ELSEVIER

Original Articles

The Evolutionary Psychology of Extrapair Sex: The Role of Fluctuating Asymmetry

Steven W. Gangestad and Randy Thornhill
Departments of Psychology and Biology, University of New Mexico, Albuquerque, New Mexico

This study explored evolutionary hypotheses concerning extrapair sex (or EPCs: extrapair copulations). Based on recent notions about sexual selection, we predicted that (a) men's number of EPCs would correlate negatively with their fluctuating asymmetry, a measure of the extent to which developmental design is imprecisely expressed, and (b) men's number of times having been an EPC partner of a woman would negatively correlate with their fluctuating asymmetry. In a sample of college heterosexual couples, both hypotheses were supported. In addition, men's physical attractiveness independently predicted how often they had been an EPC partner. Women's anxious attachment style positively covaried with their number of EPC partners, whereas their avoidant attachment style negatively covaried with their number of EPC partners.

KEY WORDS: Development; Developmental stability; Extrapair sex; Fluctuating asymmetry; Mate Choice; Sexual Selection.

As recorded by poets, novelists, and psychologists alike, sexual relationships evoke emotions distinct both in intensity and kind. And, of all events within relationships that evoke strong emotional reactions, extrapair sexual relations (or EPCs: extrapair copulations) are perhaps those that can lead to the most destructive consequences. When discovered by one's mate, EPCs not only can cause relationships to dissolve (Hite 1987), but, after reviewing the relevant empirical literature, Daly and Wilson (1988) concluded that the most

Received April 29, 1995; revised October 14, 1996.

Address reprint requests and correspondence to: Steven W. Gangestad, Department of Psychology, University of New Mexico, Albuquerque, NM 87131, U.S.A.

Evolution and Human Behavior 18: 69–88 (1997)

655 Avenue of the Americas, New York, NY 10010
1090-5138/97/$17.00
PII S1090-5138(97)00003-4

common cause of spousal homicide is male suspicion of his mate's infidelity (see also Wilson and Daly 1992).

In light of the clear significance of EPCs to the lives of individuals and relationships, systematic and theoretically motivated research examining the factors that give rise to them is surprisingly sparse. Most research on extramarital sex (for a review, see Thompson 1983) or nonmarital extradyadic sex (Hansen 1986) has been atheoretical (for recent exceptions, see Baker and Bellis 1993; Bellis and Baker 1990). The paucity of theoretically motivated research cannot be due merely to the infrequency of EPCs. Large surveys of married women in the U.S. estimate that between 15% (Laumann et al. 1994) and 70% (Hite 1987) have had extramarital sex, with the median estimate being about 30% (for a review, see Thompson 1983; also Kinsey et al. 1953). Typically, 25%–50% of married U.S. men surveyed report having had extramarital sex (Thompson 1983; see also Kinsey et al. 1948; Laumann et al. 1994). And, 6% of a sample of British women with one main partner reported their *last* act of sexual intercourse to be an EPC (Bellis and Baker 1990). Blood group studies of paternity in England have revealed levels of nonpaternity for the purported father of about 6% (Edwards 1957).

In the research reported here, we adopted an evolutionary perspective to explore individual difference factors associated with EPCs of college students involved in romantic relationships. While sometimes leading to marriage, college romantic relationships may, on average, differ from more long-lasting mateships in a number of ways. Nevertheless, these relationships are convenient to study, extrapair sex outside of them is not uncommon, and theory and data indicate that in a variety of ways we should expect the factors associated with phenomena in them to be similar to those associated with the same phenomena in long-term mateships (Hansen 1986). Moreover, EPCs in college relationships can bring about many of the same disruptive consequences that extrapair sex in marriages brings about. Hence, EPCs in student relationships may shed light on evolutionary hypotheses.

EVOLUTIONARY PSYCHOLOGY AND EPCs

From an evolutionary psychological perspective, relatively long-term sexual and romantic relationships partly represent the expression of adaptations, individuals' design features forged through the accumulative effects of differential replication of genes during the course of human history. Purportedly, one overarching function of the propensity to form long-term sexual relationships is that such relationships provide a social context in which childrearing would have been efficient and successful within ancestral environments (Mellen 1981). Of course, in this age of readily available and reliable contraception, long-term sexual relationships can be completely unlinked with reproduction and parenting. This fact, however, in no way gainsays a historically adaptive, reproductive significance of the psychological design that underlies the formation and maintenance of sexual relationships (Buss 1991, 1995; Symons 1987, 1992; Thornhill 1990; Tooby and Cosmides 1992).

From an adaptationist perspective, why do EPCs occur? Because the roles that men and women play in reproduction differ, the functional significance of EPCs

should partly differ for the sexes. Whereas men can potentially have many offspring within a short time frame, women can conceive and successfully bear a child at most once a year or so. For this reason, men's EPCs historically may have increased their quantity of offspring, whereas women's EPCs probably affected only offspring quality. With this notion in mind, we derived and tested specific evolutionary hypotheses about EPCs rooted in ideas about the differential developmental quality of male partners.

Factors Affecting Men's EPC Opportunities

Because of men's potentially slight investment in offspring, their reproductive success has covaried historically with their number of mates. Number of mates in turn may have covaried with the extent to which men could obtain mates with minimal mating effort and parental investment (e.g., short-term mates) and, therefore, men's reproductive success is likely to have covaried with their short-term mating ability (Betzig 1986; Buss and Schmitt 1993). As a result, although men's evolved design should not necessarily dispose them to pursue short-term matings under all circumstances, it should dispose them to do so under certain conditions (Buss and Schmitt 1993).

EPCs are often short-term matings in which effort put toward the matings (i.e., energy expenditure, time, accumulated material resources) is relatively small. The success with which men can pursue such short-term matings necessarily is a function of women's evolved psychological design and, more specifically, the conditions under which women would accept mates who invest little into their relationships. Multiple sexual selection processes that could have forged women's psychological design in this regard have been proposed (Bradbury and Andersson 1987; Cronin 1991; Kirkpatrick and Ryan 1991). Our focus is one particular sexual selection process, "good genes" sexual selection (for a review, see Cronin 1991).

"Good genes." A number of theorists propose that women will accept men for short-term matings to the extent that their genes confer viability fitness to offspring, that is, to the extent that they possess "good genes" (Benshoof and Thornhill, 1979; Gangestad and Simpson 1990; Simpson and Gangestad 1991; Smith 1984; Thornhill and Gangestad 1993). Proposals that mate choice is based on genetic benefits offspring receive have been controversial, for they require heritable fitness (that is, the genetic "quality" [in a highly restricted, evolutionary sense—that is, quality for purposes of survival and reproduction] of mates must vary). And, under classical population genetic models, selection drives out heritable fitness (Fisher 1930; Kirkpatrick 1982, 1985; Lande 1981). These models have assumptions, however, that have recently been questioned.

One assumption is that the selective environment is constant. Recently, population biologists have noted that at least certain aspects of the environment are clearly not constant. Specifically, pathogens and the immune defenses of their hosts coevolve in response to one another, such that their nature continually changes across generations (Anderson and May 1978, 1982). Host–parasite coevolution has been one of the most important concepts to be introduced into evolutionary genetics in

the past several decades, having been applied to our understanding of the immense genetic diversity in the natural world, sexual recombination, and the evolution of sex itself (Hamilton 1980, 1982; Tooby 1982)—three major issues in evolutionary biology. In addition, it has been applied to sexual selection. Specifically, Hamilton and Zuk (1982) have noted that, because host–parasite coevolution maintains heritable fitness in host populations in the form of variation in pathogen resistance, host individuals should evolve to choose mates who possess indicators of pathogen resistance.

A second assumption is that new genetic variants enter the population at a negligible rate. One process through which new variants are introduced, of course, is mutation. Although this process has been recognized as an important genetic phenomenon for decades, until recently it was thought that new, slightly deleterious alleles introduced through mutation would be removed by selection quickly and have a negligible effect on heritable fitness. In fact, mutation–selection balance can maintain considerable heritable fitness (Rice 1988). Hence, perhaps individuals should evolve to choose mates who possess indicators of a relative lack of mildly deleterious alleles (Pomiankowski et al. 1991).

Biologists have attempted to identify markers of pathogen resistance and lack of mildly harmful, relatively new genetic variants in a variety of species. The most successful of these attempts probably concerns *fluctuating asymmetry*. Fluctuating asymmetry is absolute asymmetry of the two sides of bilateral characters (e.g., wings, fins, hands, feet, ears) for which the signed differences between the two sides have a population mean of zero and are normally distributed (Van Valen 1962). Because the two sides of such characters are not controlled by different genes, it is thought that their asymmetry represents the imprecise expression of underlying developmental design due to developmental perturbations (developmental instability). Although a variety of factors can cause developmental perturbation (e.g., extreme temperatures, poor nutritional status, toxins; see Lerner 1954; Parsons 1990; Thoday 1955; Waddington 1957), pathogens (Bailit et al. 1970; Møller 1992a; Parsons 1990) and mutations (Parsons 1990) are two important causes of perturbation in natural populations. As might be expected if pathogen resistance and mutation effects are heritable, fluctuating asymmetry appears to be heritable across a variety of species, including humans (Møller and Thornhill, in press).[1]

Low fluctuating asymmetry is associated with high male mating success (or with sexually selected characters associated with mating success) in a variety of species, including barn swallows (Møller 1992b), scorpionflies (Thornhill 1992a, 1992b; Thornhill and Sauer 1992), Drosophila (Markow and Ricker 1992), primates (Manning and Chamberlain 1993), and others (for reviews, see Møller and Pomiankowski, 1993; Møller and Swaddle, in press; Watson and Thornhill 1994). Some of the best evidence for the importance of fluctuating asymmetry in mating success, however, comes from humans. In research we have previously reported, we measured fluctuating asymmetry by measuring the two sides of seven bilateral charac-

[1]Heritability of fluctuating asymmetry is relevant because *some* phenomenon (or phenomena) must have maintained its additive genetic variance despite apparent directional selection for low fluctuating asymmetry. Host–parasite coevolution and mutation–selection balance are just such phenomena.

ters (feet, ankles, hands, wrists, elbows, ear length, ear width), taking the difference for each, and creating a composite index. Men who possess low fluctuating asymmetry tend to be judged as more attractive than other men (Gangestad et al. 1994; Thornhill and Gangestad 1994) and have relatively large body mass (Manning 1994; Thornhill et al. 1996). Moreover, men who possess low fluctuating asymmetry tend to have had relatively many sexual partners (Gangestad and Thornhill 1996a; Thornhill and Gangestad 1994).

Hypothesis. Short-term mating outside of a long-term relationship has obvious potential costs. Detection by a mate may lead to dissolution of the relationship. The partner may reduce his or her investment in the relationship. Bodily injury may result (Daly and Wilson 1988). Moreover, short-term mating efforts are not without costs in the currency of time, energy expenditure, and the like. Finally, sexually transmitted diseases have probably been around throughout the microevolution of *Homo sapiens*, and multiple partners increase the chances of contracting them. Men should have an evolved design that disposes them to pursue short-term matings under low-cost conditions, one of which is that they are preferred by women as short-term partners. One factor that leads men to be preferred by females as sexual partners (in absence of a long-term relationship) is their developmental quality, a marker of which is fluctuating asymmetry. The following prediction can hence be made concerning men's EPCs: Men's number of EPC partners will correlate positively with men's developmental quality and thus negatively with men's fluctuating asymmetry.

Factors Affecting Women's EPC Partnerships

Due to internal gestation, women's reproductive success, unlike that of men, historically should not have been a function of their number of sexual partners. After all, women can conceive only once every year or so and, hence, multiple mates in a short period of time do not convert into multiple conceptions. In light of this fact, what potential benefits of extrapair sexual relations could have forged an evolved design disposing women to pursue them under certain conditions? One benefit is once again based on notions about "good genes" sexual selection (Smith 1984).

Genetic benefits. To the extent that men's fitness is heritable, from an evolutionary perspective women should be faced with trading off men's heritable fitness and their investment in the mateship (Gangestad 1993; Gangestad and Thornhill 1996b). The reason is that men who can successfully achieve short-term matings (e.g., men with heritable fitness) may not be disposed to invest exclusively in a single mateship. Men most willing to invest in a mateship, by contrast, may be those less able to achieve short-term matings. Historically, however, women may have been able to achieve genetic benefits as well as investment by obtaining genetic benefits from one male and investment from another, that is, by engaging in extrapair sex (Benshoof and Thornhill 1979; Smith 1984). In part, a woman would have been reproductively advantaged by doing so to the extent that she could improve on the genetic

benefits of her mate. One evolutionary view, then, suggests that women's propensities to engage in extrapair sex should partly depend upon this factor.

Hypothesis. Based on these notions, then, we can derive a prediction about women's extrapair sex: Women's EPC partners will tend to exhibit developmental quality, as revealed by low fluctuating asymmetry. Hence, men's fluctuating asymmetry should negatively correlate with the number of times they have been a woman's EPC partner.

Overview of the Study

Heterosexual college students involved in romantic relationships completed a series of questionaires about their relationship and sexual history. Included were questions about: (1) Number of EPC Partners: Whether they had ever had sex with a person of the opposite sex other than a relationship partner during a romantic relationship and, if so, with how many persons had they had such sex; and (2) Number of Times an EPC Partner: Whether they had ever had sex with a person of the opposite sex they knew was involved romantically with another person at that time and, if so, with how many such persons. Seven anatomic fluctuating asymmetries were measured and summed into an index. Regression analyses were then conducted to examine the association between men's and women's fluctuating asymmetry and number of EPC partners or number of times an EPC partner. Also included in regression models were measures of age, socioeconomic status (SES) of family of origin, expected future salary, physical attractiveness, and attachment style (Hazan and Shaver 1987; Simpson 1990).

Hazan and Shaver (1987) suggested that romantic relationship styles can be thought of in terms similar to conceptualizations of mother–infant attachment (Bowlby 1973; see also Bartholomew 1990; Bartholomew and Horowitz 1991; Collins and Read 1990; Feeney and Noller 1990; Kobak and Hazan 1991; Simpson 1990; Simpson et al. 1992). They also constructed a measure designed to categorize individuals into one of three styles based on work with mother–infant interactions (Ainsworth et al. 1978): avoidant, anxious, and secure. Simpson et al. (1992) adopted a dimensional perspective, in which romantic relationship styles can be construed as varying along (a) an avoidant (distant, nonintimate) to secure (open to intimacy) dimension, and (b) an anxious (fearful of abandonment) to nonanxious (not fearful of adandonment) dimension. We included measures of attachment styles in this study because research indicates that these variations in openness to intimacy and fear of abandonment importantly predict a variety of relationship phenomena (Collins and Read 1990; Hazan and Shaver 1987; Simpson 1990; Simpson et al. 1992). It may be important to control for these variations in any attempt to examine the contributions of other factors, such as fluctuating asymmetry, to relationship phenomena. In addition, however, the associations between attachment styles and EPCs may be interesting in their own right. We used Simpson et al.'s measures of the two dimensions of avoidant and anxious attachment in this research.

METHODS

Participants

Participants were 203 heterosexual couples (203 men, 203 women) involved in a romantic relationship for at least 1 month. At least one member of each couple was enrolled in a psychology course and received, in return for participation, credit toward a class research requirement. To provide an incentive for partners to participate, we held a raffle drawing at the end of each of the two semesters during which the study was conducted, at which time one couple was awarded $100. The mean age of the men was 21.06 years (*SD* = 3.55, range = 17–40); the average age of the women was 19.95 years (*SD* = 3.24, range 17–39). In total, 53% of participants reported themselves as Caucasian, 36% as Hispanic, 5% Native American, 3% African American, 1% Asian, and 2% other. Twenty couples were married. Nine had children together, and another six men and eight women had children with previous partners. The mean length of the couples' current relationships at the time of the study was 20.6 months (*SD* = 18.6, range = 1–108).

Procedure

Couples reported in groups of 1–4. After reading and signing an informed consent form, each individual was escorted to a separate room and given a series of questionnaires to complete in privacy. The fact that responses were completely confidential, anonymous, and would in no way be seen by one's partner was stressed.

Questionnaires. The questionnaires included: (1) A brief basic information sheet, including age, height, weight, ethnicity, SES of home of origin (upper class, upper-middle class, middle class, lower-middle class, or lower class), marital status, duration of current relationship, number of offspring, and number of offspring with the current partner. This basic information sheet also asked whether the participant had ever broken or sprained within the past 3 months a foot, ankle, hand, wrist, or elbow. These reports were taken into account when we calculated our measure of fluctuating asymmetry (see next section).

(2) Extrapair Sex, Current Relationship: Participants were asked whether they had had sex with someone other than their partner while involved with their current partner and, if so, with how many partners.

(3) Extrapair Sex, Ever: Participants were also asked whether they had had sex outside of a relationship with any partner prior to the current relationship and, if so, with how many partners. This figure was added to the number of EPC partners that a participant reported to have during the current relationship to provide a measure of each individual's total number of EPC partners. On average, men reported 1.62 EPC partners (*SD* = 2.67, range = 0–16) and women reported 0.50 EPC partners (*SD* = 0.99, range = 0–7).

(4) Number of Times an EPC Partner: Participants were asked whether they had had sex with a person who they knew was seriously involved in a relationship

with another person or married and, if so, with how many such partners. On average, men reported having been an EPC partner with 0.76 partners (SD = 1.99, range = 0–13). Women reported having been an EPC partner with an average of 0.33 partners (SD = 1.66, range = 0–3). Only participants in the latter half of the study (N of couples = 99) were asked these questions.

(5) Self- and Partner-Estimated Earnings: Participants were asked to estimate the yearly earnings they and their partners would achieve in 10 years (median values: male self-reported, $55K; male partner-reported, $50K; female self-reported, $40K; female partner-reported, $50K). Inspection of these reports revealed that a small proportion of men and women reported values over $100,000 (up to $500,000) (8%). Because these values were clear outliers, we decided to truncate each variable at $100,000. Self- and partner-reports were correlated .40 for men ($p < .001$) and .29 for women ($p < .001$). We averaged the self- and partner-reports to estimate expected future earnings.[2]

(6) Attachment Indices (Simpson et al. 1992): Two factor-analytically derived scales constructed from items based on Hazan and Shaver's (1987) paragraph descriptions of attachment types: avoidant versus secure attachment (which we refer to as avoidant attachment here; eight items) and anxious attachment (five items). Sample items for each scale are: for avoidant attachment, "I am nervous whenever anyone gets too close to me"; for anxious attachment, "I often worry that my partner(s) doesn't really love me."

Fluctuating asymmetry measures. After putting individuals in their separate rooms to fill out the questionnaires, the experimenters (2) interrupted each, one at a time, to measure fluctuating asymmetry. For these measurements, the participant was escorted to a separate room reserved for measurements alone. One of the two experimenters then measured the participant's left and right sides of seven bilateral characters: foot width, ankle width, hand width, wrist width, elbow width, ear length, and ear width. Measurements were made with steel calipers to the nearest 0.1 mm (0.01 mm for the last 99 participants of each sex). Because measurements may involve some measurement error, remeasurements were taken when the left and right sides differed by more than 3 mm (determined on the basis of previous studies to be relatively extreme asymmetry). In total, about 10% of the measurements met this criterion. On such characters, the two measurements were averaged. For the 99 couples run during our second semester of data collection, we added two characters: index (second) finger length and fifth finger length. A total fluctuating asymmetry index (FA) was calculated for each participant by taking the absolute difference between the two sides on each character, dividing by the mean size of the character for the participant, and summing these values across all characters (Palmer and Strobeck 1986). Because FA for the two semesters of data collection involved different numbers of characters, we standardized FA (through z-score transformation) within semester and used this standardized index for all analyses.

[2]Truncated estimates were correlated more highly than untruncated estimates, a fact that provides additional justification for truncating.

Some asymmetry of skeletal characters may be due to breaks or sprains, not developmental instability. In previous research, we did not take account of these factors, but in this study we attempted to do so. For any feature for which a participant reported a break (ever) or sprain (within the past 3 months) on one side or the other, we (a) assigned the sex-specific mean asymmetry in cases in which the asymmetry exceeded the mean, or (b) assigned the participant's measured asymmetry in cases in which the asymmetry was less than the mean asymmetry. In so doing, we assumed that breaks and sprains more often increase than decrease asymmetry. This procedure affected 4.1% of the fluctuating asymmetry calculations for individual characters (5.9% for men, 2.4% for women). The resultant measures of asymmetry were correlated .92 and .94 with unaltered measures for men and women, respectively.

Given the small mean asymmetry of individual characters (< 2 mm), measurement error is a potential concern. To assess interrater reliability, then, we had two experimenters take measurements for 47 individuals (23 men and 24 women). The two experimenters were blind to each other's measures. The intraclass correlation between the two measurers' FAs for individuals was .63 (.65 within each sex). Hence, it appears that these measures of fluctuating asymmetry possess interrater reliability sufficient for correlational work.[3]

The authors measured approximately 25% of the participants. A substantial proportion (about 50%) of the other participants were measured by experimenters familiar with the general prediction that low FA men should have more sex partners, even if not familiar with the specific hypothesis of the current study. Any result from this study could potentially be due to experimenter biases in measurement (Rosenthal 1976). Nonetheless, we believe that this possibility is unlikely. The intraclass correlation between two measurements of FA in an independent sample of individuals (n = 78) by measurers totally unfamiliar with the notion of FA, its association with developmental instability, or its role in sexual selection processes was almost identical to that observed in the present study (intraclass correlation = .63; Simpson et al. 1995). If reliable experimenter biases were present in the current study, one would expect the intermeasurer agreement to be higher in the current study than in a study using naive measurers (because of the additional source of covariation across measurements). Of course, we cannot fully rule out effects of experimenter bias in the current study; future research should examine this possibility.

Photographs and physical attractiveness ratings. After measuring a participant's fluctuating asymmetry, an experimenter took two black-and-white, head-on facial photographs of the participant. For these photos, participants were asked to retain a neutral expression. After processing, one of the two photos of each individual was selected for rating (the one that was most clearly head-on, in which the participant did not close his or her eyes or smile, and for which the focus was best). On the basis of these photos, the physical attractiveness of participants was rated by eight raters (second semester) or 10 raters (first semester) on a scale of 1 (least attractive) to 10

[3]For those participants for whom we had two FA measures, we averaged across them. Because a subset of our participants had more reliable measures due to aggregation, then, the reliability of FA in the total sample was probably close to .7.

(most attractive). The raters' judgments for each participant were averaged to yield a composite attractiveness measure. Despite fewer raters for the second semester, Cronbach's alphas were .84 for both semesters. Due to camera mishaps, processing problems, or unsuitable poses, we did not obtain ratings of 14 men and 13 women.

At the end of the study, participants were fully debriefed.

RESULTS

Number of EPC Partners

We first examined predictors of the number of EPC partners men and women reported through a series of multiple regression analyses (using SPSSX). In the first model, we included five variables: age, FA, expected salary, SES, and physical attractiveness. Physical attractiveness was included because it is generally considered to be a factor that importantly influences romantic relationships (Berscheid and Walster 1974). Expected salary and SES were included because they may be expected to affect individuals' attractiveness in a short-term relationship (perhaps particularly men's attractiveness; Buss and Schmitt 1993).

Table 1 presents the results for men and women. As can be seen, only one variable significantly predicted men's number of EPC partners: FA (beta = −.17, $t[168] = 2.22$, $p < .02$). As expected, low FA men reported having more EPC partners than high FA men.

No variable significantly predicted women's number of EPC partners, all $|t|$s < 1.4, *ns*.

To control for additional variables, we conducted a second set of regression analyses. Here, we added the two attachment style variables (anxious attachment

Table 1. Multiple Regression Analyses Predicting EPC Partners From FA, Age, SES, Expected Income, and Facial Attractiveness

Men			
Predictor variable	Beta	$t(168)$	p
FA	−.17	−2.22	< .02
Age	.01	.19	*ns*
SES	.06	.82	*ns*
Expected income	.02	.20	*ns*
Facial attractiveness	−.02	−.21	*ns*
Women			
Predictor variable	Beta	$t(164)$	p
FA	−.03	−.40	*ns*
Age	.11	1.37	*ns*
SES	−.05	−.68	*ns*
Expected income	−.07	−.92	*ns*
Facial attractiveness	−.09	−1.21	*ns*

Note. For these and all other analyses, a one-tailed test was used for male FA; two-tailed tests were used for all other variables.

and avoidant attachment) as predictors. Results are presented in Table 2. As can be seen, men's FA remained a significant predictor of their number of EPC partners, beta = −.17, $t(164) = 2.27$, $p < .05$. No other variables predicted men's number of EPC partners at the .05 level of significance.

Women's number of EPC partners was significantly predicted by both attachment variables. Their anxious attachment positively predicted their number of EPC partners, beta = .20, $t(161) = 2.60$, $p < .01$. Their avoidant attachment negatively predicted their number of EPC partners, beta = −.21, $t(161) = 2.69$, $p < .01$. No other variables significantly predicted women's number of EPC partners.

Number of Times an EPC Partner

Next, we examined predictors of the number of times men and women reported themselves to have been an EPC partner of another person. To do so, we first regressed this variable on five variables, including FA, age, expected salary, SES, and physical attractiveness. Results are presented in Table 3.

The number of times men had been an EPC partner was significantly predicted by three variables. As expected men of lower FA tended to have been an EPC partner more times than did men of high FA, beta = −.27, $t(80) = 2.67$, $p < .005$. Second, older men had been an EPC partner more often than younger men, beta = .24, $t(80) = 2.30$, $p < .05$. Third, more facially attractive men had been an EPC partner more often than less facially attractive men, beta = .27, $t(80) = 2.52$, $p < .02$.

The number of times women had been an EPC partner was predicted only by their age, beta = .66, $t(72) = 7.14$, $p < .001$.

Table 2. Multiple Regression Analyses Predicting EPC Partners From FA, Age, SES, Expected Income, Facial Attractiveness, and Attachment Styles

Men			
Predictor variable	Beta	$t(164)$	p
FA	−.17	−2.27	< .02
Age	.01	.09	*ns*
SES	.07	.87	*ns*
Expected income	.02	.24	*ns*
Facial attractiveness	−.02	−.22	*ns*
Anxious attachment	.09	1.11	*ns*
Avoidant attachment	.13	1.71	< .10
Women			
Predictor variable	Beta	$t(161)$	p
FA	−.04	−.58	*ns*
Age	.13	1.73	< .10
SES	−.06	−.71	*ns*
Expected income	−.05	−.64	*ns*
Facial attractiveness	−.07	−.87	*ns*
Anxious attachment	.20	2.60	< .01
Avoidant attachment	−.21	−2.69	< .01

Table 3. Multiple Regression Analyses Predicting Times an EPC Partner From FA, Age, SES, Expected Income, and Facial Attractiveness

Men			
Predictor variable	Beta	$t(80)$	p
FA	−.27	−2.69	< .005
Age	.24	2.30	< .05
SES	.08	.78	*ns*
Expected income	−.17	−1.61	*ns*
Facial attractiveness	.27	2.52	< .02
Women			
Predictor variable	Beta	$t(72)$	p
FA	.06	.63	*ns*
Age	.66	7.15	< .001
SES	−.04	−.45	*ns*
Expected income	−.05	−.50	*ns*
Facial attractiveness	.08	.83	*ns*

When measures of men's attachment styles were added, all three variables that had been significant predictors for men in the previous analysis remained significant predictors (Table 4). Neither anxious attachment nor avoidant attachment significantly predicted the number of times a man had been an EPC partner. Similarly, a woman's anxious attachment and avoidant attachment did not significantly predict the number of times she had been an EPC partner (Table 4).

Table 4. Multiple Regression Analyses Predicting Times an EPC Partner From FA, Age, SES, Expected Income, Facial Attractiveness, and Attachment Styles

Men			
Predictor variable	Beta	$t(77)$	p
FA	−.26	−2.55	< .005
Age	.25	2.35	< .05
SES	.10	.97	*ns*
Expected income	−.16	−1.50	*ns*
Facial attractiveness	.27	2.51	< .02
Anxious attachment	.15	1.48	*ns*
Avoidant attachment	.10	.95	*ns*
Women			
Predictor variable	Beta	$t(70)$	p
FA	.08	.85	*ns*
Age	.66	7.07	< .001
SES	−.04	−.39	*ns*
Expected income	−.07	−.77	*ns*
Facial attractiveness	.07	.78	*ns*
Anxious attachment	−.11	−1.13	*ns*
Avoidant attachment	.06	.63	*ns*

Controlling for Number of Sex Partners

Previously, we reported a correlation between number of self-reported sex partners in a lifetime and men's FA (in an independent sample; Thornhill and Gangestad 1990). Was men's FA correlated in the current sample with their number of EPC partners and the number of times they had been an EPC partner simply because low FA men have more partners overall than high FA men? To assess this possibility, we performed one additional set of regression analyses, this time controlling for men's number of sex partners other than EPC partners or partners for whom the man was a woman's EPC partner. Results are presented in Tables 5 and 6.

Independent of men's number of partners other than EPC partners, men's FA continued to significantly predict their number of EPC partners, beta = $-.13$, $t(159) = 1.83$, $p < .05$. Moreover, a man's FA significantly predicted the number of times he had been an EPC partner, independent of the number of sex partners other than those for whom the man was an EPC partner, beta = $-.24$, $t(73) = 2.49$, $p < .01$. Men's physical attractiveness predicted the number of times they had been EPC partners at a marginally significant level, beta = .17, $t(73) = 1.73$, $p < .09$.

Independent of women's number of sex partners other than EPC partners, their avoidant attachment and anxious attachment continued to significantly predict their number of EPC partners, betas = $-.21$ and .19, respectively, $t(159) = -2.72$, $p < .01$ and 2.45, $p < .05$.

The number of EPC partners an individual reported was predicted by the number of non-EPC partners he or she reported. Moreover, the number of partners for

Table 5. Multiple Regression Analyses Predicting EPC Partners From FA, Age, SES, Expected Income, Facial Attractiveness, Attachment Styles, and Other Sex Partners

Men			
Predictor variable	Beta	$t(159)$	p
FA	−.13	−1.83	< .05
Age	−.11	−1.48	*ns*
SES	.05	.75	*ns*
Expected income	−.01	−.08	*ns*
Facial attractiveness	−.06	−.86	*ns*
Anxious attachment	.11	1.53	*ns*
Avoidant attachment	.09	1.20	*ns*
Other sex partners	.44	5.92	< .001
Women			
Predictor variable	Beta	$t(159)$	p
FA	−.04	−.58	*ns*
Age	.07	.86	*ns*
SES	−.05	−.69	*ns*
Expected income	−.04	−.58	*ns*
Facial attractiveness	−.07	−.95	*ns*
Anxious attachment	.19	2.45	< .02
Avoidant attachment	−.21	−2.72	< .01
Other sex partners	.18	2.24	< .05

whom sex was an EPC an individual reported was predicted by the number of other partners he or she reported (Tables 5 and 6).

Zero-Order Correlations

So that the reader can more fully understand the relationships between predictors and criterion variables in the multiple regression analyses presented thus far, we include a table of zero-order correlations between variables (Table 7). Most notable, perhaps, is no significant correlation between men's facial attractiveness and FA in this sample, $r = .00$, in contrast to two previous studies in which significant negative associations were found (Gangestad et al. 1994; Thornhill and Yeo 1994).

DISCUSSION

The present research focused on hypotheses about men's and women's EPCs based on "good genes" notions about sexual selection processes in humans. The first of these hypotheses concerned men's EPCs, whereas the second concerned women's EPCs.

Both hypotheses received support. As predicted, low FA men have more EPC partners compared to high FA men. Moreover, this association existed when the potential confounding variables of age, SES of family of origin, expected future salary, physical attractiveness, and attachment style were statistically controlled.

The prediction about women's extrapair sex also received empirical support. As predicted, low FA men claimed to have been EPC partners more often than high

Table 6. Multiple Regression Analyses Predicting Times an EPC Partner From FA, Age, SES, Expected Income, Facial Attractiveness, Attachment Styles, and Other Sex Partners

Men			
Predictor variable	Beta	$t(73)$	p
FA	−.24	−2.49	< .01
Age	.07	.69	*ns*
SES	.07	.70	*ns*
Expected income	−.09	−.97	*ns*
Facial attractiveness	.17	1.73	< .09
Anxious attachment	.08	.88	*ns*
Avoidant attachment	.05	.50	*ns*
Other sex partners	.46	4.59	< .001
Women			
Predictor variable	Beta	$t(68)$	p
FA	.10	1.19	*ns*
Age	.60	6.58	< .001
SES	−.03	−.31	*ns*
Expected income	−.07	−.80	*ns*
Facial attractiveness	.07	.82	*ns*
Anxious attachment	−.15	−1.64	*ns*
Avoidant attachment	.05	.61	*ns*
Other sex partners	.26	3.02	< .005

FA men. Once again, this association existed when the potential confounding variables of age, SES of family of origin, expected future salary, physical attractiveness, and attachment style were statistically controlled.

In addition, men's facial attractiveness predicted the number of partners for whom they had been EPC partners. Perhaps interestingly, a man's facial attractiveness did not predict his own number of EPC partners. A woman's number of EPC partners was predicted by her attachment styles: Whereas anxious attachment was associated with women's EPC partners positively, avoidant attachment was associated with women's EPC partners negatively.

To examine whether associations between predictor variables and reports of EPC behavior might be due merely to an increased number of sex partners in general, we also performed regression analyses controlling for sex partners other than EPC partners and times an EPC partner. With these variables controlled, men's FA continued to significantly predict the number of times they had been EPC partners and (more weakly) their number of EPC partners. Women's attachment styles continued to significantly predict their number of EPC partners.

Implications for Sexual Selection Theory Applied to Humans

EPCs and men's fluctuating asymmetry. What do these findings reveal about the nature of the sexual selection history of humans? First, they suggest that men who show evidence of developmental stability are relatively likely to pursue extrapair sexual relations and be chosen as EPC partners by women, perhaps because of women's greater willingness to have sex with them in the absence of investment in a relationship. Additional evidence supports this conjecture. Specifically, research on an independent sample revealed that men with low fluctuating asymmetry tend to have relatively many sexual partners in general (Thornhill and Gangestad 1994). Moreover, men who have low fluctuating asymmetry tend to sexualize (e.g., flirt with) women other than their partners more than do men with relatively high fluctuating asymmetry (Gangestad and Thornhill 1996b). Together, these findings are

Table 7. Zero-Order Correlations Between Predictors and Criterion Variables

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1. Times an EPC partner	–	.28**	−.28**	.16	.11	−.07	.17	.13	.13	.73**
2. EPC partners	.12	–	−.17**	.04	−.01	.02	−.03	.02	.10	.59**
3. FA	.07	−.01	–	−.09	−.05	−.09	.00	.10	.00	−.20**
4. Age	.65**	.12	−.01	–	−.06	.06	−.10	−.11	.19**	.21**
5. SES	−.19	−.03	−.01	−.08	–	.16*	.09	−.11	.07	.07
6. Expected income	−.04	−.04	−.08	.04	.11	–	.18**	−.04	.01	.16*
7. Facial attractiveness	−.09	−.12	.01	−.13	.10	.06	–	−.02	.01	.05
8. Anxious attachment	−.08	.14	.05	−.11	−.19**	−.17*	−.13	–	.04	.07
9. Avoidant attachment	.10	−.14	−.03	.01	−.14	−.03	−.01	.16*	–	.19**
10. No. sex partners	.48**	.42**	−.02	.35**	−.02	−.02	−.06	.03	−.04	–

Note. Correlations for males are above the diagonal; correlations for females are below the diagonal.

*$p < .05$.

**$p < .01$.

consistent with the notion that "good genes" sexual selection has partly forged the design of human psychological adaptations that underlie mating.

Research on women's orgasms is also consistent with a "good genes" interpretation of these findings. Baker and Bellis (1993) found that, when women have multiple sex-partners, the pattern of their sexual response (orgasm) tends to favor retention of sperm from the extra pair, rather than inpair, partner. Bellis and Baker (1990) furthermore found that women tend to have EPCs during peak periods of fertility, whereas their inpair sex was more evenly distributed across the cycle. Finally, we recently reported a result (obtained on a subset of the current sample) that women's orgasms—in particular, purportedly high sperm retention orgasms (Baker and Bellis 1993)—are correlated with their partner's fluctuating asymmetry (Thornhill et al. 1996).

This research cannot rule out all other explanations for our findings. Perhaps low FA men provide nongenetic benefits as EPC partners and to their own EPC partners. For instance, low FA men are seen as more able to provide physical protection to their partners than high FA men. Perhaps, because nonpaternal men were a threat to a woman's offspring, women's evolved EPC preferences favor men who could provide benefits of physical protection against other men's threats (cf. Hrdy 1981). Future research should attempt to tease apart alternative explanations.

The findings raise additional questions:

(1) What are the observed phenotypic features that account for these findings? Men's body mass, muscularity, and social dominance are related to fluctuating asymmetry and may function as cues (Gangestad and Thornhill 1996a). Do these cues mediate the relationships between men's FA and their EPC behavior? What other cues might mediate these associations?

(2) How does men's fluctuating asymmetry and increased probability of extrapair sex affect their relationships?

Men's material resources. We included other variables that some evolutionary perspectives might expect to be related to men's or women's EPCs. If women look to obtain material resources in short-term relationships (Buss and Schmitt 1993), we might expect men who come from families with money or men who are expected to earn much money to be particularly likely to have EPCs or to be women's EPC partners. We found no support for the notion that men's resources substantially influence either the number of their own EPC partners or their likelihood of being an EPC partner. Indeed, the average beta weight for these variables across all analyses was near zero (.07 for SES and −.07 for expected income). Of course, the student population we examined is a relatively affluent one, in which immediate access to large amounts of money or other material resources is nevertheless relatively rare. Perhaps the predictions would be better tested in another population; however, the one additional study we know of that is pertinent to this prediction found no support for it either. In a large community sample, Pérusse (1993) correlated a measure of men's status with a measure intended to predict the reproductive consequences of their sexual encounters in an ancestral environment (assuming no contraception), one highly correlated with their number of sex partners. Although single men's status reliably predicted this measure (see also Pérusse 1994), married men's status did

not. Thus, Pérusse (1993) found no evidence that married men's status predicts their extramarital sex.

Women's fluctuating asymmetry. Unlike men's fluctuating asymmetry, women's asymmetry did not predict the number of their own EPCs or thee number of times they had been EPC partners. The average beta weight across all analyses was near zero (−.04 for number of EPC partners, .08 for times an EPC partner). This matches expectations, since sexual selection theory gives no reason to expect that women advantaged on the mating market would convert their advantage into short-term matings. We have no evidence that low FA women are advantaged on the mating market but, even if they are, we would have no reason to expect that their FA would be associated with their number of EPC partners or number of times an EPC partner.

Women's Attachment Styles and Sexual History

Interestingly, two variables did predict women's number of EPC partners in multiple regression analyses: their anxious and avoidant attachment styles. Whereas women's anxious attachment was positively associated with their number of EPC partners, women's avoidant attachment was negatively associated with their number of EPC partners. These effects persisted even when total number of EPC sex partners was statistically controlled. It appears, then, that women most likely to engage in EPCs are those who are open to intimacy (nonavoidant) yet fearful of abandonment (anxious). Possibly, these women have been exposed during development to cues of noninvestment by men (cf. Belsky et al. 1991; Cashden 1993), which lead them to engage in EPCs as hedges against abandonment. The fact that these same women were *not* more likely to be the EPC partners of men is consistent with this speculation. (That is, it is not apparent how *being* an EPC partner, as opposed to *having* an EPC partner, would hedge against abandonment.) Future research should explore further how women's adult romantic attachment styles might reflect adaptive, evolved variations in women's mating psychology.

Summary

This research demonstrated that a heritable indicator of men's developmental health, FA, predicted the number of EPC partners they had as well as the number of times they reported having been EPC partners. This finding is consistent with the notion that men's and women's mating psychologies have evolved partly in response to the presence of genetic variation in fitness and viability. Additional research should address whether low FA men might also provide nongenetic benefits to EPC partners.

The authors thank Randall Comer, Joy Thornhill, Ellen Roots, Bryant Furlow, Tara Armijo-Prewitt, Steve Aeschliman, Dede Brown, Sherri Dabovich, Otto Han, and Donny Johnson for considerable assistance with this research.

REFERENCES

Ainsworth, M.D.S., Blehar, M.C., Waters, E., and Wall, S. *Patterns of Attachment: A Psychological Study of the Strange Situation*, Hillsdale, NJ: Erlbaum, 1978.

Anderson, R.M., and May, R.M. Regulation and stability of host-parasite population interactions, I: Regulatory processes. *Journal of Animal Ecology* 47:219–247, 1978.

Anderson, R.M., and May, R.M. Coevolution of host and parasites. *Parasitology* 85:411–426, 1982.

Bailit, H.L., Workman, P.L., Niswander, J.D., and Maclean, J.C. Dental asymmetry as an indicator of genetic and environmental conditions in human populations. *Human Biology* 42:626–638, 1970.

Baker, R.R., and Bellis, M.A. Human sperm competition: Ejaculate manipulation by females and a function for the female orgasm. *Animal Behaviour* 46:887–909, 1993.

Bartholomew, K. Avoidance of intimacy: An attachment perspective: *Journal of Social and Personal Relationships* 7:147–178, 1990.

Bartholomew, K. and Horowitz, L.M. Attachment styles among young adults: A test of a four-category model. *Journal of Personality and Social Psychology* 61:226–244, 1991.

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

Belsky, J., Steinberg, L., and Draper, P. Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialization. *Child Development* 62:647–670, 1991.

Benshoof, L., and Thornhill, R. The evolution of monogamy and concealed ovulation in humans. *Journal of Social and Biological Structures* 2:95–106, 1979.

Berscheid, E., and Walster, E. Physical attractiveness. In *Advances in Experimental Social Psychology* (Vol. 7), L. Berkowitz (Ed.). New York: Academic Press, 1974; pp. 157–215.

Betzig, L. *Depotism and Differential Reproduction: A Darwinian View of History*, Hawthorne, NY: Aldine de Gruyter, 1986.

Bowlby, J. *Attachment and Loss: Vol. 2 Separation: Anxiety and Anger*, New York: Basic Books, 1973.

Bradbury, J.W., and Andersson, M.B. (Eds.). *Sexual Selection: Testing the Alternatives*. Chichester, England: Wiley, 1987.

Buss, D.M. Evolutionary personality psychology. *Annual Review of Psychology* 42:459–491, 1991.

Buss, D.M. Evolutionary psychology: A new paradigm for psychological science. *Psychological Inquiry* 6:1–30, 1995.

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

Cashden, E. Attracting mates: Effects of parental investment on mate attraction strategies. *Ethology and Sociobiology* 14:1–24, 1993.

Collins, N.L., and Read, S.J. Adult attachment, working models, and relationship quality in dating couples. *Journal of Personality and Social Psychology* 58:644–663, 1990.

Cronin, H. *The Ant and the Peacock*, Cambridge: Cambridge University Press, 1991.

Daly, M., and Wilson, M. *Homicide*, Hawthorne, NY: Aldine de Gruyter, 1988.

Edwards, J.H. A critical examination of the reputed primary influence of ABO phenotype on fertility and sex ratio. *British Journal of Preventive and Social Medicine* 11:79–89, 1957.

Feeney, J.A., and Noller, P. Attachment style as a predictor of adult romantic relationships. *Journal of Personality and Social Psychology* 58:281–291, 1990.

Fisher, R.A. *The Genetical Theory of Natural Selection*: Oxford: Claredon, 1930.

Gangestad, S.W. Sexual selection and physical attractiveness: Implications for mating dynamics. *Human Nature* 4:205–235, 1993.

Gangestad, S.W., and Simpson, J.A. Toward an evolutionary history of female sociosexual variation. *Journal of Personality* 58:69–96, 1990.

Gangestad, S.W., and Thornhill, R. An evolutionary psychological analysis of human sexual selection: Developmental stability, male sexual behavior, and mediating features. Manuscript submitted for publication, 1996a.

Gangestad, S.W., and Thornhill, R. Sexual selection and relationship dynamics: Trade-offs between partner exclusivity and fluctuating asymmetry. Unpublished manuscript, University of New Mexico, 1996b.

Gangestad, S.W., Thornhill, R., and Yeo, R.A. Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology* 15:73–85, 1994.

Hamilton, W.D. Sex vs. non-sex vs. parasite. *Oikos* 35:282–290, 1980.

Hamilton, W.D Pathogens as causes of genetic diversity in their host populations. In *Population Biology of Infectious Diseases*, R.M. Anderson and R.M. May (Eds.). New York: Springer-Verlag, 1982, pp. 269–296.

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

Hansen, G.L. Extradyadic relations during courtship. *Journal of Sex Research* 22: 382–390, 1986.

Hazan, C., and Shaver, P. Romantic love conceptualized as an attachment process. *Journal of Personality and Social Psychology* 48:502–511, 1987.

Heywood, J.S. Sexual selection by the handicap principle. *Evolution* 43:1387–1397, 1989.

Hite, S. *Women and Love: A Cultural Revolution in Progress*, New York: Knopf, 1987.

Hrdy, S.B. *The Woman That Never Evolved*, Cambridge, MA: Harvard University Press, 1981.

Kinsey, A.C., Pomeroy, W.B., and Martin, C.E. *Sexual Behavior in the Human Male*, Philadelphia: W.B. Saunders,1948.

Kinsey, A.C., Pomeroy, W.B., Martin, C.E., and Gebhard, P.H. *Sexual Behavior in the Human Female*, Philadelphia: W.B. Saunders, 1953.

Kirkpatrick, M. Sexual selection and the evolution of female choice. *Evolution* 36:1–12, 1982.

Kirkpatrick, M. Evolution of female choice and male parental investment in polygynous species: The demise of the "sexy son." *American Naturalist* 125:788–810, 1985.

Kirkpatrick, M., and Ryan, M.J. The evolution of mating preferences and the paradox of the lek. *Nature* 350:33–38, 1991.

Kobak, R.R., and Hazan, C. Attachment in marriage: Effects of security and accuracy of working models. *Journal of Personality and Social Psychology* 60:861–869, 1991.

Lande, R. Models of speciation by sexual selection on polygenic characters. *Proceedings of the National Academy of Sciences (USA)* 70:3721–3725, 1981.

Laumann, E.O., Gagnon, J.H., Michael, R.T., and Michaels, S. *The Social Organization of Sexuality*, Chicago: University of Chicago Press, 1994.

Lerner, I.M. *Genetic Homeostasis*, Edinburgh: Oliver and Boyd, 1974.

Manning, J.T., and Chamberlain, A.T. Fluctuating asymmetry, sexual selection, and canine teeth in primates. *Proceedings of the Royal Society of London B* 251:83–87, 1993.

Markow, T., and Ricker, J.P. Male size, developmental stability, and mating success in natural populations of three Drosophila species. *Heredity* 69:122–127, 1992.

Mellen, S.L.W. *The Evolution of Love*, Oxford: Freeman, 1981.

Møller, A.P. Female swallow preference for symmetrical male sexual ornaments. *Nature* 357:238–240, 1992a.

Møller, A.P. Parasites differentially increase the degree of fluctuating asymmetry in secondary sexual characters. *Journal of Evolutionary Biology* 5:691–700, 1992b.

Møller, A.P., and Pomiankowski, A. Fluctuating asymmetry and sexual selection. *Genetica* 1993.

Møller, A.P., and Swaddle, J. *Developmental Stability and Evolution*, Oxford: Oxford University Press (in press).

Møller, A.P., and Thornhill, R. The heritability of fluctuating asymmetry. *Journal of Evolutionary Biology* (in press).

Palmer, A.R., and Strobeck, C. Fluctuating asymmetry: Measurement, analysis, patterns. *Annual Review in Ecology and Systematics* 17:392–421, 1986.

Parsons, P.A. Fluctuating asymmetry: An epigenetic measure of stress. *Biological Review* 65:131–145, 1990.

Pérusse, D. Cultural and reproductive success in industrial societies: Testing the relationship at the proximate and ultimate levels. *Behavioral and Brain Sciences* 16:267–322, 1993.

Pérusse, D. Mate choice in modern societies: Testing evolutionary hypotheses with behavioral data. *Human Nature* 5:255–278, 1994.

Pomiankowski, A., Iwasa, Y., and Nee, S. The evolution of costly mate preferences, I: Fisher and biased mutation. *Evolution* 45:1422–1430, 1991.

Rice, W.R. Heritable variation in fitness as a prerequisite for adaptive female choice: The effect of mutation-selection balance. *Evolution* 42:817–820, 1988.

Rosenthal, R. *Experimenter Effects in Behavioral Research*, New York: Irvington, 1976.

Simpson, J.A. Influence of attachment styles on romantic relationships. *Journal of Personality and Social Psychology* 59:971–980, 1990.

Simpson, J.A., and Gangestad, S.W. Personality and sexuality: Empirical relations and an integrative the-

oretical model. In *Sexuality in Close Relationships*, K. McKinney and S. Sprecher (Eds.). Hillsdale, NJ: Erlbaum, 1991, pp. 71–92.

Simpson, J.A., Gangestad, S.W., and Christensen, N. Fluctuating asymmetry and interpersonal presentation. Unpublished research, Texas A&M University, 1995.

Simpson, J.A., Rholes, W.S., and Nelligan, J.S. Support seeking and support giving within couples in an anxiety-provoking situation: The role of attachment styles. *Journal of Personality and Social Psychology* 62:434–446, 1992.

Smith, R.L. Human sperm competition. In *Sperm Competition and the Evolution of Animal Mating Systems*, R.L. Smith (Ed.). London: Academic Press, 1984, pp. 601–660.

Soule, M.E. Allometric variation. I. The theory and some consequences. *American Naturalist* 120:765–785, 1982.

Symons, D. If we're all Darwinians, what's the fuss about? In *Sociobiology and Psychology: Ideas, Issues, and Applications*, C.B. Crawford, M.F. Smith, and D.L. Krebs (Eds.). Hillsdale, NJ: Erlbaum, 1987, pp. 121–146.

Thoday, J.M. Balance, heterozygosity and developmental stability. *Cold Spring Harbor Symposium on Quantitative Biology* 20:318–326, 1955.

Thompson, A.P. Extramarital sex: A review of the research literature. *Journal of Sex Research* 19:1–22, 1983.

Thornhill, R. The study of adaptation. In *Interpretation and Explanation in the Study of Animal Behavior* (Vol. 2), M. Bekoff and D. Jamieson (Eds.). Boulder, CO: West View, 1990, pp. 31–62.

Thornhill, R. Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*: Mecoptera). *Behavioral Ecology* 3:277–283, 1992a.

Thornhill, R. Fluctuating asymmetry and the mating system of the Japanese scorpionfly (*Panorpa japonica*). *Animal Behavior* 44:867–879, 1992b.

Thornhill, R., and Gangestad, S.W. Human facial beauty: Averageness, symmetry, and parasite resistance. *Human Nature* 4:237–269, 1993.

Thornhill, R., and Gangestad, S.W. Fluccuating asymmetry and human sexual behavior. *Psychological Science* 5:297–302, 1994.

Thornhill, R., Gangestad, S.W., and Comer, R. Human female orgasm and mate fluctuating asymmetry. *Animal Behaviour* 50:1601–1615, 1996.

Thornhill, R., and Sauer, K.P. Paternal genetic effects on the fighting ability of sons and daughters and mating success of sons in a scorpionfly (*Panorpa vulgaris*). *Animal Behaviour* 43:255–264, 1992.

Tooby, J. Pathogens, polymorphism, and the evolution of sex. *Journal of Theoretical Biology* 97:557–576, 1982.

Tooby, J., and Cosmides, L. The psychological foundations of culture. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, J.H. Barkow, L. Cosmides, and J. Tooby (Eds.). New York: Oxford University Press, 1992, pp. 19–136.

Van Valen, L. A study of fluctuating asymmetry. *Evolution* 16:125–142, 1962.

Watson, P.J., and Thornhill, R. Fluctuating asymmetry and sexual selection. *Trends in Ecology and Evolution* 9:21–25, 1994.

Wilson, M., and Daly, M. The man who mistook his wife for a chattel. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, J. Barkow, L. Cosmides, and J. Tooby (Eds.). New York Oxford University Press, 1992, pp. 289–322.