



Strangers With Benefits: Attraction to Outgroup Men Increases as Fertility Increases Across the Menstrual Cycle

Joseph F. Salvatore¹, Andrea L. Meltzer², David S. March³,
and Lowell Gaertner³

Abstract

Research typically reveals that outgroups are regarded with disinterest at best and hatred and enmity at worst. Working from an evolutionary framework, we identify a unique pattern of outgroup attraction. The small-group lifestyle of pre-human ancestors plausibly limited access to genetically diverse mates. Ancestral females may have solved the inbreeding dilemma while balancing parental investment pressures by mating with outgroup males either via converting to an outgroup or cuckolding the ingroup. A vestige of those mating strategies might manifest in human women as a cyclic pattern of attraction across the menstrual cycle, such that attraction to outgroup men increases as fertility increases across the cycle. Two studies, one using a longitudinal method and the other an experimental method, evidenced the hypothesized linear relationship between attraction to outgroup men and fertility in naturally cycling women.

Keywords

intergroup processes, evolution, attraction

Received May 17, 2016; revision accepted October 12, 2016

Outgroups are typically regarded with disinterest at best and enmity and hatred at worst. Such an orientation arises, in part, from a complex interplay of identity processes and structures of intragroup and intergroup interdependence (Brewer, 2007; Gaertner & Dovidio, 2010). In the current research, we use an evolutionary framework to identify a pattern of outgroup attraction, rather than enmity, that varies across a woman's menstrual cycle.

The social group was of fundamental importance to human evolution. Groups afforded ancestors advantages such as shared resources, protection from predators, and cooperative child-rearing (Caporael, 1997, 2001; Foley, 1996; Tattersall, 2012). More than a survival strategy, the social group served as a selection environment for cognitive, emotional, and behavioral functioning (Caporael, 1997, 2007; Dunbar, 1993; Fiske, 2000; Sedikides & Skorowonski, 1997; Stevens & Fiske, 1995). Requirements for the viability of the group (e.g., internal coordination, organization) exerted pressures that shaped sociality, including plausible selection for a favorable orientation to the ingroup (Brewer, 1999; Brewer & Caporael, 2006; Caporael & Brewer, 1991; Gaertner, Iuzzini, Witt, & Oriña, 2006).

Likewise, a variety of ancestral conditions presumably promoted an aversion of outgroups that manifests in humans as different forms of prejudice. For example, the prevalence of aggression and physical attack by outgroups may have led

to the natural selection of fear-based prejudices in that ancestors who feared outgroups were better able to avoid and survive such attacks than did ancestors who lacked such fear (Schaller & Neuberg, 2012; Van Vugt, 2009). Relatedly, ancestral females who feared sexual attack by outgroup males may have better retained reproductive control than did females who lacked such rape fear (Navarrete, Fessler, Fleischman, & Geyer, 2009). Xenophobia and disgust-based prejudices may have evolved in response to threats of socially transmitted disease—ancestors who avoided individuals whose behavior or physical appearance deviated from normative standards may have better avoided pathogen transmission (Schaller & Neuberg, 2012). Hence, much outgroup antipathy is plausibly rooted in the social dynamics of our evolutionary past.

Nevertheless, a particular aspect of ancestral group-life gives reason to consider the possibility of attraction, rather than disinterest or disdain, toward outgroups. The small-group

¹Florida Atlantic University, Boca Raton, USA

²Florida State University, Tallahassee, USA

³University of Tennessee, Knoxville, USA

Corresponding Author:

Lowell Gaertner, University of Tennessee, Department of Psychology,
Knoxville, TN 37996-0900, USA.

Email: gaertner@utk.edu

lifestyle of pre-human ancestors necessarily posed a challenge in the form of restricted access to genetically diverse mates, thereby precluding the fitness benefit of heterozygous offspring (Charlesworth & Willis, 2009; Penn & Potts, 1999; Roberts & Little, 2008). The size of ancestral residential groups (i.e., demes, bands), which is estimated to have ranged from 20 to 130 members (Aiello & Dunbar, 1993; Caporael, 2007; Marlow, 2005; Tattersall, 2012; Wobst, 1974), falls perilously below the estimated minimum-necessary size for a population of mammals to remain viable (3,876 members; Traill, Bradshaw, & Brook, 2007). Such estimates, although not without controversy (Garnett & Zander, 2011; but see Brook, Bradshaw, Traill, & Frankham, 2011), suggest that *Homo sapiens* would not have evolved if their small-group living ancestors did not overcome their inbreeding dilemma by mating outside of their groupings (Chapais, 2008, 2013; Hill et al., 2011).

So, how might have ancestral outgroup mating occurred? At least four strategies are plausible (and not necessarily mutually exclusive). Whereas two strategies lacked ancestral-female choice to mate with an outgroup male, two other strategies involved female choice. It is those choice-based strategies that might manifest in human women as a pattern of attraction to outgroup men that varies across the menstrual cycle. We review all four strategies in turn.

One strategy lacking female choice could have been a mutual intergroup exchange of reproductively able females (Caporael, 2007; Wobst, 1974). Perhaps groups gathered annually or seasonally to exchange females. Such an exchange likely obviated female choice as the decision to mate with an outgroup male would have been actively imposed (e.g., “you must go”) or normatively engaged as social convention. Of course, an exchange of males could also have been possible. A male exchange, however, may have been less likely if there was division of labor between the sexes, with males serving as warriors and hunters (Van Vugt, 2009; Van Vugt, De Cremer, & Janssen, 2007). The other strategy lacking female choice could have been rape (Thornhill & Thornhill, 1992). As an inbreeding solution, rape would have had to have been perpetrated more consistently against outgroup than ingroup females and, as a counter strategy, females may have developed a fear of outgroup males (McDonald, Asher, Kerr, & Navarrete, 2011; Navarrete et al., 2009).

The two female-choice strategies both account for the greater parental investment required by ancestral females than males (Trivers, 1972; Buss, 1989), but they do so differently. One strategy could have been for females to mate with an outgroup male with the provision that he and his group invest in the offspring’s survival. That is, some ancestral females may have volitionally “converted” to the outgroup male’s collective (Clutton-Brock, 1989). The other strategy could have been for ancestral females to furtively mate with outgroup males in an act of cuckoldry against an existing partner and ingroup. Secrecy would have been essential

because her partner and group would have resisted investing in the survival of an outgroup offspring.¹

If outgroup mating solved the inbreeding dilemma and provided a fitness benefit to ancestral females who chose an outgroup mate relative to those who did not, then a trace of the fitness-affording choice should persist in human women (e.g., Thornhill & Gangestad, 2008). Research on menstrual cycle shifts in women’s behavior is consistent with the possibility that ancestral females avoided inbreeding and were drawn to males who could provide heterozygous offspring. For example, women on more (than less) fertile days of their cycle report stronger disgust of aberrant sexual behavior such as incest (Fessler & Navarrete, 2003), are more avoidant of their fathers but not their mothers (Lieberman, Pillsworth, & Haselton, 2011), and experience greater sexual attraction to extra-pair men to the extent that those women and their partners have genetically similar immune systems (Garver-Apgar, Gangestad, Thornhill, Miller, & Olp, 2006).²

If conversion and cuckolding were successful gene-capturing strategies of ancestral outgroup mating, a vestige of those strategies might manifest in human women as a cyclic pattern of attraction across the menstrual cycle such that attraction to outgroup men increases as fertility increases across the cycle. Furthermore, if the attraction-fertility pattern is indeed a footprint of an ancestral-female strategy for genetic diversity, then it should occur uniquely in response to outgroup men and should not occur in response to ingroup men or to women of either group. Finally, the pattern might best manifest in naturally cycling women but not in women whose cycle is altered by hormonal contraceptives, given that hormonal contraceptives alter psychological phenomenon that are synced to the menstrual cycle by suppressing ovulation (e.g., Alvergne & Lummaa, 2010).

We test in two studies whether attraction to outgroup men increases with increased fertility across the cycle. Study 1 uses a longitudinal design that measures women’s desire to go on a date with a different-race man at three points of their menstrual cycle. Study 2 uses a between-subjects design that compares women who are on different days of their cycle in terms of how physically attractive they find a standardized set of male and female targets whose presumed ethnicity is experimentally manipulated to be the same as (i.e., ingroup member) or different than (i.e., outgroup member) the women’s own ethnicity. We estimate fertility by calculating a woman’s menstrual cycle day (Garver-Apgar, Gangestad, & Thornhill, 2008) and assigning her a corresponding actuarial-based risk score of conceiving an offspring (i.e., conception risk; Wilcox, Dunson, Weinberg, Trussell, & Baird, 2001).³

Study 1

Method

A total of 118 women enrolled in introductory psychology at a Southeastern university completed an online screener to

assess their eligibility (i.e., not using hormonal contraception, regular menstrual cycle length of 24 through 35 days, heterosexual, and of college age). We invited the 50 eligible women to participate, 39 of whom accepted and participated for partial course credit. Two women provided incomprehensible menstrual information, leaving an effective sample of 37 women (27 Caucasian, seven African American, two Asian, and one Hispanic; $M_{\text{age}} = 18.73$ years, $SD = 0.99$, range = 18–22).

Based on their reported cycle length and date they began their recent cycle, we standardized women to a 28-day cycle (following Garver-Apgar et al., 2008). We attempted to schedule women to participate at three points of their cycle (early, middle, and late) to allow within-person variation in conception risk. A total of 14 women began the study early cycle (before day 10), eight began midcycle (days 10–15), and 15 began late cycle (after day 15). The number of days between the first and second sessions varied among women ($M = 8.37$ days, $SD = 4.16$), as did the number of days between the second and third sessions ($M = 8.63$ days, $SD = 2.91$). Neither the point of the cycle on which women began the study nor the number of days between sessions moderated the predicted effect.⁴

We emailed participants a web-link the morning of each session. In addition to responding to items included for other purposes, women reported the date they began their recent cycle and responded to two hypothesis-relevant items. They indicated their current desire to go on a date with a different-race man: “how interested would you be in going out on a date with a man of a different race tonight?” To ensure that responses are not an artifact of a mere desire to go on a date, they also indicated: “how interested would you be in going out on a date with a man tonight?” Women responded on scales ranging from 0 = *not at all* to 100 = *completely*, with the desire-to-date-a-man item preceding the desire-to-date-a-different-race-man item.

Results

For each session, we calculated a woman’s menstrual cycle day standardized to a 28-day cycle (based on cycle length, start date of most recent cycle, and session date; see Garver-Apgar et al., 2008) and assigned her a conception risk using estimates reported in Table 1 of Wilcox et al. (2001) for “all women” (conclusions based on direction of effects, and p values are the same using Wilcox et al.’s estimates for “regular cycles”).

Nested within women are ratings of their desire to go on a date with a different-race man (and desire to go on a date) and corresponding conception risk for as many as 3 cycle-days. We accounted for the nesting using multi-level regression in Proc Mixed of SAS. To test the within-person association between desire to date a different-race man and conception risk, we person-centered each woman’s conception-risk score and controlled her average conception risk

(i.e., mean conception risk across her sessions; Raudenbush & Bryk, 2002; Wang & Maxwell, 2015). For each analysis, we conducted model comparisons (using restricted maximum likelihood and log-likelihood tests) to identify the most appropriate structure of random effects (i.e., which random slopes and covariances should be estimated along with a random intercept). We report analyses that do not control participant race, but note that conclusions based on direction of effects and p values are the same when race is covaried.

We regressed desire-to-go-on-a-date-with-a-different-race-man onto conception risk (person-centered Level 1 variable), the woman’s average conception risk (grand-mean-centered Level 2 variable), and a random effect for the intercept. Consistent with the outgroup-mating hypothesis, desire to date a different-race man *increased* with within-person increases in conception risk, $B = 144.19$, $SE = 72.42$, $F(1, 58) = 3.96$, $p = .0512$, 95% confidence interval (CI) = $[-0.78, 289.16]$. As a woman became more likely to conceive, she reported a stronger desire to go on a date with a different-race man.

We conducted a second analysis to ensure that the latter pattern is not an artifact of an increased desire to go on a date in general. Indeed, the two desire variables correlate at $r = .62$. We regressed desire-to-go-on-a-date-with-a-different-race-man onto conception risk (person-centered Level 1 variable), the woman’s average conception risk (grand-mean-centered Level 2 variable), desire-to-go-on-a-date-with-a-man (person-centered Level 1 variable), the woman’s average desire-to-go-on-a-date-with-a-man (grand-mean-centered Level 2 variable), and random effects for the intercept and slope of person-centered desire-to-go-on-a-date-with-a-man. Desire to date a different-race man increased with within-person increases in desire to go on a date, $B = 0.63$, $SE = 0.09$, $F(1, 18) = 48.07$, $p = .0001$, and was stronger among women who on average reported a greater desire to go on a date, $B = 0.36$, $SE = 0.13$, $F(1, 39) = 7.90$, $p = .0077$. Independent of those effects, however, desire to date a different-race man continued to *increase* with within-person increases in conception risk, $B = 92.96$, $SE = 36.89$, $F(1, 39) = 6.35$, $p = .0160$, 95% CI = $[18.33, 167.59]$.

These data suggest that the positive within-person association between conception risk and desire to go on a date with a different-race man is not an artifact of a corresponding desire simply to go on a date. Indeed, regressing desire-to-go-on-a-date-with-a-man onto conception risk (person-centered Level 1 variable), the woman’s average conception risk (grand-mean-centered Level 2 variable), and a random effect for the intercept reveals no association with within-person changes in conception risk, $B = 58.59$, $SE = 91.58$, $F(1, 58) = 0.41$, $p = .5248$. Only desire to go on a date with a different-race man increases with increased conception risk.

Discussion

Women reported their desire to go on a date with a different-race man on as many as 3 different days of their menstrual

cycle. Desire to date a different-race man increased as conception risk increased. This pattern is consistent with the possibility that ancestral females solved the inbreeding dilemma of small-group living by choosing to mate with outgroup males.

One limitation of the current method is that we lacked control over the different-race men who women envisioned dating on the different days of their cycle. A skeptic might suggest that at higher conception risk, women imagined men who were distinct from the men they imagined at lower conception risk. Stated otherwise, desire to date a different-race man may have remained constant across the cycle and what fluctuated was the desirability of the imagined men. However, this alternative might simply be a restatement of the hypothesis. Absent the conversion or cuckold strategies, it is unclear why women would envision more desirable different-race men as conception risk increased. Another way to test the hypothesis would be to hold constant the outgroup man and assess whether his perceived attractiveness increases with conception risk. The cuckold and conversion strategies imply that outgroup men will appear more attractive with increased conception risk. Such is what we test in Study 2.

A second limitation is that we did not assess fear of rape. Rape fear is potentially important in that research on sexual-coercion avoidance (McDonald et al., 2011; Navarrete et al., 2009) suggests that a menstrual cycle shift in ingroup favoritism is moderated by perceived vulnerability to sexual assault (e.g., rape fear, associating the outgroup more than the ingroup with physical formidability). For example, Caucasian women who have a higher (than lower) rape fear evaluate the social category of White people more favorably than they evaluate the social category of African American people at higher than lower conception risk (Navarrete et al., 2009). In Study 2, we measure rape fear to assess its moderating potential.

Study 2

In the current study, we manipulated the presumed ingroup versus outgroup membership of male and female faces, and women who were on a different day of their respective cycle rated the physical attractiveness of each face. Hence, women saw the same faces and the only systematic variation was the manipulated membership of each face. Both the conversion and cuckold strategies of ancestral-female outgroup mating imply that the perceived attractiveness of outgroup men (but not ingroup men or women of either group) will increase with increased conception risk.

Furthermore, we employed a distinction in the mate preference literature to empirically distinguish the conversion and cuckold strategies. Based on the possibility that our ancestors faced trade-offs between nurturing existing offspring and conceiving additional offspring, different preferences evolved for the qualities of long-term relationship partners and short-term sex partners (Gangestad & Simpson,

2000). Conversion and cuckolding both involved capturing outgroup genes and similarly imply that human women will find outgroup men increasingly physically attractive and appealing as short-term sex partners as conception risk increases. Only the conversion strategy, in addition, implies that women will find outgroup men increasingly appealing as long-term relationship partners as conception risk increases because according to only the conversion strategy did ancestral outgroup males serve a child-rearing role.

Pilot Study

We sought photographs of the faces of moderately attractive (to avoid floor and ceiling effects), college-aged men and women who could be perceived as being either Caucasian or Hispanic (so we could manipulate their presumed group membership in the main study in regard to our Caucasian participants). We presented 108 faces that approximated our criteria to two samples of college-aged Caucasian American women via Mechanical Turk.

One sample ($n = 16$, $M_{\text{age}} = 22.44$ years) rated the ethnicity of each face on a scale anchored at the extremes by 1 = *could only be Hispanic* and 9 = *could only be Caucasian* and anchored at the midpoint by 5 = *could be either Hispanic or Caucasian*. The other sample ($n = 21$, $M_{\text{age}} = 22.66$ years) rated the physical attractiveness of each face on a scale anchored at the extremes by 1 = *extremely unattractive* and 9 = *extremely attractive* and anchored at the midpoint by 5 = *neither unattractive nor attractive*.

We selected 16 male faces and 16 female faces that received average ratings near the midpoint of both the Ethnicity and Attractiveness scales. Hence, we obtained a set of 32 faces of college-aged persons who could pass for either ethnicity ($M = 5.11$, $SD = 0.73$) and are moderately attractive ($M = 5.77$, $SD = 0.88$).

Method

In total, 142 non-Hispanic Caucasian women at a Southeastern university participated for credit in an introductory psychology course. Upon arrival to the laboratory, participants sat in private computer cubicles. Instructions noted that the purpose of the study was to obtain, for future research, photos of Hispanics and Caucasians who vary in attractiveness.

Each of the 32 pilot-tested faces (see Supplemental Material) was presented with a label indicating whether the person was Hispanic or Caucasian. The label was assigned randomly to each face for each participant but constrained so that half of the male and female faces for a given participant were labeled Hispanic, and half were labeled Caucasian. Participants rated the physical attractiveness of each face ("How physically attractive do you find this individual?") and additionally rated the attractiveness of each male face for a long-term relationship ("How attractive do you find this individual for a long-term relationship?") and a short-term

relationship ("How attractive do you find this individual for a short-term relationship, that is, a one-night stand?"), with ratings made on 9-point scales (1 = *extremely unattractive* to 9 = *extremely attractive*). Each face was presented separately for each rating, and the order of the faces and ratings was randomized for each participant (the ethnic label for a given face was held constant across ratings within participants). Hence, all participants viewed the same faces and what varied was whether a given face was an ingroup (Caucasian) or outgroup (Hispanic) member. Participants subsequently reported whether they were using hormonal contraception, the typical length of their menstrual cycle, and (with aid of a calendar) the date they began their recent menstrual cycle, and completed the *Fear of Rape* scale ($\alpha = .92$; Senn & Dzinis, 1996).

Results

We excluded 25 participants because they reported dates for a future (rather than recent) menstrual cycle ($n = 4$), had aberrant cycle lengths greater than 40 or less than 20 days ($n = 12$), or were 10 or more days late for their period ($n = 9$). Our effective sample consisted of 117 women ($M_{\text{age}} = 18.25$ years, $SD = 0.59$, range = 18–22), 77 of whom were not using hormonal contraception. We computed each woman's mean rating for the physical-attraction, short-term, and long-term items, respectively, as a function of target sex and target group and, as in Study 1, assigned her a conception risk based on her estimated cycle day standardized to a 28-day cycle.

Physical attraction. We regressed physical attraction on a factorial crossing of conception risk (mean centered), hormonal contraception, target sex, and target group, with the latter two as within-subject variables. Consistent with the conversion and cuckold strategies, there was a significant interaction of Conception Risk \times Hormonal Contraception \times Target Sex \times Target Group, $F(1, 113) = 8.36$, $p = .0046$. The interaction is such that conception risk predicted physical attraction only when women not using hormonal contraception rated outgroup men (see Table 1 and Figure 1). In particular, as the conception risk of naturally cycling women *increased*, they perceived outgroup men to be *increasingly* physically attractive, $B = 11.19$, $SE = 4.88$, $F(1, 113) = 5.25$, $p = .0238$, $\eta^2 = .044$, 95% CI = [1.52, 20.86]. No other combination of group, sex, and contraception evidenced a conception-risk effect.

We added to the prior analysis the main and interactive effects of mean-centered rape fear and found no evidence of moderation. The four-way interaction of Conception Risk \times Hormonal Contraception \times Target Sex \times Target Group remained, $F(1, 109) = 9.84$, $p = .0022$, and did not vary by rape fear (i.e., five-way interaction), $F(1, 109) = 0.37$, $p = .5422$. Likewise, conception risk continued to positively predict the perceived attractiveness of outgroup men for naturally cycling women, $B = 11.15$, $SE = 4.84$, $F(1, 109) = 5.31$, $p = .0231$, $\eta^2 = .043$, and

Table 1. Effect of Conception Risk on Attraction (Regression Parameter, F Value, p Value, and η^2 Effect-Size Estimate) as a Function of Hormonal Contraception, Target Sex, and Target Group.

Targets	Hormonal contraception							
	Not Using				Using			
	B	F	p	η^2	B	F	p	η^2
Physical attraction								
Male								
Outgroup	11.19	5.25	.0238	.044	-2.91	0.20	.6528	.002
Ingroup	2.39	0.30	.5875	.003	8.58	2.18	.1425	.019
Female								
Outgroup	3.69	0.83	.3629	.007	6.27	1.38	.2422	.011
Ingroup	4.02	1.12	.2916	.009	4.19	0.70	.4049	.006
Long-term attraction								
Male								
Outgroup	12.47	4.93	.0284	.042	-3.70	0.25	.6185	.002
Ingroup	0.38	0.01	.9364	.000	4.96	0.63	.4299	.005
Short-term attraction								
Male								
Outgroup	13.10	4.65	.0331	.040	-0.29	0.00	.9708	.000
Ingroup	4.02	0.58	.4477	.005	9.52	1.87	.1745	.016

Note. All values are based on $F(1, 113)$.

did not vary by rape fear (i.e., Conception Risk \times Rape), $F(1, 109) = 0.11$, $p = .7357$, $\eta^2 = .001$.

Attraction as a short-term versus long-term partner. We regressed the short-term and long-term ratings of the male faces onto a factorial crossing of conception risk (mean centered), hormonal contraception, target group, and rating type (short, long), with the latter two as within-subject variables. Consistent with the conversion strategy, there was a three-way interaction of Conception Risk \times Hormonal Contraception \times Target Group, $F(1, 113) = 7.04$, $p = .0091$, which did not vary by rating type (i.e., four-way interaction), $F(1, 113) = 0.16$, $p = .6924$. The three-way interaction is such that conception risk predicted short-term or long-term attraction only when women not using hormonal contraception rated outgroup men (see Table 1 and Figure 2). In particular, as the conception risk of naturally cycling women *increased*, they perceived outgroup men to be *increasingly* attractive as short-term partners, $B = 13.10$, $SE = 6.07$, $F(1, 113) = 4.65$, $p = .0331$, $\eta^2 = .040$, 95% CI = [1.07, 25.12], and long-term partners, $B = 12.47$, $SE = 5.62$, $F(1, 113) = 4.93$, $p = .0284$, $\eta^2 = .042$, 95% CI = [1.34, 23.59]. No other combination of group and contraception evidenced a conception-risk effect on short-term or long-term attraction.

We added to the prior analysis the main and interactive effects of mean-centered rape fear and found no evidence of moderation. The three-way interaction of Conception Risk \times Hormonal Contraception \times Target Group remained, $F(1, 109) = 9.52$, $p = .0026$, and did not vary by rape fear (i.e.,

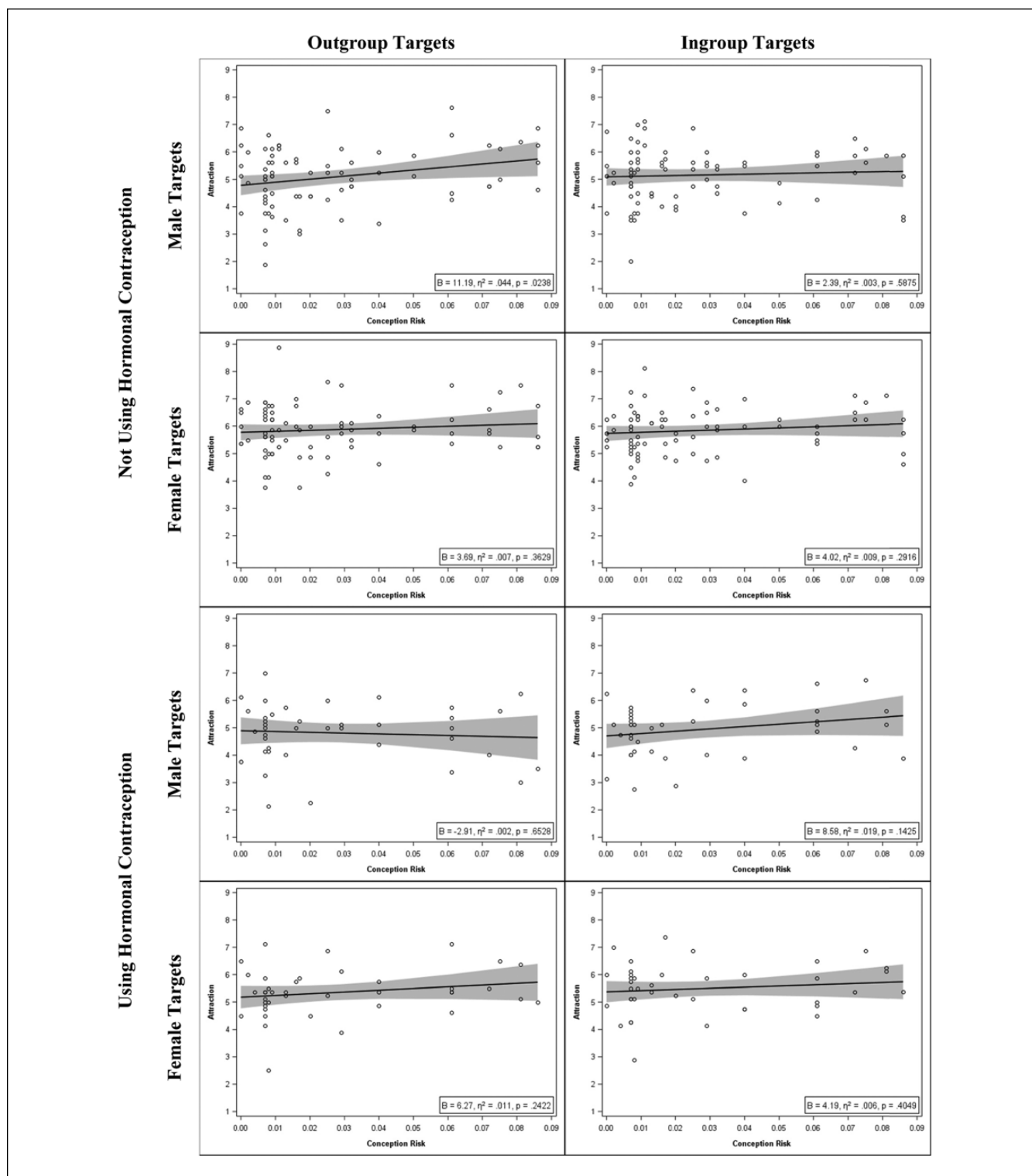


Figure 1. Physical attraction (with 95% confidence limits and η^2 effect-size estimate of conception risk) as a function of conception risk, contraception, target sex, and target group.

four-way interaction), $F(1, 109) = 0.21, p = .6480$. Likewise, conception risk continued to positively predict naturally cycling women's short-term, $B = 13.11, SE = 6.11, F(1, 109) = 4.61, p = .0340, \eta^2 = .039$, and long-term, $B = 12.59, SE =$

$5.58, F(1, 109) = 5.08, p = .0262, \eta^2 = .042$, attraction to outgroup men, and neither varied by rape fear (i.e., Conception Risk \times Rape), $F_{\text{short}}(1, 109) = 0.18, p = .6575, \eta^2 = .002$ and $F_{\text{long}}(1, 109) = 0.00, p = .9611, \eta^2 = .000$.

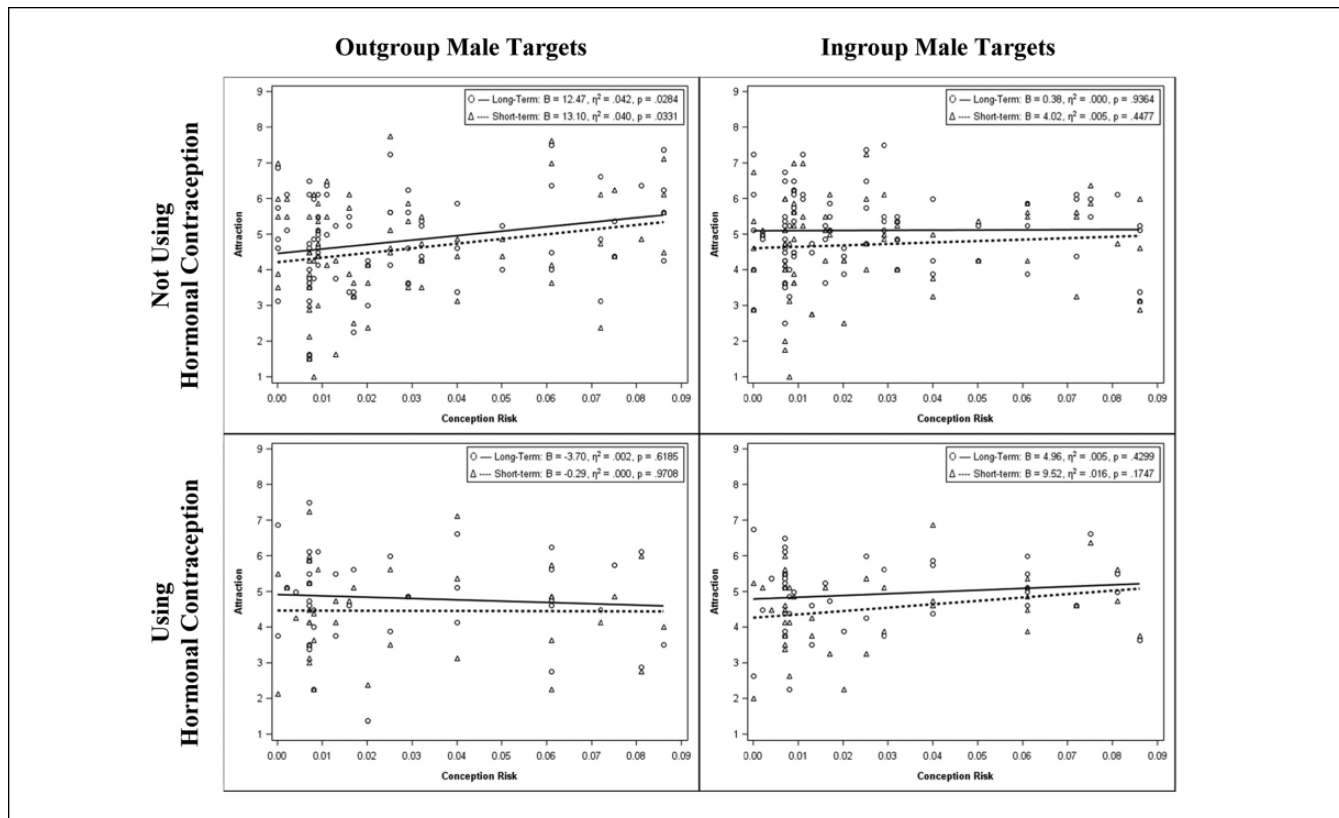


Figure 2. Attraction (with η^2 effect-size estimate of conception risk) as a long-term partner (circles and solid lines) and short-term partner (triangles and dotted lines) as a function of conception risk, contraception, and target group.

Discussion

We manipulated the ethnicity of male and female faces such that half were labeled ingroup members and half were labeled outgroup members. Despite viewing the *same* faces, women's perception of the faces varied across the menstrual cycle, as we predicted, based on the conversion and cuckold strategies of ancestral-female mating. Naturally cycling women perceived outgroup men (but not ingroup men or women of either group) to be increasingly physically attractive with increased conception risk.

That this attraction-fertility pattern occurred uniquely to outgroup men is consistent with the genetic-diversity function of the conversion and cuckold strategies. It was not the case that women perceived all men to be increasingly attractive with conception risk: It occurred in response to outgroup men but not ingroup men. Likewise, it was not the case that women perceived all outgroup members to be increasingly attractive with increased conception risk: It occurred in response to outgroup men but not outgroup women. For small-group living ancestral females, the benefit provided by outgroup males (but not ingroup males or females of either group) was a solution to the inbreeding dilemma in the possibility of genetically diverse progeny. That attraction increased uniquely to outgroup men with

increased conception risk for naturally cycling women is consistent with the hypothesized ancestral-female outgroup-mating strategies.

To distinguish between vestiges of the cuckolding and conversion strategies, we additionally had women rate male faces in terms of their attractiveness as short-term and long-term partners. The cuckold strategy implies that the attractiveness of outgroup men as short-term (but not long-term) partners will increase with increased fertility across the cycle because ancestral outgroup mating was solely for gene capturing, with long-term child care having been provided by the cuckolded ingroup. The conversion strategy, in contrast, implies that the attractiveness of outgroup men as short-term and long-term partners will increase with increased fertility across the cycle because ancestral outgroup males served as both a source of genetic diversity and child care. That naturally cycling women perceived outgroup (but not ingroup) men to be increasingly attractive as both short-term and long-term partners as conception risk increased across the cycle is consistent with the conversion strategy.

Readers familiar with the cycle-shift literature will be quick to note that cycle-shift effects are typically found in regard to short-term but not long-term attraction. In that literature (as reviewed by Gildersleeve, Haselton, & Fales, 2014; but also see Wood, Kressel, Joshi, & Louie, 2014),

short-term attraction varies in response to male displays that ostensibly signal genetic quality (e.g., symmetry), and the cycle shift reflects a sexual motive to capture genes. Ancestral females did not necessarily rely on males displaying such cues for child-rearing and balanced parental investment pressures in other ways, which is why such cues yield cycle shifts in short-term but not long-term attraction. Unique to the conversion strategy of outgroup mating is that it simultaneously balanced ancestral concerns with genetic variability and parental investment: The outgroup was a source of genetic diversity and child-rearing. Sex for genes *and* parental investment co-occurred with conversion. What manifests in human women as a cycle shift in both short-term and long-term attraction to outgroup men is presumably evidence of the reproductive utility of ancestral outgroup males as both sex and relationship partners.

Of course, the current empirical distinction between short-term and long-term attraction is far from definitive support for the conversion strategy. There are other plausible explanations for the long-term ratings that do not involve the possibility that ancestral females converted groups. One explanation is that a halo-effect (Thorndike, 1920) drives the long-term ratings as a function of the short-term ratings. If, as implied by the cuckold strategy, women at increased fertility are increasingly attracted to outgroup men as sex partners, then a general favorableness could color ratings of outgroup men across multiple dimensions. In which case, the observed pattern in long-term ratings is not diagnostic of the long-term appeal of outgroup men. Another explanation is that the long-term ratings were driven by a motivated bias that unconstrained ancestral females from parental investment pressures and enabled them to engage in short-term sexual relationships with genetically advantageous males. Durante, Griskevicius, Simpson, and Li (2012), for example, demonstrate that ovulating women over-estimate the fatherly quality of physically attractive and dominant men (i.e., men who ostensibly signal “good-genes,” but are less apt to maintain long-term relationships). Although our data are consistent with the conversion strategy, additional research is necessary to further clarify the cuckold and conversion strategies.

Finally, we acknowledge that women could evidence attraction to outgroup men for reasons other than a vestige of an ancestral genetic-diversity strategy. Women, for example, might seek an outgroup mate for upward mobility. Such an account of the current data, however, is rendered less plausible given that Hispanics (the outgroup) are a group of *lower* status and power in the United States than Caucasians (the ingroup; Bobo & Zubrinsky, 1996). Nonetheless, women could find outgroup men appealing for reasons other than vestiges of ancestral mating.

General Discussion

By contemplating a challenge faced by pre-human ancestors, we identified a shifting pattern of outgroup attraction that

previously remained latent to intergroup science and contrasts with the typically observed tendency to disregard, if not despise, outgroups. We reasoned that some ancestral females solved the inbreeding dilemma of their small-group lifestyle by choosing an outgroup mate and managed parental investment concerns by cuckolding the ingroup or converting to the outgroup. We hypothesized that a footprint of that fitness-affording choice would manifest in women as a pattern of attraction to outgroup men that increases with increased fertility across the menstrual cycle.

We observed the hypothesized pattern among naturally cycling women in two studies. We used a longitudinal design in Study 1 and observed within-person increases in desire to date a different-race man increase with within-person increases in conception risk. That pattern was unique to a desire to go on a date with a different-race man and did not occur simply in regard to a desire to go on a date with a man. We used an experimental design in Study 2 and compared Caucasian women on different cycle-days in regard to how attractive they perceived male and female faces that we randomly assigned as Caucasian (ingroup) or Hispanic (outgroup). The perceived attractiveness of outgroup men (but not ingroup men or women of either group) increased across women with increased conception risk.

That two different methods revealed the same conceptual pattern of attraction to outgroup men suggests that the pattern reflects a relatively complex intergroup orientation in women. In what follows, we consider remaining issues and broader implication of this work.

Remaining Issues

Some issues constitute alternative explanations and others involve potentially important nuances. When possible, we empirically address the issues with data.

Is it masculinity? Perhaps the observed pattern of outgroup attraction is derivative from more basic work in the cycle-shift literature. An outgroup might simply be a proxy for masculinity, which women find appealing at increased fertility (Gildersleeve et al., 2014; Meltzer, 2016; cf. Wood et al., 2014). Consequently, women at higher conception risk in Study 1 might have imagined more masculine different-race men and in Study 2 perceived the outgroup men to be more masculine. We consider this masculinity explanation unlikely particularly for the standardized photos of Study 2 because in the cycle-shift literature, women respond to visible (not imagined) cues. Nonetheless, we tested this possibility with a sample of 133 women via Mechanical Turk screened as Caucasian, 18 to 25 years, and not using hormonal contraception.

Participants rated the masculinity of the 32 faces used in Study 2 (“How masculine is this face?” 1 = *not at all masculine* to 7 = *extremely masculine*). Each face was randomly assigned a label so that half of the male and female faces were “Hispanic” and the others were “Caucasian.” Participants

subsequently reported the typical length of their menstrual cycle and the date they began their recent cycle. We standardized women to a 28-day cycle and assigned them a conception risk as in Study 1 and 2. We excluded 18 women who reported an aberrant date of their recent cycle ($n = 4$; ranged from 9 months to 24 years before the session), an aberrant cycle length greater than 40 or less than 20 days ($n = 11$), or were 10 or more days late for their period ($n = 3$), which yielded an effective sample of 115 women.

We computed each woman's mean masculinity rating as a function of target sex and group and regressed those ratings on a factorial crossing of conception risk (mean centered), target sex, and target group (with the latter two as within-subject variables). As one would expect, women perceived male faces as more masculine than female faces: Women perceived (a) Caucasian men as more masculine ($M = 5.47$, $SD = 0.80$) than Caucasian women ($M = 1.86$, $SD = 0.70$), $F(1, 113) = 1,046.39$, $p = .0001$, and (b) Hispanic men as more masculine ($M = 5.52$, $SD = 0.81$) than Hispanic women ($M = 1.78$, $SD = 0.63$), $F(1, 113) = 1,071.93$, $p = .0001$, and neither varied by conception risk, $F_s(1, 113) < 0.79$, $p_s > .37$. Notably inconsistent with the masculinity explanation of outgroup male attraction is that women perceived Hispanic men as *no more* masculine than Caucasian men, $F(1, 113) = 1.14$, $p = .2874$, and that did not vary by conception risk, $F(1, 113) = 0.24$, $p = .6240$. Even at the highest value of conception risk, women did not perceive masculinity differences between Hispanic men ($M = 5.46$) and Caucasian men ($M = 5.45$), $F(1, 113) = 0.00$, $p = .9588$. Thus, the attraction-fertility pattern to outgroup men is an improbable product or proxy of imagined or perceived masculinity.

Outgroup attraction and outgroup fear? Research on sexual-coercion avoidance (McDonald et al., 2011; Navarrete et al., 2009) indicates that women high in rape-fear evidence more favorable ingroup than outgroup evaluations on days of higher than lower conception risk. The explanation is that in the ancestral environment, outgroup males frequently perpetrated rape, and females who feared them better retained reproductive choice and, thereby, reaped a fitness benefit. The pattern observed in the sexual coercion-avoidance literature for women high in rape fear is opposite in form to the pattern detected in the current research. Of course, sexual-coercion-avoidance and genetic-diversity-promoting processes can coexist. We offer two reasons as to how we were able to observe the previously undetected genetic-diversity process.

One reason is that observation of the opposing processes requires assessments that are differentially sensitive to their differing manifestations (e.g., Boldry, Gaertner, & Quinn, 2007). The sexual-coercion-avoidance pattern is typically assessed with the Implicit Association Test (IAT; Greenwald, Nosek, & Banaji, 2003), which assesses the associative strength between two social groups (e.g., Blacks and Whites) and two valenced-attribute categories (e.g., good and bad) by

tracking the speed with which persons simultaneously categorize exemplars of the group and the attribute. In Study 2 of the current research, in contrast, participants made judgments about exemplars (face photos) that were informed by group membership (Hispanic or Caucasian). The important distinction is that the IAT is influenced more so by associations with the groups than with the exemplars of those groups (De Houwer, 2001; Olson & Fazio, 2003). To the extent that an assessment focuses on the group (e.g., IAT), associations with the group (e.g., Black-Bad, White-Good) might reveal patterns differently than an assessment that focuses on specific group members (e.g., is *he* attractive? for example, Insko & Schopler, 1998; Sears, 1983). In both instances, the group influences responding, but different processes are tapped.

Another reason is that the processes are influenced by different cues. Navarrete et al. (2009) suggest that hostile stereotypes mute the expression of the genetic-diversity process:

in the event that both coercion-avoidance processes and heterogeneity-attraction processes are operative, it may be difficult to find evidence of the latter in a cultural milieu where negative stereotypes (including those involving victimization) of social out-groups are pervasive. . . . heterogeneity-attraction processes may be detectable only in contexts where negative stereotypes are not cognitively accessible or do not include associations with danger. (p. 664)

A coercion-avoidance pattern has been detected primarily with Blacks as the outgroup. In contrast, we detected a genetic-diversity pattern in Study 2 with Hispanics as the outgroup (we did not assess the race of the different-race men who women envisioned in Study 1).

We conducted a study examining whether Caucasian women differentially associate White, Black, and Hispanic men with sexual violence. We recruited from Mechanical Turk 87 non-Hispanic Caucasian American women between the ages of 18 and 24 who were not using hormonal contraceptives. Women rated the extent (1 = *not at all* to 7 = *very much*) that White, Black, and Hispanic men are sexually violent, sexually forceful, and sexually hostile; completed the fear of rape scale (Senn & Dzinis, 1996); and provided menstrual cycle information (i.e., cycle length and when their recent cycle began). We excluded 12 women who reported aberrant cycle lengths greater than 40 or less than 20 days ($n = 9$) or were 10 or more days late for their period ($n = 3$). We averaged the violent, forceful, and hostile items to create a sexual-violence index for each ethnicity ($\alpha > .85$). A repeated-measures ANOVA indicated that Caucasian women perceived Hispanic men as no more sexually violent ($M = 3.78$, $SD = 1.45$) than White men ($M = 3.77$, $SD = 1.36$), $F(1, 74) = 0.00$, $p = .9543$, but they perceived Black men ($M = 4.04$, $SD = 1.55$) as more sexually violent than both Hispanic men, $F(1, 74) = 6.77$, $p = .0112$, and White men, $F(1, 74) = 6.42$, $p = .0134$. Adding mean-centered rape fear and conception risk revealed no moderating effects of rape, $F(2, 70) = 1.48$, $p = .2358$; conception risk, $F(2, 70) = 0.40$, $p = .6696$;

nor Rape \times Conception Risk, $F(2, 70) = 0.14, p = .8697$. Such data suggest that we were able to detect a genetic diversity, rather than coercion-avoidance, process in Study 2 because women do not associate Hispanic men with sexual violence.

Hence, it is plausible that vestiges of coercion-avoidance and genetic-diversity strategies coexist in women. Category-based versus exemplar-based assessments might differentially tap the processes, and different cues might differentially activate each process (e.g., Neuberg, Kenrick, & Schaller, 2010; Schaller, Simpson, & Kenrick, 2006). Indeed, the genetic-diversity process would not activate in response to any outgroup man, but likely requires that fertile women feel safe and in control of mate choice. Given that there is now evidence consistent with both processes, an important next-step is to identify and explore the constellation of cues on which outgroup fear and attraction are contingent.

Is outgroup attraction limited to ethnic groups? Related to the latter issue is the nature of groups to which genetic diversity-based outgroup attraction extends. Studies 1 and 2 provided evidence in regard to ethnically defined groups. To provide a strong test of generalization, we conducted a study using the minimal-group paradigm—a procedure in which participants are categorized into novel groups. Indeed, evidence of coercion avoidance has been observed in minimal groups (McDonald et al., 2011, Study 2).

A total of 244 naturally cycling Caucasian women at a Southeastern university completed an ostensible perceptual-task in which they had to quickly assess the number of target symbols that appeared among distractor symbols (see Gramzow & Gaertner, 2005). Instructions explained that the task classifies people as belonging to Perceptual Group A or B, and participants learned that they are in Group A. Participants then rated the physical attractiveness of the 16 male faces from Study 2, which we randomly labeled such that half were in Group A and half were in Group B. Participants reported the typical length of their menstrual cycle and the date they began their recent cycle and completed the fear of rape scale. We computed each woman's mean attraction rating as a function of target group and assigned her a conception risk as in Studies 1 and 2. We regressed attraction ratings onto a factorial crossing of conception risk (mean centered), rape (mean centered), and target group (a within-subject variable). Conception risk (a) did not differentially predict ingroup versus outgroup attraction (i.e., Conception Risk \times Group), $F(1, 240) = 0.03, p = .8547$ —and that two-way interaction was not moderated by rape fear (i.e., Conception Risk \times Group \times Rape), $F(1, 240) = 0.13, p = .7150$ —and (b) it did not predict either attraction to the ingroup, $B = -3.23, SE = 2.07, F(1, 240) = 2.44, p = .1198, \eta^2 = .010$, nor outgroup, $B = -2.89, SE = 2.15, F(1, 240) = 1.80, p = .1804, \eta^2 = .007$.

These data imply that genetic diversity-based outgroup attraction does not extend to minimal groups. We should note

that other effects, particularly the outgroup homogeneity effect, are less pronounced in minimal than natural groups (Boldry et al., 2007; Mullen & Hu, 1989; Ostrom & Sedikides, 1992). We began our research using ethnically defined groups because persons consider and use ethnicity as a meaningful basis of social categorization (Hewstone, Hantzi, & Johnston, 1991). If meaningfulness matters for the fertility-attraction effect, perhaps we could have done more to imbue the categories with substance. McDonald et al. (2011), for example, had participants additionally wear T-shirts symbolizing their minimal-group membership. They also assessed rape fear (in the form of perceived ingroup-outgroup physical formidability) before assessing ingroup-outgroup attitudes, and that order may have activated the coercion-avoidance process.

It is also possible that in our minimal-group study processes of coercion avoidance and genetic diversity, each canceled the expression of the other, thereby yielding a null effect of conception risk. Unfortunately, our attraction-rating task is incapable of indexing such response competition. One could imagine a paired-comparison task in which women indicate the more attractive face in a paired presentation of an ingroup man and outgroup man. Mouse (or eye) tracking could be used to assess the trajectory of the response when selecting between paired faces. Opposing processes for outgroup fear and attraction would manifest as vacillation between faces, and we would anticipate greater midcycle (than earlier or later cycle) vacillation. Nonetheless, the most accurate data-driven statement that we can offer at this point is that the attraction-fertility pattern to outgroup men occurs with ethnically defined groups but not minimal groups.

Does relationship status moderate fertility-linked outgroup attraction? Readers might wonder whether women's relationship status (i.e., paired or not) moderates the manifestation of the cuckolding versus conversion strategy such that a cuckolding pattern emerges more strongly among relationally paired women. This is an interesting but potentially complicated issue. For ancestral females, the cuckold strategy of outgroup mating would have been successful only if outgroup paternity remained secretive. Two possibilities that would have enabled a guise of ingroup paternity would have been a stable ancestral pattern of either pair-bonding or polyandry. The former, but not necessarily the latter, would have increased the likelihood that a cuckolding pattern of outgroup attraction would emerge for relationally paired women. Of course, another possibility is that natural selection may simply have yielded the persistence in women of a midcycle desire for outgroup men without such desire being conditioned on their relationship status; in which case, fertility-linked outgroup attraction in human women might not be responsive to own relationship status. Nonetheless, future research should certainly examine relationship status as a moderator and, perhaps, the qualities of those relationships

(Drigotas, Safstrom, Gentilia, 1999) or partners (Garver-Apgar et al., 2006).

Why no cycle-shift in attraction to ingroup males? Readers familiar with the cycle-shift literature might wonder why we did not predict (nor find) a cycle-shift in response to ingroup men. It is important to keep in mind that past research varied male displays presumably indicative of genetic quality (e.g., symmetry, masculinity; Gildersleeve et al., 2014; but see Wood et al., 2014). The current research, in contrast, did not vary such displays. Study 1 did not present any displays. Study 2 held such displays constant by presenting participants with the same photographs of men (and women) who (based on pilot-testing) were moderately attractive. The only systematic variation was the manipulation of their group membership. A question for future research is whether cycle-shifts to male displays (e.g., symmetry) are moderated by his ingroup versus outgroup membership. Perhaps displays of genetic quality were more important for small-group living ancestral females when selecting an ingroup than outgroup mate because outgroup mates provided the fitness benefit of heterozygous offspring. Consequently, women might evidence stronger cycle-shift effects in response to ingroup than outgroup male displays.

Broader Implications

The attraction-fertility pattern to outgroup men is interesting in its own right given the typically observed tendency for outgroup disinterest or disdain. The pattern, however, has broader implications for human intergroup relations. For example, intergroup contact under the appropriate conditions effectively reduces intergroup prejudice (Pettigrew & Tropp, 2006). Interestingly, there is also evidence of an extended-contact effect such that a friendship with an ingroup member who is friends with an outgroup member reduces prejudice (Wright, Aron, McLaughlin-Volpe, & Ropp, 1997). Relevant to the attraction-fertility pattern to outgroup men is the nature of those between-group interpersonal relationships: Do romantic, more than platonic, relations between members of opposing groups spearhead the contact and extended-contact effects (e.g., Olsson, Ebert, Banaji, & Phelps, 2005)? Extending this inquiry back to the ancestral context provides another plausible role of outgroup mating. Outgroup mating, particularly that achieved by the conversion strategy, may have tempered intergroup conflicts. When considered in terms of multi-level selection (e.g., Wilson & Sober, 1994), perhaps groups whose members engaged in outgroup mating experienced less conflict with those outgroups and out-produced groups whose members did not mate with outgroups. Although it is a strange thought exercise, it is possible that humans as a species are *less* antagonistic at the intergroup level than they would have been if not for ancestral outgroup mating. Nonetheless,

collaborative explorations of the frequently insulated fields of relationships and groups might spawn novel insights.

Another implication of ancestral outgroup mating, particularly stemming from the conversion strategy, is a plausible sex difference in the collective-self concept (i.e., social identity). A tendency for ancestral females to leave the ingroup and join an outgroup might manifest in women as a relatively flexible social identity (at least more so than that of men). Such flexibility might enable women to readily bond and connect with disparate groups while men remain steadfastly connected to ingroups. Such a possibility provides another explanation for the tendency for men to be more apt to engage in intergroup conflict and display stronger ingroup loyalty than do women (Van Vugt, 2009; Van Vugt et al., 2007; but see Schopler et al., 2001). Similarly, while both men and women experience a need to belong (Baumeister & Leary, 1995), the possible flexibility of female social identity might yield a stronger expression of the belongingness need among women (than among men) for dyadic (i.e., interpersonal) than group (i.e., collective) connections.

Conclusion

In contrast to the typical tendency of disinterest, if not disdain, toward outgroups, we observed in two methodologically divergent studies a pattern of attraction to outgroup men that increased with increased fertility across the menstrual cycle. We suggest that this pattern is a vestige of an ancestral-female solution to the inbreeding dilemma of their small-group lifestyle.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) received no financial support for the research, authorship, and/or publication of this article.

Supplemental Material

The online supplemental material is available at <http://pspb.sagepub.com/supplemental>.

Notes

1. It is unlikely that phenotypic markers of group membership would have compromised the cuckold strategy (e.g., "the baby doesn't look like us!") given the time scale and geographic proximity of ancestral groups (Stringer & McKie, 1997). Furthermore, some readers might accept that female ancestors cuckolded a partner in the genetic sense of his lost reproductive potential, but question whether cuckolding a group is plausible. We suggest that exploitation of a group's cooperative structure and energy expenditure (e.g., gathering and sharing nutrients

that could have been directed to other mothers and offspring) constitutes cuckolding.

2. We excluded from review a broader literature addressing cycle-shifts in mate preference. That literature examines attraction on days of higher versus lower fertility to male displays that ostensibly signal genetic quality, for example, facial-masculinity (Penton-Voak & Perrett, 2000), vocal-masculinity (Puts, 2005), symmetry (Gangestad & Thornhill, 1998), and behavior (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004). That literature is not without controversy due to two meta-analyses that offer opposing conclusions regarding the presence of a cycle-shift (Gildersleeve et al., 2014; Wood et al., 2014).
3. Our conclusions are not unique to using conception risk. We reach the same conclusions testing a quadratic trend across menstrual cycle days (i.e., inverted "U" with a midcycle peak).
4. Five women responded on only two sessions. Another five responded on only one session. Conclusions (based on *p* values and direction of effects) are the same with and without those women. Reported results are based on the responses of all participants.

References

- Aiello, L. C., & Dunbar, R. I. M. (1993). Neocortex size, group size, and the evolution of language. *Current Anthropology*, 34, 184-193.
- Alvergne, A., & Lummaa, V. (2010). Does the contraceptive pill alter mate choice in humans? *Trends in Ecology & Evolution*, 25, 171-179.
- Baumeister, R. F., & Leary, M. R. (1995). The need to belong: Desire for interpersonal attachment as a fundamental human motivation. *Psychological Bulletin*, 117, 497-529.
- Bobo, L., & Zubrinsky, C. L. (1996). Attitudes on residential integration: Perceived status differences, mere in-group preference, or racial prejudice? *Social Forces*, 74, 883-909.
- Boldry, J. G., Gaertner, L., & Quinn, J. (2007). Measuring the measures: A meta-analytic investigation of the measures of out-group homogeneity. *Group Processes & Intergroup Relations*, 10, 157-178.
- Brewer, M. B. (1999). The psychology of prejudice: Ingroup love or outgroup hate? *Journal of Social Issues*, 55, 429-444.
- Brewer, M. B. (2007). The social psychology of intergroup relations: Social categorization, ingroup bias, and outgroup prejudice. In A. W. Kruglanski & E. T. Higgins (Eds.), *Social psychology: Handbook of basic principles* (2nd ed., pp. 695-715). New York, NY: Guilford Press.
- Brewer, M. B., & Caporael, L. R. (2006). An evolutionary perspective on social identity: Revisiting Groups. In M. Schaller, J. A. Simpson, & D. T. Kenrick (Eds.), *Evolution and social psychology* (pp. 141-161). New York, NY: Psychology Press.
- Brook, B. W., Bradshaw, C. J. A., Traill, L. W., & Frankham, R. (2011). Minimum viable population size: Not magic, but necessary. *Trends in Ecology & Evolution*, 26, 619-620.
- Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, 12, 1-49.
- Caporael, L. R. (1997). The evolution of truly social cognition: The core configurations model. *Personality and Social Psychology Review*, 1, 276-298.
- Caporael, L. R. (2001). Parts and wholes: The evolutionary importance of groups. In C. Sedikides & M. B. Brewer (Eds.), *Individual self, relational self, collective self* (pp. 241-258). Philadelphia, PA: Psychology Press.
- Caporael, L. R. (2007). Evolutionary theory for social and cultural psychology. In A. W. Kruglanski & E. T. Higgins (Eds.), *Social psychology: Handbook of basic principles* (2nd ed., pp. 3-18). New York, NY: Guilford Press.
- Caporael, L. R., & Brewer, M. B. (1991). Reviving evolutionary psychology: Biology meets society. *Journal of Social Issues*, 47, 187-195.
- Chapais, B. (2008). *Primeval kinship*. Cambridge, MA: Harvard University Press.
- Chapais, B. (2013). Monogamy, strongly bonded groups, and the evolution of human social structure. *Evolutionary Anthropology*, 22, 52-65.
- Charlesworth, D., & Willis, J. H. (2009). The genetics of inbreeding depression. *Nature Reviews Genetics*, 10, 783-796.
- Clutton-Brock, T. H. (1989). Female transfer and inbreeding avoidance in social mammals. *Nature*, 337, 70-72.
- De Houwer, J. (2001). A structural and process analysis of the Implicit Association Test. *Journal of Experimental Social Psychology*, 37, 443-451.
- Drigotas, S. M., Safstrom, C. A., & Gentilia, T. (1999). An investment model prediction of dating infidelity. *Journal of Personality and Social Psychology*, 77, 509-524.
- Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size, and language in humans. *Behavioral and Brain Sciences*, 16, 681-735.
- Durante, K. M., Griskevicius, V., Simpson, J. A., & Li, N. P. (2012). Ovulation leads women to perceive sexy cads as good dads. *Journal of Personality and Social Psychology*, 103, 292-305.
- Fessler, D. M. T., & Navarrete, C. D. (2003). Domain-specific variation in disgust sensitivity across the menstrual cycle. *Evolution & Human Behavior*, 24, 406-417.
- Fiske, S. T. (2000). Stereotyping, prejudice, and discrimination at the seam between the centuries: Evolution, culture, mind, and brain. *European Journal of Social Psychology*, 30, 299-322.
- Foley, R. (1996). The adaptive legacy of human evolution: A search for the environment of evolutionary adaptedness. *Evolutionary Anthropology*, 4, 194-203.
- Gaertner, L., Iuzzini, J., Guerrero, W. M., & Oriña, M. M. (2006). Us without them: Evidence for an intragroup origin of positive ingroup regard. *Journal of Personality and Social Psychology*, 90, 426-439.
- Gaertner, S. L., & Dovidio, J. F. (2010). Intergroup bias. In S. T. Fiske, D. T. Gilbert, & G. Lindzey (Eds.), *Handbook of social psychology* (5th ed., pp. 1084-1121). Hoboken, NJ: John Wiley & Sons.
- Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, 23, 573-644.
- Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, P. N. (2004). Women's preferences for male behavioral displays change across the menstrual cycle. *Psychological Science*, 15, 203-207.
- Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings of the Royal Society of London: Biological Sciences*, 265, 927-933.

- Garnett, S. T., & Zander, K. K. (2011). Minimum viable population limitations ignore evolutionary history. *Trends in Ecology & Evolution*, 26, 618-619.
- Garver-Apgar, C. E., Gangestad, S. W., & Thornhill, G. R. (2008). Hormonal correlates of women's mid-cycle preference for the scent of symmetry. *Evolution & Human Behavior*, 29, 223-232.
- Garver-Apgar, C. E., Gangestad, S. W., Thornhill, R., Miller, R. D., & Olp, J. J. (2006). Major histocompatibility complex alleles, sexual responsivity, and unfaithfulness in romantic couples. *Psychological Science*, 17, 830-835.
- Gildersleeve, K. A., Haselton, M. G., & Fales, M. (2014). Do women's mate preferences change across the ovulatory cycle? A meta-analytic review. *Psychological Bulletin*, 140, 1205-1259.
- Gramzow, R. H., & Gaertner, L. (2005). Self-esteem and favoritism toward novel in-groups: The self as an evaluative base. *Journal of Personality and Social Psychology*, 88, 801-815.
- Greenwald, A. G., Nosek, B. A., & Banaji, M. R. (2003). Understanding and using the Implicit Association Test: I. An improved scoring algorithm. *Journal of Personality and Social Psychology*, 85, 197-216.
- Hewstone, M., Hantzi, A., & Johnston, L. (1991). Social categorization and person memory: The pervasiveness of race as an organizing principle. *European Journal of Social Psychology*, 21, 517-528.
- Hill, K. R., Walker, R. S., Bozicevic, M., Eder, J., Headland, T., Hewlett, B., . . . Wood, B. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science*, 331, 1286-1289.
- Insko, C. A., & Schopler, J. (1998). Differential distrust of groups and individuals. In C. Sedikides, J. Schopler, & C. A. Insko (Eds.), *Intergroup cognition and intergroup behavior* (pp. 75-107). Mahwah, NJ: Lawrence Erlbaum.
- Lieberman, D., Pillsworth, E. G., & Haselton, M. G. (2011). Kin affiliation across the ovulatory cycle: Females avoid fathers when fertile. *Psychological Science*, 22, 13-18.
- Marlow, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology*, 14, 54-67.
- McDonald, M. M., Asher, B. D., Kerr, N. L., & Navarrete, C. D. (2011). Fertility and intergroup bias in racial and minimal-group contexts: Evidence for shared architecture. *Psychological Science*, 22, 860-865.
- Meltzer, A. L. (2016). Wives with masculine husbands report increased marital satisfaction near peak fertility. *Evolutionary Behavioral Sciences*. Advance online publication. doi:10.1037/ebs0000083
- Mullen, B., & Hu, L. (1989). Perceptions of ingroup and outgroup variability: A meta-analytic integration. *Basic and Applied Social Psychology*, 10, 233-252.
- Navarrete, C. D., Fessler, D. M. T., Fleischman, D. S., & Geyer, J. (2009). Race bias tracks conception risk across the menstrual cycle. *Psychological Science*, 20, 661-665.
- Neuberg, S. L., Kenrick, D. T., & Schaller, M. (2010). Evolutionary social psychology. In S. T. Fiske, D. T. Gilbert, & G. Lindzey (Eds.), *Handbook of social psychology* (5th ed., pp. 761-796). Hoboken, NJ: John Wiley & Sons.
- Olson, M. A., & Fazio, R. H. (2003). Relations between implicit measures of prejudice. What are we measuring? *Psychological Science*, 14, 636-639.
- Olsson, A., Ebert, J. P., Banaji, M. R., & Phelps, E. A. (2005). The role of social groups in the persistence of learned fear. *Science*, 309, 785-787.
- Ostrom, T. M., & Sedikides, C. (1992). Out-group homogeneity effects in natural and minimal groups. *Psychological Bulletin*, 112, 536-552.
- Penn, A. J., & Potts, W. K. (1999). The evolution of mating preferences and major histocompatibility complex genes. *The American Naturalist*, 153, 145-164.
- Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically—Further evidence. *Evolution & Human Behavior*, 21, 39-48.
- Pettigrew, T. F., & Tropp, L. R. (2006). A meta-analytic test of Intergroup Contact Theory. *Journal of Personality and Social Psychology*, 90, 751-783.
- Puts, D. (2005). Mating context and menstrual phase affect women's preferences for male voice pitch. *Evolution & Human Behavior*, 26, 388-397.
- Raudenbush, S. W., & Bryk, A. S. (2002). *Hierarchical linear models: Applications and data Analysis models*. Thousand Oaks, CA: SAGE.
- Roberts, S. C., & Little, A. C. (2008). Good genes, complementary genes, and human mate preferences. *Genetica*, 132, 309-321.
- Schaller, M., & Neuberg, S. L. (2012). Danger, disease, and the nature of prejudice(s). *Advances in Experimental Social Psychology*, 46, 1-54.
- Schaller, M., Simpson, J. A., & Kenrick, D. T. (Eds.). (2006). *Evolution and social psychology*. New York, NY: Psychology Press.
- Schopler, J., Insko, C. A., Wieselquist, J., Pemberton, M., Witcher, B., Kozar, R., . . . Wildschut, T. (2001). When groups are more competitive than individuals: The domain of the discontinuity effect. *Journal of Personality and Social Psychology*, 80, 632-644.
- Sears, D. O. (1983). The person-positivity bias. *Journal of Personality and Social Psychology*, 44, 233-250.
- Sedikides, C., & Skorowski, J. J. (1997). The symbolic self in evolutionary context. *Personality and Social Psychology Review*, 1, 80-102.
- Senn, C. Y., & Dzinis, K. (1996). Measuring fear of rape: A new scale. *Canadian Journal of Behavioral Science*, 28, 141-144.
- Stevens, L. A., & Fiske, S. T. (1995). Motivation and cognition in social life: A social survival perspective. *Social Cognition*, 13, 189-214.
- Stringer, C., & McKie, R. (1997). *African exodus: The origins of modern humanity*. London, England: Cape.
- Tattersall, I. (2012). *Masters of the planet: In search for our human origins*. New York, NY: Palgrave Macmillan.
- Thorndike, E. L. (1920). A constant error in psychological ratings. *Journal of Applied Psychology*, 4, 25-29.
- Thornhill, R., & Gangestad, S. W. (2008). *The evolutionary biology of human female sexuality*. Oxford, UK: Oxford University Press.
- Thornhill, R., & Thornhill, N. W. (1992). The evolutionary psychology of men's coercive sexuality. *Behavioral and Brain Sciences*, 15, 363-421.
- Traill, L. W., Bradshaw, C. J. A., & Brook, B. W. (2007). Minimum viable population size: A meta-analysis of 30 years of published estimates. *Biological Conservation*, 139, 159-166.

- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871-1971* (pp. 136-179). Chicago, IL: Aldine.
- Van Vugt, M. (2009). Sex differences in intergroup competition, aggression, and warfare: The male warrior hypothesis. *Annals of the New York Academy of Sciences*, 1167, 124-134.
- Van Vugt, M., De Cremer, D., & Janssen, D. P. (2007). Gender differences in cooperation and competition: The male-warrior Hypothesis. *Psychological Science*, 18, 19-23.
- Wang, L., & Maxwell, S. E. (2015). On disaggregating between-person and within-person effects with longitudinal data using multilevel models. *Psychological Methods*, 20, 63-83.
- Wilcox, A. J., Dunson, D. B., Weinberg, C. R., Trussell, J., & Baird, D. D. (2001). Likelihood of conception with a single act of intercourse: Providing benchmark rates for assessment of post-coital contraceptives. *Contraception*, 63, 211-215.
- Wilson, D. S., & Sober, E. (1994). Reintroducing group selection to the human behavioral sciences. *Behavioral and Brain Sciences*, 17, 585-654.
- Wobst, H. M. (1974). Boundary conditions for Paleolithic social systems: A simulation approach. *Society for American Archaeology*, 39, 147-178.
- Wood, W., Kressel, L., Joshi, P., & Louie, B. (2014). Meta-analysis of menstrual cycle effects on women's mate preferences. *Emotion Review*, 6, 229-249.
- Wright, S. C., Aron, A., McLaughlin-Volpe, T., & Ropp, S. A. (1997). The extended contact effect: Knowledge of cross-group friendships and prejudice. *Journal of Personality and Social Psychology*, 73, 73-90.