more relevant to how women chose extra-pair mates if experience helped women better understand the costs and benefits of extra-pair mateships.

Main analysis: Predictors of women's choices. An analysis of covariance was used to compare women's choices of men in the long-term versus extra-pair mateship condition, controlling for the effects of marital experience, age, and parity. As a group, the covariates accounted for a significant amount of the variance in women's choices of men $(R^2 = .10; F(3, 155) = 7.00, p < .001)$. No individual covariate was a significant predictor (all ps > .05), although, the effect of one covariate, marital experience, was marginal ($R^2 = .01$; F(1,155) = 3.09, p = .08). The lack of significant individual covariates is probably due to the fact that they were highly correlated with each other (see Table 1). With the effects of the covariates removed, experimental condition still accounted for a significant amount of unique variance in women's choices of men ($R^2 =$.16; F(1, 155) = 33.90, p < .001). Women chose fewer men with good character but lower attractiveness for extra-pair mateships $(M_{\rm adj} = 2.3)$ than for long-term mateships ($M_{adi} = 3.6$). That is, a greater number of physically attractive men were chosen for extra-pair mateships than for long-term mateships. Overall, the model accounted for 27% of the variance in women's choice of stimulus men.

In sum, women's preferences varied according to the type of mateship they considered. When considering a long-term mateship, women chose in greater numbers men with good character who were less physically attractive. Men with good character were chosen significantly less often than physically attractive men in the extra-pair condition.

Experiment 2

One possibility, however, was that the relative importance of physical attractiveness in Experiment 1 was not specific to extrapair mateships but instead reflected a more general effect of attending to and preferring individuals with cues of attractiveness in one's short-term interactions. In social contexts, physically attractive individuals are often attributed positive traits (Dion, Berscheid, & Walster, 1972). Therefore, it is possible that the benefits subjects expected to gain from their short-term interactions with the physically attractive men in Experiment 1 outweighed the imagined costs imposed by the men's less desirable character, with such an effect occurring regardless of whether the interaction was sexual or not. If this is true, such an effect would be due to a general mechanism, not one specific to a sexual psychology. Alternatively, if the increased preference for physically attractive men in short-term interactions is limited to sexual contexts, then it would support the idea that the effect is due to a mechanism specific to the sexual domain.

To test these ideas, a separate group of women completed the same experimental procedures, except that they were asked to choose the stimulus men for a nonsexual interaction of working on a short-term versus long-term project. This provided a test of whether the preference for physically attractive individuals, and the tolerance for less desirable character, was specific to a sexual context (specifically extra-pair mateships) or was a more general effect of preferences for individuals in short-term interactions.

Method

Participants. Seventy-five female undergraduate students participated in the study for experimental course credit. Three additional undergraduates participated but were not included in the sample because they did not identify themselves as heterosexual. Participant age ranged from 17 to 34 years, with a mean of 20.5 (SD = 3.2). Eight (10.7%) participants were married or in marriage-like unions. A slightly greater proportion (13.3%) had marital experience. One had children.

Materials and procedure. The materials were the same as those used in Experiment 1, with the modification that participants were now asked to imagine that they were employed at a company and were being asked to choose the men they would prefer to work with on an important project. Thirty-eight participants were asked to choose coworkers for a brief short-term project, whereas 37 participants were asked to choose coworkers for a long-term project. In addition to this task, women were asked to provide their marital status, age, and parity.

Results and discussion

Correlational analyses indicated that none of the potential covariates (i.e., marital status, marital experience, age, and parity) were related to a woman's choice of stimulus men. Therefore, a simple t-test was used to compare women's choices of coworkers in the short-term versus long-term work condition. In contrast to the findings from Experiment 1, no difference was found between the number of men chosen with good character for a short-term (M = 3.6) as compared with a long-term (M = 3.6) project, t < 1.0, ns. In addition, a contrast between women's choices in Experiments 1 and 2 indicated that the difference in means between the long-term and extra-pair conditions in the mateship context was significantly larger than the difference between the long-term and short-term conditions in the coworker context (interaction F(1, 231)) = 11.56, p < .005; a follow-up analysis of covariance which included the covariates used in Experiment 1 confirmed the significant interaction and pattern of means, F(1,(227) = 13.13, p < .001). These findings suggest that the preference in Experiment 1 for physically attractive individuals with less desirable character was specific to the sexual context of an extra-pair mateship.

General Discussion

In Experiment 1, women's preferences differed for long-term and extra-pair mates. For long-term mates, women preferred men with good character (defined by attributes indicative of being a good cooperator and parent), even if they were less physically attractive. In the extra-pair condition, however, women chose a greater number of physically attractive men who had less desirable character. That is, they were more likely to forgo good character in favor of physical attractiveness, suggesting that phenotypic quality, as cued by attractiveness, was weighted more heavily in this context. This trade-off is most consistent with the hypothesis that extra-pair mateships function as a way to obtain high quality gametes, with offspring potentially benefiting from greater developmental stability and pathogen resistance (a major selection pressure on humans; see Gangestad & Simpson, 2000; Thornhill & Gangestad, 1999a).

The effect of mating context was significant even after three correlated characteristics of the female study participants (age, parity, and marital experience) were covaried. As a group, however, these variables also significantly predicted women's mate choices, suggesting that older women with more marital and parenting experiences were more likely to choose men with good character, regardless of the type of mateship. Of these variables, the one most strongly related to mate choice was marital experience. This result is not surprising. The experience of sustained, long-term interactions with a person, such as those found in marriages, is likely to increase a woman's sensitivity to the benefits of good-character attributes in potential mates.

The effects of mating context and marital experience on mate choice in Experiment 1 was specific to choice of a sexual partner. In Experiment 2, where women chose between short- and long-term work partners, they tended to favor men with good character regardless of the length of the work relationship. These choices were not related to the participants' age and experience with marriage or parenting. Thus, the relative importance of physical attractiveness in the context of an extra-pair mateship seems related to the inclusion of sex in the relationship.

Contribution to previous research

Results of the current research advance our understanding of women's mate preferences in several ways. First, previous research has revealed relatively few differences in women's preferences for long-term and extra-pair mates, although some have found an increased emphasis on physical attractiveness in the related, but not identical, context of short-term relationships (e.g., Regan 1998). It should be emphasized, however, that the extra-pair context is different from the more general short-term context because of the greater risks to the woman of pursuing a relationship when she already has a primary mate. Therefore, it is critical to examine women's preferences when such risks are salient, and, thus, it is necessary to be explicit that the mateship being considered is extra-pair not just short-term. Only a few studies have examined the extra-pair context specifically. For example, Gangestad and Thornhill (1997a) found that attractiveness predicted how often men reported being chosen as an extra-pair partner, which suggests that women prefer attractive men. Also, Gangestad, Simpson, Cousins, and Christensen (2001) have found that women with an unrestricted sociosexual orientation are more likely than restricted women to prefer physically attractive men as extra-pair mates. The present research adds to these findings. Women's preferences were assessed directly and showed that, indeed, preferences for longterm and extra-pair mates differ. In addition, not only was physical attractiveness weighted more heavily in decisions about an extra-pair mate, it also overrode the general importance of good character in a mate, contrary to women's decisions about longterm mates. Thus, these results do not provide support for the hypothesis that mate

replacement is the primary function of extra-pair mateships.

Second, requiring women to trade off good character for attractiveness provided a methodology that revealed the priority given to physical attractiveness in the extrapair context. It prevented women from choosing men with the best overall attributes and provided a way to test whether women ever prefer physically attractive men who likely provide higher quality gametes but who would not make good mate replacements. Thus, it provided a way to test the mate replacement and good genes hypotheses more directly and eliminated the ambiguous result of women choosing men with the best attributes overall.

Third, Experiment 2 provided a test of the specificity of women's preference for physical attractiveness over good character in the extra-pair context. These preferences did not generalize to the context of a shortterm work project, suggesting that the psychological mechanisms underlying women's preferences for extra-pair mates are specific to the sexual domain.

Finally, it should be emphasized that women's decisions about a long-term mate revealed the great importance attributed to mates being good cooperators and parents (i.e., having good character). This has been documented in previous studies but is sometimes overlooked because of the emphasis placed on sex differences in preferences for resources and physical attractiveness. Women's decisions about long-term mates also reveal that there may be both benefits and costs with having these preferences. Some men who are good long-term mates may be so because they are unlikely to be able to attract other mates and consequently re-direct energy and resources to other women. Conversely, men who appeal as extra-pair mates may make inferior longterm mates because they have less time and energy to direct to their primary relationship (see Gangestad & Simpson, 2000, and associated commentaries for a discussion of this issue). Thus, the preferences that women expressed for long-term and extrapair mates in the present research suggest one possible solution, or facultative strategy, to the problem of how to choose the best mate. Women can choose men who make the best long-term mates, and, in certain circumstances, they can also form extra-pair mateships with physically attractive men who offer higher quality gametes—the good genes hypothesis of extra-pair mateships.

Future Directions

In the current research, women's preference for attractiveness in extra-pair mates appears to be best explained by a good genes hypothesis of extra-pair mateships. However, physical attractiveness is multiply determined (e.g., symmetry, masculinity, clear skin connoting healthiness, etc.) and likely signals information about other attributes, in addition to developmental stability and immunocompetence. For example, masculinity, which signals immunocompetence, may also signal a man's ability to deal with intrasexual competition (see Furlow, Gangestad, & Armijo-Prewitt, 1998, for the finding that more symmetrical men have more physical fights with other men). Thus, when women form extra-pair mateships, they may benefit in multiple ways, such as obtaining protection, as well as good genes, from extra-pair mates. In the current research, the physically attractive men were slightly taller than the men with good character. Thus, it is possible that women might have gained additional protection benefits by choosing the attractive men. However, information was not available about other attributes (e.g., masculinity) associated with providing protection. Future studies need to test whether women obtain good genes alone, protection alone, or both simultaneously in extra-pair mateships.

In the current research, cues of phenotypic quality were limited to physical attractiveness. In addition, only limited information was available about the participants, none of which appeared to be strong predictors of mate choice. Future studies could include the same stimuli (i.e., visual information, vignettes, and inherent tradeoffs) but with additional measures of phenotypic quality (e.g., fluctuating asymmetry) in the stimuli and more information about the participants, such as their current risk of conception. If extra-pair mateships functioned as a way to obtain high quality gametes, then women's preferences for men with cues of high phenotypic quality should be strongest when conception is most likely. Both Gangestad and Thornhill (1998; Thornhill & Gangestad, 1999b) and Penton-Voak and colleagues (1999; Penton-Voak & Perrett, 2000) have found such relationships. For example, Gangestad and Thornhill (1998) had women rate the odor of Tshirts worn by men. The women never saw the men nor did they know anything about their degree of symmetry. Nevertheless, women rated the T-shirts worn by more symmetrical men to be more attractive (i.e., less offensive) than the T-shirts worn by less symmetrical men, but this effect was limited to those who were in the pre-ovulatory phase of their cycles (i.e., were most likely to conceive). This suggests that women may be more sensitive to cues of phenotypic quality when they are most likely to conceive and may preferentially choose men of better phenotypic quality at this time. These results have been replicated, with the further finding that women also preferred the scent of T-shirts worn by men with greater facial attractiveness (again, women never saw the men; Thornhill & Gangestad, 1999b). Thus, these studies suggest that cues of male phenotypic quality may be olfactory as well as visual (e.g., facial attractiveness).

Penton-Voak and colleagues (1999) have focused on another potential marker of immunocompetence and phenotypic quality facial masculinity (Folstad & Karter, 1992; Scheib et al., 1999)—and found similar cyclical variation in women's preferences (see also Franklin & Johnston, 2000). When asked to select the most physically attractive face, women preferred the more masculinized faces during the pre-ovulatory phase (when there was the highest risk of conception). Moreover, when women were asked to choose faces for short-term and longterm relationships, the preference for more masculinized faces was observed only for short-term relationships, providing further evidence for the possibility that one function of extra-pair mateships could be to obtain high-quality gametes.

The current research provided a preliminary examination of the role of individual differences in women's choice of long-term and extra-pair mates. Having experience in marital relationship slightly biased a women's choices toward choosing men with good character and away from physically attractive men, regardless of the mating context. Other individual differences, such as the propensity to engage in sexual relationships without commitment (e.g., Simpson and Gangestad's [1991] sociosexuality orientation measure [SOI]), may account for additional variation in women's choices. For example, in a study on romantic partner choice, Simpson and Gangestad (1992) required women to choose between men who were high on physical attractiveness and social visibility or high on good personal/parenting qualities. Women who were more unrestricted tended to choose the former, whereas those who were more restricted chose the latter. Additionally, as discussed earlier, Gangestad, Simpson, Cousins, and Christensen (2001) found that women who scored the highest on the SOI were most likely to prefer physically attractive men as extra-pair partners.

Other factors, such as the environment in which women live, would also be expected to influence women's choices (see Gangestad & Simpson, 2000, for a review). For example, Gangestad and Buss (1993) found that women valued physical attractiveness more in long-term mates when they lived in environments characterized by high pathogen loads. Also, in mobile hunter-gatherer societies, it may be critical to a child's survival to have more than two parents who are willing to care for him or her. The Ache seem to have solved this problem in a social system that recognizes more than one father, and, hence, women's choices of extra-pair mates may be strongly influenced by such a factor (Hill & Hurtado, 1996). Future studies are needed to

address variability in women's choices of mates, both long-term and extra-pair, at the level of individual differences in personality and in one's social and physical environment.

In conclusion, by using an experimental manipulation in which women had to trade off good character for physical attractiveness, differences emerged in women's criteria for extra-pair and long-term mates.

References

- Anderson, K. G., Kaplan, H., & Lancaster, J. (1999). Paternal care by genetic fathers and stepfathers. I: Reports from Albuquerque men. Evolution and Human Behavior, 20, 405-431.
- Baker, R.R., & Bellis, M. A. (1993). Human sperm competition: Ejaculate manipulation by females and a function for the female orgasm. *Animal Behaviour*, 46, 887–909.
- Batten, M. (1992). Sexual strategies: How females choose their mates. New York: Tarcher/Putnam.
- Beckerman, S., Lizarralde, R., Ballew, C., Schroeder, S., Fingelton, C., Garrison, A., & Smith, H. (1998). The Bari partible paternity project: Preliminary results. *Current Anthropology*, 39, 164–167.
- Bellis, M. A., & Baker, R. R. (1990). Do females promote sperm competition? Data for humans. Animal Behaviour, 40, 997–999.
- Benshoof, L., & Thornhill, R. (1979). The evolution of monogamy and concealed ovulation in humans. *Journal of Social and Biological Structures*, 2, 95– 106.
- Betzig, L. (1988). Mating and parenting in Darwinian perspective. In L. Betzig, M. Borgerhoff Mulder, & P. Turke (Eds.), human reproductive behaviour: A Darwinian perspective (pp. 3-20). New York: Cambridge University Press.
- Betzig, L. (1997). People are animals. In L. Betzig (Ed.), Human nature: A critical reader (pp. 1–17). Oxford: Oxford University Press.
- Blurton Jones, N. G., Marlowe, F. W., Hawkes, K., & O'Connell, J. F. (2000). Parental investment and hunter-gatherer divorce rates. In L. Cronk, N. Chagnon, & W. Irons (Eds.), Adaptation and human behavior: An anthropological perspective (pp. 69–90). New York: Aldine de Gruyter.
- Borgerhoff Mulder, M. (1990). Kipsigis women's preferences for wealthy men: Evidence for female choice in mammals? *Behavioral Ecology and Sociobiology*, 27, 255–264.
- Brown, L., Shumaker, R. W., & Downhower, J. F. (1995). Do primates experience sperm competition? American Naturalist, 146, 302–306.
- Bullock, H. L. & Montgomerie, R. D. (2000). Mate attraction. II: Facial attractiveness. Paper presented at the meeting of the Human Behavior and Evolution Society, Amherst, MA.
- Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. Behavioral and Brain Sciences, 12, 1-49.

Women chose in greater numbers men with good character for long-term mateships, whereas physically attractive men with less desirable character were chosen more often for extra-pair mateships. These results provide further evidence for a good genes hypothesis for the function of extra-pair mateships, in that women were willing to trade off a man's good character for his greater physical attractiveness.

- Buss, D. M. (1994). The evolution of desire: Strategies of human mating. New York: Basic Books.
- Buss, D. M., & Barnes, M. (1986). Preferences in human mate selection. Journal of Personality and Social Psychology, 50, 559–570.
- Buss, D. M., Larsen, R. J., Westen, D., & Semmelroth, J. (1992). Sex differences in jealousy: Evolution, physiology, and psychology. *Psychological Science*, 3, 251–255.
- Buss, D. M. & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, 100, 204–232.
- Cashdan, E. (1996). Women's mating strategies. Evolutionary Anthropology, 5, 134–143.
- Charlesworth, B. (1987). The heritability of fitness. In J. W. Bradbury & M. B. Andersson (Eds.), Sexual selection: Testing the alternatives (pp. 21-40). New York: Wiley.
- Charlesworth, B. (1990). Mutation-selection balance and the evolutionary advantage of sex and recombination. *Genetical Research*, 55, 199–221.
- Charlesworth, B., & Hughes, K. A. (2000). The maintenance of genetic variation in life history traits. In R. S. Singh & C. B. Krimbas (Eds.), *Evolutionary genetics from molecules to morphology*. Cambridge, UK: Cambridge University Press.
- Cunningham, M. R., Barbee, A. P., & Pike, C. L. (1990). What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. *Journal of Personality and Social Psychology*, 59, 61–72.
- Cunningham, M. R., Druen, P. B., & Barbee, A. P. (1997). Angels, mentors, and friends: Trade-offs among evolutionary, social, and individual variables in physical appearance. In J. A. Simpson & D. T. Kenrick (Eds.), Evolutionary social psychology (pp. 109-140). Mahwah, NJ: Lawrence Erlbaum Associates.
- Daly, M., & Wilson, M. (1998). The evolutionary social psychology of family violence. In C. Crawford & D. L. Krebs (Eds.), *Handbook of evolutionary psychology: Ideas, issues, and applications* (pp. 431– 456). Mahwah, NJ: Lawrence Erlbaum Associates.
- Davies, N. B. (1992). Dunnock behaviour and social evolution. Oxford: Oxford University Press.
- DeSteno, D. A., & Salovey, P. (1996). Evolutionary origins of sex differences in jealousy? Questioning the "fitness" of the model. *Psychological Science*, 7, 367–372.

- Dion, K., Berscheid, E., & Walster, E. (1972). What is beautiful is good. *Journal of Personality and Social Psychology*, 24, 285–290.
- Eagly, A. H., & Wood, W. (1999). The origins of sex differences in human behavior: Evolved dispositions versus social roles. *American Psychologist*, 54, 408–423.
- Ellis, B. J. (1992). The evolution of sexual attraction: Evaluative mechanisms in women. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 267–288). New York: Oxford University Press.
- Enlow, D. M., & Hans, M. G. (1996). Essentials of facial growth. Philadelphia: Saunders.
- Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford: Clarendon.
- Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist*, 139, 603–622.
- Franklin, M., & Johnston, V. (2000). Hormone markers and beauty. Paper presented at the meeting of the Human Behavior and Evolution Society, Amherst, MA.
- Furlow, B., Gangestad, S. W., & Armijo-Prewitt, T. (1998). Developmental stability and human violence. Proceedings of the Royal Society, London, B, 266, 1–6.
- Gangestad, S. W. (1993). Sexual selection and physical attractiveness: Implications for mating dynamics. *Human Nature*, 4, 205–235.
- Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology* and Sociobiology, 14, 89–96.
- Gangestad, S. W., & Simpson, J. A. (2000). The evolution of mating: Trade-offs and strategic pluralism. Behavioral and Brain Sciences, 23, 573–644.
- Gangestad, S. W., Simpson, J. A., Cousins, A. J., & Christensen, P. N. (2001). Fluctuating asymmetry, sociosexuality, and women's context-specific mate preferences. Manuscript submitted for publication.
- Gangestad, S. W., & Thornhill, R. (1997a). The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry. *Evolution and Human Behavior*, 18, 69–88.
- Gangestad, S. W., & Thornhill, R. (1997b). Human sexual selection and developmental stability. In J. A. Simpson & D. T. Kenrick (Eds.), *Evolutionary social psychology* (pp. 169–195). Mahwah, NJ: Lawrence Erlbaum Associates.
- Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings of the Royal Society, London, B, 265, 927–933.*
- Grafen, A. (1990). Biological signals as handicaps. Journal of Theoretical Biology, 144, 517–546. Grammer, K., & Thornhill, R. (1994). Human (Homo sapiens) facial attractiveness and sexual selection: The role of symmetry and averageness. Journal of Comparative Psychology, 108, 233–242.
- Greiling, H., & Buss, D. M. (2000). Women's sexual strategies: The hidden dimension of extra-pair mating. Personality and Individual Differences, 28, 929– 963.
- Haddix, K. A. (2001). Leaving your wife and your brothers: When polyandrous marriages fall apart. *Evolution and Human Behavior*, 22, 47–60.
- Hamilton, W. D. (1982). Pathogens as causes of genetic

diversity in their host populations. In R. M. Anderson & R. M. May (Eds.), *Population biology of infectious diseases* (pp. 269–296). New York: Springer-Verlag.

- Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science*, 218, 384–387.
- Harcourt, A. H., Harvey, P. H., Larson, S. G., & Short, R. V. (1981). Testis weight, body weight, and breeding system in primates. *Nature*, 293, 55–57.
- Hawkes, K. (1991). Showing off: Tests of another hypothesis about men's foraging goals. *Ethology and Sociobiology*, 11, 29-54.
- Hazan, C., & Zeifman, D. (1999). Pair bonds as attachments: Evaluating the evidence. In J. Cassidy & P. R. Shaver (Eds.), *Handbook of attachment: Theory, research, and clinical applications* (pp. 336-354). New York: Guilford Press.
- Hill, K., & Hurtado, A. M. (1996). Ache life history: The ecology and demography of a foraging people. New York: Aldine de Gruyter.
- Hill, K., & Kaplan, H. (1988). Tradeoffs in male and female reproductive strategies among the Ache: Parts 1 and 2. In L. Betzig, M. Borgerhoff Mulder, & P. Turke (Eds.), *Human reproductive behaviour:* A Darwinian perspective (pp. 277-305). New York: Cambridge University Press.
- Holekamp, K. E., & Sherman, P. W. (1989). Why male ground squirrels disperse. *American Scientist*, 77, 232–239.
- Hrdy, S. B. (1997). Raising Darwin's consciousness: Female sexuality and the prehominid origins of patriarchy. *Human Nature*, 8, 1–49.
- Hrdy, S. B. (1999). Mother nature: A history of mothers, infants, and natural selection. New York: Pantheon Books.
- Hume, D.K., & Montgomerie, R. (2001). Facial attractiveness signals different aspects of "quality" in women and men. Evolution and Human Behavior, 22, 93–112.
- Jensen-Campbell, L. A., Graziano, W. G., & West, S. G. (1995). Dominance, prosocial orientation, and female preferences: Do nice guys really finish last? *Journal of Personality and Social Psychology*, 68, 427-440.
- Jones, D. (1996). Physical attractiveness and the theory of sexual selection: Results from five populations. Museum of Anthropology, University of Michigan.
- Kenagy, G. J., & Trombulak, S. C. (1986). Size and function of mammalian testes in relation to body size. *Journal of Mammology*, 67, 1–22.
- Kenrick, D. T., Sadalla, E. K., Groth, G., & Trost, M. R. (1990). Evolution, traits and the stages of human courtship: Qualifying the parental investment model. *Journal of Personality*, 58, 97–116.
- Kenrick, D. T., Groth, G. E., Trost, M. R., & Sadalla, E. K. (1993). Integrating evolutionary and social exchange perspectives on relationships: Effects of gender, self-appraisal, and involvement level on mate selection criteria. *Journal of Personality and Social Psychology*, 64, 951–969.
- Kirkpatrick, M. (1986). The handicap mechanism of sexual selection does not work. *American Natural*ist, 127, 222–240.
- Kirkpatrick, M. (1996). Good genes and direct selection in the evolution of mating preferences. *Evolu*tion, 50, 2125–2140.
- Lancaster, J. B. (1991). A feminist and evolutionary

biologist looks at women. Yearbook of Physical Anthropology, 34, 1-11.

- Lancaster, J. B., & Lancaster, C. (1983). Parental investment: The hominid adaptation. In D.J. Ortner (Ed.), How humans adapt: A biocultural odyssey (pp. 33-56). Washington, DC: Smithsonian Institutional Press.
- Landolt, M. A., Lalumière, M. L., & Quinsey, V. L. (1995). Sex differences in intra-sex variations in human mating tactics: An evolutionary approach. *Ethology and Sociobiology*, 16, 3–23.
- Li, N. P., Bailey, J. M., & Kenrick, D. T. (2001). The necessities and luxuries of mate preferences: Testing trade-offs. Manuscript submitted for publication.
- Marlowe, F. (1999). Showoffs or Providers? The parenting effort of Hadza men. Evolution and Human Behavior, 20, 391–404.
- Mazur, A., Halpern, C., & Urdy, J. R. (1994). Dominant looking male teenagers copulate earlier. *Ethology* and Sociobiology, 15, 87–94.
- Miller, G. F., & Todd, P. (1998). Mate choice turns cognitive. Trends in Cognitive Sciences, 2, 190–198.
- Miller, L. C., & Fishkin, S. A. (1997). On the dynamics of human bonding and reproductive success: Seeking windows on the adapted-for human-environmental interface. In J. A. Simpson & D. T. Kenrick (Eds.), *Evolutionary social psychology* (pp. 197– 235). Mahwah, NJ: Lawrence Erlbaum Associates.
- Møller, A. P. (1988). Testes size, ejaculate quality and sperm competition in birds. *Biological Journal of* the Linnaean Society, 33, 273-283.
- Møller, A. P. (1990). Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Animal Behaviour*, 40, 1185–1187.
- Møller, A. P., & Swaddle, J. P. (1997). Developmental stability and evolution. Oxford, UK: Oxford University Press.
- Møller, A. P., & Thornhill, R. (1997). A meta-analysis of the heritability of developmental stability. *Journal of Evolutionary Biology*, 10, 1–16.
- Owens, I. P. F. (1993). When kids just aren't worth it: Cuckoldry and parental care. *Trends in Ecology* and Evolution, 8, 269–271.
- Parsons, P. A. (1992). Fluctuating asymmetry: A biological monitor of environmental and genomic stress. *Heredity*, 68, 361–364.
- Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically: Further evidence. *Evolution and Human Behavior*, 21, 39–48.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., & Minamisawa, R. (1999). Menstrual cycle alters face preference. *Nature* 24, 399, 741–742.
- Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A., Edwards, R. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behavior*, 20, 295–307.
- Pérusse, D. (1993). Cultural and reproductive success in industrial societies: Testing the relationship at the proximate and ultimate levels. *Behavioral and Brain Sciences*, 16, 267–283.
- Pierce, C. A. (1996). Body height and romantic attraction: A meta-analytic test of the male-taller norm. Social Behavior and Personality, 24, 143–150.
- Pound, N., Javed, M. H., Ruberto, C., Shaikh, M. A., & del Valle, A. P. (1999). Factoring affecting human ejaculate composition. Paper presented at the meet-

ing of the Human Behavior and Evolution Society, Salt Lake City, UT.

- Regan, P. C. (1998). What if you can't get what you want? Willingness to compromise ideal mate selection standards as a function of sex, mate value, and relationship context. *Personality and Social Psychology Bulletin*, 24, 1294–1303.
- Rowe, L., & Houle, D. (1996). The lek paradox and the capture of genetic variance by condition dependent traits. Proceedings of the Royal Society of London, B, 263, 1415-1421.
- Rusbult, C. E., & Buunk, B. P. (1993). Commitment processes in close relationships: An interdependence analysis. *Journal of Social and Personal Relationships*, 10, 175–204.
- Sadalla, E. K., Kenrick, D. T., & Vershure, B. (1987). Dominance and heterosexual attraction. Journal of Personality and Social Psychology, 52, 730–738.
- Scheib, J. E. (1994). Sperm donor selection and the psychology of female mate choice. *Ethology and Sociobiology*, 15, 113–129.
- Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry, and cues of good genes. Proceedings of the Royal Society of London, B, 266, 1913–1917.
- Simpson, J. A., & Gangestad, S. W. (1991). Individual differences in sociosexuality: Evidence for convergent and discriminant validity. *Journal of Personality and Social Psychology*, 60, 870–883.
- Simpson, J. A., & Gangestad, S. W. (1992). Sociosexuality and romantic partner choice. *Journal of Personality*, 60, 31–51.
- Smith, R. L. (1984). Human sperm competition. In R. L. Smith (Ed.), Sperm competition and the evolution of animal mating systems (pp. 601-659). Orlando: Academic Press.
- Symons, D. (1979). The evolution of human sexuality. Oxford: Oxford University Press.
- Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty: Averageness, symmetry, and parasite resistance. Human Nature, 4, 237–269.
- Thornhill, R., & Gangestad, S. W. (1996). The evolution of human sexuality. *Trends in Ecology and Evolu*tion, 11, 98–102.
- Thornhill, R., & Gangestad, S. W. (1999a). Facial attractiveness. Trends in Cognitive Sciences, 13, 452–460.
- Thornhill, R., & Gangestad, S. W. (1999b). The scent of symmetry: A human sex pheromone that signals fitness? Evolution and Human Behavior, 20, 175– 201.
- Tinbergen, N. (1963). On the aims and methods of ethology. Zeitschrift f
 ür Tierpsychologie, 20, 410– 433.
- Townsend, J. M., & Wasserman, T. (1998). Sexual attractiveness: Sex differences in assessment and criteria. Evolution and Human Behavior, 19, 171–191.
- Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), Sexual selection and the descent of man, 1871–1971 (pp. 136–179). Chicago: Aldine.
- Van Valen, L. (1962). A study of fluctuating asymmetry. Evolution, 16, 125–142.
- Wiederman, M. W., & Dubois, S. L. (1998). Evolution and sex differences in preferences for short-term mates: Results from a policy capturing study. *Evolution and Human Behavior*, 19, 153–170.
- Wilson, M., & Daly, M. (1992). The man who mistook his wife for a chattel. In J. H. Barkow, L. Cosmides,

& J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 289–322). New York: Oxford University Press.

- Wilson, M., & Daly, M. (1993). An evolutionary psychological perspective on male sexual proprietariness and violence against women. *Violence and Victims*, 8, 271–294.
- Wyckoff, G. J., Wang, W., & Wu, C. (2000). Rapid evolution of male reproductive genes in the descent of man. *Nature*, 403, 304–309.
- Zahavi, A. (1975). Mate selection—a selection for handicap. *Journal of Theoretical Biology*, 53, 205– 214.