When are women especially attracted to attractive men? Human mate preferences in a pathogen prevalent ecology

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Dedication

This dissertation is dedicated to my loving parents, Judy Harris and John Cantú.

Abstract

Pathogen and disease threat are known to trigger avoidant behaviors in humans, which aids in stopping the spread of infection. However, might pathogen prevalence also influence specific *approach* behaviors as well, such as who might get asked out on a date? Drawing on Strategic Pluralism Theory, three preliminary experiments test hypotheses specifying the effect of perceived pathogen prevalence on preferences for physically attractive mates. Experiments 1 and 2 reveal that when pathogen prevalence is temporarily salient, women (but not men) exhibit an exaggerated preference for physically attractive mates. Experiment 3 reveals implications for functionally adaptive behavioral responses: When pathogen prevalence is salient, women (but not men) exhibit faster approach-oriented muscle movements in response to highly physically attractive members of the opposite sex. Finally, the current study aims to tease apart *why* women prefer physically attractive mates after being primed with the threat of pathogens. I hypothesize that women specifically prefer attractive men as short-term partners, particularly when women are at a high fertility point in their ovulatory cycle. These findings suggest that women place an especially high priority on attractiveness under conditions of pathogen prevalence and do so because physical attractiveness serves as a signal of genetic fitness.

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Media coverage of the 2009 outbreak of the H1N1 influenza virus had a dramatic impact on human behavior. Within a week of the virus's discovery in Mexico, hundreds of schools were shut down, thousands of public activities were cancelled, and the Vice President of the United States publicly advised citizens to stay off subways and airplanes (O'Neill, 2009; Toppo, 2009). Fear of viral transmission led to a substantial months-long decrease in international air travel not just in the Americas, but in Asia and Europe as well (Hamamura & Park, 2010). Similar reactions have been observed in response to news about bird flu in 2006, severe acute respiratory syndrome (SARS) in 2003, and many other epidemic outbreaks throughout human history. Recent experimental evidence reveals that even the temporary psychological salience of pathogen prevalence can lead to aversive responses. Perceived pathogen prevalence leads people to be less socially gregarious, to be more prejudiced against people who appear morphologically or behaviorally unusual, to be more punitive of norm-violators, and to be more wary of risky sexual behavior (Faulkner, Schaller, Park, & Duncan, 2004; Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010; Murray & Schaller, in press; Park, Schaller, & Crandall, 2007; Tybur, Bryan, Magnan, & Hooper, 2011; for a review see Schaller, 2011).

Although avoidant responses to pathogen prevalence make good sense, there is reason to believe that perceived pathogen prevalence may sometimes affect social preferences and interpersonal behavior in additional *approach*-oriented ways, as well. Some of these approach-oriented implications may emerge specifically in the domain of mating (Tybur & Gangestad, 2011). If so, then merely reading a news story about seasonal influenza or seeing a photograph of someone sneezing might influence whom someone asks out on a date, and whether that person accepts.

In the current research, I draw upon Strategic Pluralism Theory (Gangestad & Simpson, 2000) to examine how, when, and why perceived pathogen prevalence influences what individuals find attractive in potential mates. I first review concepts from evolutionary psychology and sex differences in mate preferences. I next describe the logic of strategic pluralism, which suggests that mate preferences may be especially attuned to environmental conditions, such as the threat of pathogens. The next section outlines three preliminary experiments that tested hypotheses deduced from concepts outlined by Strategic Pluralism Theory.

The Value of an Evolutionary Psychology Perspective

The father of modern social psychology, Kurt Lewin, defined human behavior as the function of both the person and the situation (Lewin, 1936). As social psychologists, then, we are interested in examining the situational and environmental cues that influence human preference and behavior. Social psychologists often examine human behavior at a proximal level. That is, many outcome behaviors are explained as arising from a direct and readily present cause, without regarding the ultimate function of the behavior. This approach to research questions contrasts with an evolutionary perspective, which asks what adaptive function a behavior serves.

The proximate and ultimate explanations for a behavior are not mutually incompatible. Instead, these different levels of analysis provide multiple complementary explanations for a behavior (Tinbergen, 1963). For instance, when trying to understand why mothers nurse young infants, we could say that it is because infants cry and provide cues that they are hungry (proximate cause) *and* because mothers realize that nursing behaviors provide important nourishment and increase the chance of offspring survival. In this way, explaining behavior at multiple levels of analysis paints a more complete causal picture.

Social psychology has much to gain from examining situational and environmental cues that are informed by an evolutionary perspective. One environmental factor that has played a large role in shaping human psychology is the presence of pathogens. Pathogens have changed the course of human history by determining which crops survived, which army won wars, and ultimately, which people adapted and survived (Diamond, 1997; Wolfe, Dunavan, & Diamond, 2007). Based in this historical understanding of pathogenic environments, some of the earliest research on pathogens and human psychology focused on how pathogens shaped cultural and regional variation. For instance, pathogen prevalence is related to variation in cultural value orientation, mate preferences, marriage structures, and food preparation and spice use (Fincher, Thornhill, Murray, & Schaller, 2008; Gangestad & Buss, 1993; Low, 1990; Sherman & Billing, 1999).

More recently, social evolutionary psychologists have studied how the presence of pathogens influences psychological mechanisms and human behavior at the individual level. Just as the human body has physical defenses against pathogens–mucous membranes to trap bacteria and coughing reflexes to keep out toxins–an individual's mind is believed to possess a suite of psychological mechanisms that inhibit the spread of disease. This collection of mechanisms is known as the Behavioral Immune System (Schaller & Park, 2011). Drawing upon the idea of a behavioral immune system, researchers have found that making individuals aware of pathogens in the environment leads to increased xenophobia, higher levels of ethnocentrism, more interpersonal prejudice and stigmatization of morphologically abnormal individuals, increased sexual restrictedness, and decreased extraversion and openness to experience (Faulkner et al., 2004; Mortensen et al., 2010; Navarrete & Fessler, 2006; Park et al., 2007; Schaller & Murray, 2008). From a functional evolutionary perspective, holding more restricted attitudes and engaging in more prejudicial behaviors is beneficial because it encourages individuals to avoid (potentially diseased) others and to prevent possible infection.

Informed predominantly by the notion of a behavioral immune system, most research on pathogens and human behavior has focused on avoidant behaviors. In contrast, relatively little is known about how pathogens might influence other *approach-oriented* behaviors, such as the person someone might ask out on a date and whether that person says "yes." Past correlational research from various world regions suggests that pathogen prevalence is related to what individuals desire in an ideal mate, but this relation has not been thoroughly tested experimentally. Therefore, the studies presented here use experimental designs to test how pathogen prevalence influences preferences for attractiveness in potential partners.

Evolutionary Psychology and Human Mate Preferences

An evolutionary approach to social psychology examines human behavior as an adaptive solution to recurring challenges that our human ancestors faced (Cosmides & Tooby, 1992). We all exist today because our ancestors successfully solved the primary challenges of survival and reproduction. The physical and mental characteristics we possess today are all design features that enhanced our evolutionary fitness.

Evolutionary psychology is heavily informed by Darwin's theory of natural selection (Darwin, 1871). *Natural selection* posits that characteristics arise in a species because they provide some survival advantage, thereby increasing an organism's fitness. For instance, if the only available food source is found on a very tall tree, only extremely tall individuals in a population who can reach the tree can obtain nourishment from it. These tall individuals are more likely to survive and will pass on their tall genes to the next generation in higher frequencies than their shorter counterparts. Over time, the result is a taller species. In this way, natural selection often explains species-wide evolution, such as why *all* humans have two forward-facing eyes or why *all* humans are designed to walk on two legs.

A second process through which characteristics arise is *sexual selection* (Darwin, 1871). According to the concept of sexual selection, a trait arises in a species because it provides some *reproductive* advantage. That is, it allows an individual possessing that trait to produce more numerous and/or more successful offspring. Sexually selected characteristics may increase an individual's ability to outcompete same-sex rivals (known as intrasexual competition), or members of the opposite sex may universally agree that a trait is desirable (intersexual preference). Male deer antlers, for example, are intrasexually adaptive, as larger antlers lead to more victories in male-male competition. In contrast, a male peacock's tail is intersexually adaptive, as larger tails are preferred by female peahens. As illustrated by these examples, sexual selection often accounts for sex differences within a species, such as larger male size or more elaborate male ornamentation.

Sexual selection results from the differential reproductive success afforded to individuals who possess the given trait compared to those who do not. Reproductive success entails both increased mating opportunities and increased offspring survival. Although some characteristics evolve because they increase the chance of mating with multiple or more desirable partners, others evolve because they enhance the likelihood of offspring surviving to reproductive age.

Offspring survival is largely dependent on parental investment, which is defined by Parental Investment Theory as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring” (Trivers, 1972, p. 139). Thus, parental investment theory implies an inevitable trade-off between investing in parenting effort versus mating effort (i.e., investing in future offspring).

All organisms, including humans, have finite time and energy to devote to fitness-maximizing activities such as mating and parenting. Deciding how to allocate effort depends on the cost-benefit analysis of the fitness advantages to be gained. If there are great fitness-enhancing gains to be made from investing in mating effort, an organism will devote more time and energy to attracting a high quality mate or multiple mates. The cost-benefit considerations of investing in mating effort versus parenting effort differ substantially for males and females in many species, including humans. These differing cost-benefit considerations result from males and females facing different minimal obligatory parental investment to ensure offspring survival. For males of most species, the minimal obligatory parental investment is considerably less than is required of females. Males need only the time and energy necessary for a single act of copulation, whereas females must endure a lengthy gestation period and provide energetic resources to nurse young offspring through lactation. Females have a higher obligatory investment in offspring than do males, and consequently the cost of mating (and making a poor mating choice) is higher for them. Therefore, parental investment theory predicts that females in such species will be the choosier and more selective sex. That is, females will exert strong preferences for desirable male mate traits and males will accordingly attempt to outcompete each other for access to valuable female sexual resources.

Trade-offs and Conditional Mating Strategies

In humans, Parental Investment Theory suggests that women are the choosier, more selective sex and that men evolved certain characteristics contingent on women's mate preferences. Additionally, because men have more to gain from investing in mating effort and pursuing multiple mates, men tend to favor short-term mating strategies more than do women (Buss, 1989; Buss & Schmitt, 1993). The trade-off between investing in mating versus parenting effort leads to gender differences in human mating strategies that vary universally across multiple cultures, a finding predicted by Sexual Strategies Theory (Buss & Schmitt, 1993). Much of the research on human mating strategies has focused on these gender differences, which typically find that men are more sexually unrestricted, have more sexual partners, and desire sex more often than do women, consistent with a male preference for investing more in mating effort (Buss & Barnes, 1986; Buss & Schmitt, 1993; Simpson & Gangestad, 1991).

An overlooked assumption of this previous research, however, is that all men and all women were successful in adopting the sex-typical mating strategy. Depending on an individual's characteristics (i.e., mate value) or environmental conditions, an individual might increase his or her reproductive success by following an alternate strategy. That is, some men in some circumstances might enhance their reproductive output by pursuing *fewer* mates and investing more heavily in *parenting* effort (Gangestad & Simpson, 2000).

Although Sexual Strategies Theory suggests that men adopt short-term mating strategies more often than women do, it also suggests that men and women evolved to enact *both* short-term and long-term mating strategies. When a strategy is enacted due to specific environmental cues, it is said to be conditional (Gross, 1996). Strategic Pluralism Theory extends Sexual Strategies Theory by pointing out that there is greater variance in human mating strategies within each gender than between them, and that the enactment of a given mating strategy depends on environmental circumstances (Gangestad & Simpson, 2000). Different environments shift cost-benefit considerations and the trade-off between mating and parenting effort. Therefore, the same notion of trade-offs that predicts between-sex differences can also be applied to predicting within-sex variation, as well.

In some environments, offspring survival is heavily dependent on genetic quality, whereas in other environments it is more dependent on parental investment. For example, in an environment where infant mortality is largely caused by infectious disease, possessing pathogen-resistant genes is paramount, and being able to provide additional units of parental investment has rapidly diminishing returns. By contrast, in an environment where infant success depends largely on biparental care, parental investment is more important than genetic quality (Gangestad & Simpson, 2000). Because of these different valuations of parental investment, the environment determines what mating strategy–-investing in mating versus parenting effort–-an individual is likely to enact.

Some recent research indicates how individuals' resource allocation in mating versus parenting effort shifts in response to environmental conditions. In resource-scarce environments, some individuals choose to delay starting a family and decrease allocations to mating effort (Griskevicius et al., 2011). Furthermore, individuals seem to be especially attuned to the scarcity of particular resources, such as the number of available male or female mates in a population. A male-biased sex ratio, in which there is an abundance of men and very few women, increases men's financial spending and the amount of effort men invest into attracting a mate (Griskevicius et al., 2012). For women, a female-biased sex ratio, in which there are more women than men, leads them to invest more heavily in building themselves and their careers and delaying starting a family (Durante et al., 2012). These studies demonstrate how environmental circumstances influence individuals to shift their mating strategies and to allocate resources to mating effort and parenting effort.

Environmental Conditions that Trigger a Desire for Genetic Quality

In addition to shifting mating strategies, environmental cues are also thought to shift individual mate preferences. Strategic pluralism suggests that men's mating strategies should be contingent on their ability to satisfy women's mate preferences, which depends on the "exchange value" of having an investing versus genetically fit partner (Gangestad & Simpson, 2000). As described earlier, some environments favor mating with a high genetic quality individual, whereas others favor mating with a high-investment individual. The trade-off between choosing a mate with good genes versus good partner traits is especially important for women, whose mating costs are high given their higher obligatory investment (Trivers, 1972).

Strategic Pluralsim Theory therefore suggests that women in particular will shift their mate preferences in accordance with environmental cues. Although it would be ideal for a woman to secure both genetic benefits and high investment from a male partner, especially in ecologically harsh conditions, such a partnership is unlikely given that men of high genetic quality are more likely to follow a short-term, low-investment strategy (Boothroyd, Jones, Burt, DeBruine, & Perrett, 2008; Rhodes, Simmons, & Peters, 2005). In ecologically harsh conditions, then, women face a trade-off between securing a mate with good genes versus good parenting qualities.

One hypothesized harsh environment that should favor genetic quality over paternal investment is a pathogen-prevalent environment. In a pathogen-prevalent environment, infant survival and success depends significantly more on the infant's inheritance of disease-resistant genes than on incremental paternal investment. Thus, one might predict that women should desire more genetically fit male partners in pathogen-ridden ecologies.

But what cues do women use to determine a man's genetic quality? Past research suggests that women use various cues of physical attractiveness (e.g., symmetry, sexual dimorphism) to determine a man's genetic quality and heritable fitness. The most compelling evidence suggesting that physical attractiveness signals male genetic quality comes from research on ovulatory cycle shifts in facial preferences. The female ovulatory cycle spans, on average, 28 days, and a woman is likely to become pregnant during only a few days within each cycle, which is known as the ovulatory phase. Because conception probability is highest for only a few days each month, women strategically shift their preferences and behaviors to maximize fitness and reproductive success (Thornhill & Gangestad, 2008). Accordingly, the ovulatory shift hypothesis proposes that women will increase their desire for men who possess markers of genetic fitness, especially when evaluating such men as short-term sexual relationship partners.

Evidence supporting the ovulatory shift hypothesis abounds. Women at high fertility prefer more symmetric and masculine male faces, especially if they are rating the men as short-term sexual partners (Little et al., 2007; Penton-Voak et al., 1999). Furthermore, women at high fertility prefer men who are more muscular and physically attractive as short-term, but not long-term, mates (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007). The fact that women prefer physical attractiveness, symmetry, and masculinity *specifically* for short-term but not long-term mates suggests that the preference is driven by a desire to secure genetic benefits for potential offspring. Furthermore, women increase their desire for physically attractive and masculine men when their current partner lacks indicators of genetic fitness (Little et al., 2002; Pillsworth & Haselton, 2006). This converging evidence on ovulatory shifts in women's preference for physical attractiveness, symmetry, and masculinity especially in short-term male mates strongly suggests that women use such characteristics as indicators of male genetic fitness (for reviews, see Gildersleeve, Haselton, & Fales, in press; Jones et al., 2008).

Other lines of research find that physical attractiveness is positively related to an individual's perceived and actual health outcomes (Kalick et al., 1998; Shackelford & Larsen, 1999). In one study, the more physically attractive and symmetrical an individual was, the less likely s/he was to suffer from various infections (Thornhill & Gangestad, 2006). A longitudinal study also found that individuals whose high school yearbook photos were rated as more attractive lived longer (Henderson & Anglin, 2003). However, a recent review of the literature on the attractiveness-health link does not find a significant, reliable relation between actual health outcomes and judgments of body attractiveness, general facial attractiveness, or specific individual cues to attractiveness (e.g., symmetry; Weeden & Sabini, 2005). These authors found weak effect sizes for specific individual cues indicating attractiveness and small correlations between attractiveness judgments and actual health outcomes, especially for men.

The meta-analysis by Weeden and Sabini (2005) was limited to attractiveness and actual health outcomes, however, and it is possible that women use men's physical attractiveness as a marker for a wider range of desirable genetic fitness qualities, such as dominance and future mating success (Boothroyd, Jones, Burt, & Perrett, 2007; Rhodes, Simmons, & Peters, 2005). Although women may prefer to mate with physically attractive men because such men are more likely to be free of disease, physically attractive men can also pass on genes that will directly increase the reproductive success of future offspring (Gangestad, Haselton, & Buss, 2006).

In the current study, I draw on Strategic Pluralism Theory to propose that women should be especially likely to monitor environmental conditions and to respond by shifting their mate preferences accordingly. Because a pathogen-prevalent ecology presents a unique challenge to women and shifts the cost-benefit considerations to favor a genetically fit partner over an investing partner, I predict that a pathogen threat will increase women's, but not men's, preference for a physically attractive mate. Previous research across cultures provides some initial support for this hypothesis. Just as strategic pluralism predicts, individuals from regions with high pathogen load prefer mates who are physically attractive over those who possess good parenting characteristics, such as kindness or warmth (Gangestad & Buss, 1993). Furthermore, cultures that have a higher pathogen load also have higher incidences of polygyny, in which one man has sexual access to many women (Low, 1990). This marriage structure most likely reflects the value of physically attractive men and women trading off parental investment for genetic quality.

A more recent survey of women from over 30 countries found that the preference for masculine male faces increases as a nation's health index decreases (DeBruine, Jones, Crawford, Welling, & Little, 2010). Taken together, these cross-cultural studies suggest that pathogen load impacts a region's mating preferences, and hint that women may be driving this effect at an individual level. Indeed, women who report higher levels of pathogen disgust prefer more masculine male faces (DeBruine, Jones, Tybur, Lieberman, & Griskevicius, 2010). Many of these initial studies, however, are correlational and cannot directly establish whether pathogen load *causes* women to shift their preference for more physically attractive male mates.

More recently, researchers have extended these correlational findings and experimentally manipulated pathogen threat to examine the effect of disease saliency on mate preferences. Following a pathogen prime, both women and men prefer more symmetric and sexually dimorphic opposite-sex faces (Little, DeBruine, & Jones, 2010). Notably, these authors find no effect of pathogen prime on men's and women's preferences for same-sex faces, suggesting that environmental pathogen cues shift partner preferences specifically and not facial preferences more generally. Women also invest more "mate dollars" into good-genes traits than good-parent traits following a pathogen manipulation, illustrating the trade-off women make between pursuing mates of genetic quality versus investment quality (Lee & Zietsch, 2011). These experimental studies advance our understanding of how pathogen threat influences mate preferences in accordance with strategic pluralism, but some important nuances of the theory still need to be tested.

Strategic pluralism predicts a gender difference in the contingent expression of mate preferences due to environmental conditions. Specifically, because women face higher obligatory parental investment and more costly consequences from poor mating decisions, they should be especially attuned to environmental conditions that influence trade-off decisions associated with mate selection. Therefore, strategic pluralism theory posits that women's, but not men's, mating preferences should shift depending on environmental conditions, especially increased pathogen threat. Previous experimental work on pathogen prevalence and mate preferences has either failed to test for this predicted gender difference by failing to sample both genders, or has not included gender as a moderator.

Preliminary Studies Examining Pathogen Threat and Women's Mate Preferences

The current study builds on data collected for preliminary studies examining the effect of pathogen prevalence on men's and women's mate preferences. The results of three experiments provide tests of the hypothesis that the perceived prevalence of pathogens leads to a stronger preference for physically attractive mates. All experiments included both male and female participants, and thus tested the additional hypothesis that this effect is specific to female mate preferences. Experiments 1 and 2 used self-report methods, whereas Experiment 3 assessed the speed of actual approach-oriented and avoidance-oriented muscle movements in response to physically attractive and unattractive opposite-sex faces.

Experiment 1

In order to experimentally manipulate perceived pathogen prevalence, male and female participants read one of two different news articles, one of which highlighted a recent rise in contagious diseases. Participants then rated the importance of various desirable traits in a potential mate, including traits connoting physical attractiveness. These methods allowed me to: (1) test the hypothesized effect of perceived pathogen prevalence on the preference for physically attractive mates, (2) test whether this effect is specific to female mate preferences, and (3) test whether it is specific to physical attractiveness.

One hundred six participants were randomly assigned to one of two experimental conditions. In the Pathogen condition, the article began with the headline "Infectious Times Ahead: Disease in the 21st Century," and described a recent rise in contagious illnesses (e.g., "...The high prevalence of pathogens is also being seen in emerging studies from Harvard Medical School. Dr. Doug Kendrick, head of the research project, notes a worrisome pattern: 'Comparing blood samples from today to those just two decades ago, we find that people today have nearly twice the pathogen load of people merely a generation ago...'"). In the Control condition, the article was of similar length but had no obvious pathogen-relevant content (the article was about sorting mail; see Griskevicius, Shiota, & Nowlis, 2010).

After reading the news article, participants responded to a brief survey on mate preferences, ostensibly to allow time for their memory to decay. Participants were presented, one at a time, with a series of desirable traits that a person might have. For each trait, they were asked, "If you were going out on a date tonight, how important is the following characteristic to you in a potential date?" Responses were recorded on 7-point rating scales (1 = "*Not at all important*"; 7 = "*Very important*"). Of primary interest were ratings on two traits relevant to physical attractiveness: *attractiveness* and *sexiness*. Because the two ratings were highly correlated, I computed the mean rating on those two traits to create a measure of the importance of a mate's physical attractiveness. To determine whether effects were specific to physical attractiveness or generalized to other desirable traits, I also computed two other 2-item measures of the importance of a mate's dependability as a partner (computed as the mean rating of *reliability* and *dependability*) and the importance of a mate's mental ability (computed as the mean rating of *intelligence* and *creativity*).

The three mate preference measures were subjected to a 2 (Experimental Condition) x 2 (Participant Sex) x 3 (Mate Preference Measure) mixed-model analysis of variance (ANOVA). Results revealed a non-significant three-way interaction, $F(2, 212) = 2.87$, $p = .122$, $\eta^2 = .020$. To test my specific predictions, I examined the results separately for men and women.

For women, a 2 (Experimental Condition) x 3 (Mate Preference Measure) mixed-model ANOVA indicated a significant two-way interaction, $F(2, 140) = 4.70$, $p = .011$, $\eta^2 = .063$. Compared to the Control condition, women in the Pathogen condition rated physical attractiveness as a more important characteristic in a potential mate, $t(70) = 2.57$, *p* = .012 (see Figure 1). The manipulation did not affect the importance that women placed on dependability (*p* = .24) or mental ability (*p* = .55).

For men, the experimental manipulation had no effects. That is, there was no difference between the Pathogen and Control conditions in the importance that men placed on physical attractiveness (*p* = .51), nor were there any effects on the importance that men placed on dependability (*p* = .85) or mental ability (*p* = .99).

These results support the hypothesis that the temporary salience of pathogen prevalence leads women—but not men—to place a higher priority on the physical attractiveness of a potential mate. Not only was this effect specific to women, but it was also specific to physical attractiveness. Thus, consistent with the predictions of strategic pluralism (Gangestad & Simpson, 2000), the temporary salience of pathogen prevalence did not influence the importance that women (or men) placed on traits indicating dependability as a partner and parent, nor did the manipulation influence the importance that women placed on a mate's intelligence or creativity. Previous research suggests that mental abilities such as creative intelligence may provide some indirect indication of general fitness (Haselton & Miller, 2006), but physical appearance is likely to be more diagnostic of fitness pertaining specifically to health outcomes for oneself and one's offspring (Miller & Todd, 1998). The pattern of results suggests that when the threat of disease transmission is perceived to be especially high, women have a stronger preference for the particular traits that are most especially diagnostic of fitness outcomes in a pathogen prevalent ecology.

Experiment 2

This experiment was designed to provide a conceptual replication of Experiment 1 using a different methodology. To manipulate the salience of pathogen prevalence, women and men in Experiment 2 read a message encouraging them to take precautions to prevent the spread of disease or, in a control condition, they read no message. They then were presented with pairs of profiles describing opposite-sex individuals, and were asked to choose which individual they would prefer as a potential mate. The pairs of profiles were designed so that participants had to choose between someone who was highly physically attractive (but not dependable or caring) and someone who was highly dependable and caring (but not so physically attractive)—the essential trade-off articulated by Strategic Pluralism Theory. I expected that when pathogen prevalence was highly salient, women (but not men) would be especially likely to resolve that trade-off in favor of physical attractiveness.

Ninety-nine participants completed the study on computers in private cubicles in a computer lab. In the Pathogen condition, immediately prior to completing the dependent measure, participants saw a “public disclaimer message” on the computer screen. The message informed participants that they were in a public space using a computer that was being used by many other people. In addition, the message informed participants about several symptoms of a virus (e.g., runny nose, vomiting, coughing) and encouraged them to take precautions to prevent the spread of this disease. Participants in the Control condition did not see any message before proceeding to complete the dependent measure.

Participants next read two pairs of profiles describing opposite-sex individuals. Within each pair, the two individuals were labeled "Person A" and "Person B." One of the individuals was described as being highly physically attractive, but not particularly dependable or caring (e.g., "Person A is attractive is considered very sexy... however, Person A is not always the most reliable, dependable, or nurturing person..."), whereas the other person was described as being very dependable and caring, but not particularly attractive (e.g., "Person B is not too attractive, and few people would deem [him/her] sexy... Person B has a friendly, helpful, and comforting gentle nature..."). For each pair of profiles, participants indicated which person they would most like to go out on a date with that night. These choices were made on two 6-point rating scales, with "*Definitely Person A*" and "*Definitely Person B*" anchoring the two endpoints.

Participants also used the same 6-point rating scale to indicate which trait cluster in general was more desirable in a potential date: Attractiveness/sexiness or Reliability/dependability. I computed the mean rating across all three items, with higher values indicating a preference to date the physically attractive person (rather than the dependable, caring, but relatively unattractive person).

A 2 (Participant Sex) x 2 (Experimental Condition) ANOVA revealed a non-significant interaction, $F(1, 95) = 1.77$, $p = .187$, $\eta^2 = .018$ (see Figure 2). However, among women, the experimental manipulation had a statistically significant effect on the mate preference measure, $F(1, 95) = 4.51$, $p = .036$, $\eta^2 = .075$. Compared to the Control condition, women in the Pathogen condition indicated a stronger preference to go out on a date with a man who was physically attractive rather than one who was dependable and caring. In contrast, the manipulation had no significant effect on preferences expressed by men ($p = .74$).

These results conceptually replicate the findings of Experiment 1. A different procedure was used to manipulate the salience of pathogen prevalence, and a different measure was used to assess mate preferences. Regardless, the results were consistent with those of Experiment 1: When pathogen prevalence was psychologically salient, women—but not men—expressed a stronger preference to date opposite-sex individuals who were physically attractive.

The results of both experiments are consistent with predictions derived from the logic of strategic pluralism (Gangestad & Simpson, 2000). The fact that the effects are specific to female mate preferences is especially notable because it is consistent with the premise that physical attractiveness is used by women not merely as a cue connoting a man's health, but also as a cue connoting his genetic fitness; specifically, a man's likelihood of producing offspring who have stronger immunological defenses that would be especially beneficial to reproductive fitness in pathogen prevalent ecologies (Gangestad & Buss, 1993; Tybur & Gangestad, 2011).

Both Experiments 1 and 2 used methods that assessed a relative preference for highly attractive compared to less attractive opposite-sex individuals. Accordingly, I could not distinguish whether pathogen prevalence led women to respond more favorably to relatively attractive men, or to respond more aversely to relatively unattractive men, or both. This distinction is relevant to the question of whether women use attractiveness as a signal of “good genes,” unattractiveness as a signal of “bad genes,” or both (Zebrowitz & Rhodes, 2004). Recent research suggests that the link between pathogen disgust and preferences for physical attractiveness might be driven by a desire to avoid especially unfit (i.e., unattractive) partners (Park, van Leeuwen, & Stephen, 2012).

Another limitation of Experiments 1 and 2 pertains to the control conditions used. In both experiments, the control conditions were affectively neutral, allowing for the possible alternative explanation that effects on female mate preferences may be attributable not to a concern with pathogen transmission specifically, but to negative affect more generally. Although there is no obvious conceptual rationale for such an alternative explanation, it can be rendered less plausible by the use of a control condition that also elicits negative affect. A third limitation of both experiments was the reliance on self-report rating scales. Experiment 3 was designed to redress all of these limitations.

Experiment 3

Experiment 3 tested the effects of a pathogen prevalence manipulation on responses to attractive and unattractive opposite-sex faces. Responses were measured with a behavioral task adapted from previous research assessing the speed of approach-oriented and avoidance-oriented physical movements (Chen & Bargh, 1999; Mortensen et al., 2010). This methodology provides a more rigorous test (using a behavioral measure) of the hypothesis that the salience of pathogen prevalence leads women to show an exaggerated preference for attractive men. It also allows me to determine whether the pathogen prevalence manipulation leads women to show exaggerated approach responses to attractive men, an exaggerated avoidance response to relatively unattractive men, or both.

As part of a study ostensibly on memory for reading material, one hundred forty one participants read a short news article, the contents of which varied systematically. In the Pathogen condition, the article was the same as that used in Experiment 1 ("Infectious Times Ahead: Disease in the 21^{st} Century"). In the Control condition, the article was of similar length and style and focused instead on a different kind of threat: the prevalence of electrical outages, data loss from computers, and other mechanical failures. Thus, the

Control article was entirely irrelevant to infectious disease, but it was designed to elicit a similar level of arousal and negative affect elicited by the Pathogen Condition.

Following the experimental manipulation, participants completed 60 trials of a computer-based task in which they made different hand movements in response to two different geometric figures (a Circle and a Square) that appeared on a computer screen. Before beginning this task, the computer keyboard was rotated 90° clockwise so that the "Esc" key was farthest away from each seated participant. Nine keys (Q, W, E, A, S, D, Z, X, C) had Circle stickers affixed to them, and another nine keys on the number pad had Square stickers affixed to them. The "?" key in the middle of the keyboard had a sticker with an "X" on it. Participants were instructed to press this key to start each trial, and to keep their finger there until prompted (by the appearance of a Circle or Square on the computer screen) to press another key. At the beginning of each trial, a central fixation point ("X") appeared in the center of the computer screen for 1500 ms, followed by a photograph of an opposite-sex face, which was displayed for 500 ms. Immediately following the display of the face, a geometric figure (either a Circle or a Square) appeared on the screen. Upon seeing the geometric figure, participants were instructed to move their hand "as quickly and as accurately as possible" to press any of the keyboard keys marked with the corresponding geometric figure (i.e., to press a key marked with a Circle when they saw a Circle, or to press a key marked with a Square when they saw a Square). Participants had to make a correct response to move to the next trial. Given the placement of the stickers on the keys and the orientation of the keyboard, when participants moved their hand to press a Circle key, it represented an avoidance response (a movement away from the body); and when they moved their hand to press a Square key, it represented an approach response (a movement toward the body).

Across the 60 behavioral response trials, participants were presented with 20 different facial photographs of opposite-sex faces three times each. All facial photographs were of college-aged individuals and had been used in previous research on facial attractiveness (see Maner, Gailliot, Rouby, & Miller, 2007). Half of the photographs were of relatively attractive opposite-sex faces, and half were of relatively unattractive opposite-sex faces. Circles and Squares were paired equal numbers of times with relatively attractive and relatively unattractive opposite-sex faces. Therefore, there were 15 trials each on which participants made: (a) an approach response to a relatively attractive opposite-sex face, (b) an approach response to a relatively unattractive opposite-sex face, (b) an avoidance response to a relatively attractive opposite-sex face, (d) an avoidance response to a relatively unattractive opposite-sex face.

Response time was recorded (i.e., the number of milliseconds that elapsed between when the geometric figure appeared on the screen and when the participant pressed a corresponding key). Similar to previous research (e.g., Mortensen et al., 2010), outlier responses were defined as any response faster than 300 ms or slower than 2,000 ms. Across all participants, 2.8% of responses met these criteria, and were removed prior to computing the primary dependent measures. I computed four measures for each participant, representing the mean time (in milliseconds) taken to make a particular kind of movement in response to a particular category of opposite-sex face: (a) *approach* movements in response to relatively *attractive* faces, (b) *approach* movements in response to relatively *unattractive* faces, (c) *avoidance* movements in response to relatively *attractive* faces, and (d) *avoidance* movements in response to relatively *unattractive* faces.

A 2 (Participant Sex) x 2 (Experimental Condition) x 2 (Face) x 2 (Response) mixed model ANOVA revealed a non-significant 4-way interaction, $F(1, 137) = 1.63$, $p = .20$. To test specific predictions, however, results were analyzed separately for approach movements and for avoidance movements.

For approach movements, a 2 (Participant Sex) x 2 (Experimental Condition) x 2 (Face) mixed model ANOVA revealed a non-significant 3-way interaction, $F(1, 137) = 1.58$, $p = .20$. However, my specific predictions involved examining the simple 2-way interactions between the priming condition and face type within each sex. For women, a 2 (Experimental Condition) x 2 (Face) mixed model ANOVA revealed a significant 2-way interaction, $F(1, 138) = 4.16$, $p = .04$. This interaction is depicted in Figure 3. Compared to the Control condition, women in the Pathogen condition made marginally faster approach movements in response to faces of relatively attractive men, $F(1, 138) = 2.76$, $p = .099$. In contrast, the experimental manipulation had no effect on women's approach movements in response to relatively unattractive men ($p = .57$).

As expected, the manipulation had no effect on men's approach movements ($p = .84$). As Figure 3 reveals, among men, there was virtually no difference between the Control and Pathogen conditions in approach movements made in response to either relatively attractive ($p = .82$) or unattractive female faces ($p = .74$).

There were no inferentially meaningful effects on the speed of avoidance movements ($p = .50$). Among women, avoidance movements in response to both relatively attractive and relatively unattractive male faces tended to be somewhat faster in the Pathogen condition, but neither difference was statistically significant (*p*'s = .47 and .14, respectively). Among men, avoidance movements tended to be slower in the Pathogen condition but, again, neither effect was statistically significant (*p*’s = .53 and .60 for relatively attractive and unattractive female faces, respectively).

These results provide further evidence that perceived pathogen prevalence leads women (but not men) to respond more favorably to physically attractive opposite-sex faces. The use of an affectively negative control condition suggests that the impact of the pathogen prevalence manipulation results from a concern with pathogen transmission specifically, not from negative affect more generally. This motivational specificity is consistent with other findings documenting the effects of perceived pathogen prevalence on social cognition and behavior (Faulkner et al., 2004; Murray & Schaller, in press). The fact that the effect emerges not only on self-reported preferences, but also on the speed of approach-oriented motor movements implicates an automatized, non-conscious impact on actual behavior. This is consistent with the conceptual logic of strategic pluralism, which emphasizes the adaptive implications of preferences for reproductive behavior. It is also notable that the pathogen prevalence manipulation had an effect specific to approach movements, but did not influence avoidance movements. This pattern of findings is consistent with an interpretation that pathogen prevalence amplifies women's positive responses to men with "good genes." It does not appear to amplify aversion to men with "bad genes."

It is perhaps especially striking that the pathogen prevalence manipulation led women to make faster approach movements to attractive men, given previous results showing that pathogen threat can lead women (and men) to make relatively faster avoidance movements in response to social stimuli (Mortensen et al., 2010). These results therefore suggest that although the conclusions of Mortensen et al. (2010) may apply to social dispositions in general, they do not seem to apply to the specific domain of mating behavior in which specific kinds of approach movements have specific kinds of beneficial implications for reproductive fitness, perhaps especially in pathogen prevalent ecologies.

These results also reveal effects that are sex-specific: Pathogen prevalence amplifies female preference for attractive male mates, but does not amplify male preference for attractive female mates. These findings are consistent with an explanatory mechanism in which women implicitly use a man's physical attractiveness as a cue connoting genetic fitness.

Functional Explanations for Women's Preference for Physical Attractiveness

Thus far, I have assumed that women's desire for physically attractive mates increases following a pathogen prime because women desire to extract genetic benefits from men who possess markers of genetic fitness. However, physical attractiveness can serve not only as a signal of an individual's heritable genetic fitness, but also as a signal of the individual's current and future health status. These different inferential mechanisms have different implications for contexts under which pathogen prevalence may be expected to predict exaggerated preferences for attractive men.

Healthier mates are less likely to transmit infections. If perceived pathogen prevalence leads women to be more concerned with their own vulnerability to pathogen transmission, women who have higher personal vulnerability to disease or higher pathogen sensitivity might express exaggerated preferences for physically attractive men following a pathogen threat. Moreover, the relationship context in which women rate men should not influence their preferences because such women are most concerned with disease avoidance rather than securing genetic benefits for potential offspring.

However, healthier mates are also more likely to make better long-term partners and parents, partly because they are likely to live longer. If perceived pathogen prevalence leads women to be more concerned with the likelihood that their mate will be a long-lived, highly investing partner and parent, they might express exaggerated preferences for physically attractive men in a long-term relationship in which the father provides extended care for children.

In contrast, if perceived pathogen prevalence leads women to be more concerned with the genetic fitness of their offspring, they might express exaggerated preferences for physically attractive men in a reproductive context in which a man's genetic fitness has implications for the genetic fitness of her offspring. As previously mentioned, the monthly female ovulatory cycle provides a unique context in which securing genetic benefits from genetically fit males is prioritized. When women are most fertile, it is especially important to mate with men who possess markers of genetic fitness, even if the relationship is only short-term and sexual in nature.

Current Study Overview and Hypotheses

The current study tested the plausibility of these various functional explanations and the underlying psychological mechanism for *why* women prefer physically attractive mates following a pathogen prime. I chose to study the effect of a pathogen prevalence manipulation on women's mate preferences across the ovulatory cycle. Given the extant literature on women's mate preference shifts across the ovulatory cycle and the previous findings demonstrating how experimentally manipulated pathogen threat increased women's desire for physically attractive mates, I tested the following hypotheses.

First, I sought to replicate previous research on women's desire for physically attractive mates across the ovulatory cycle. As described previously, women in the fertile ovulatory phase of their menstrual cycle desire men who possess markers of genetic fitness, such as symmetry, masculinity, dominance, and general attractiveness (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Little et al., 2007; Penton-Voak et al., 1999). These traits are especially preferred when women rate men in a short-term relationship context because women prioritize securing genetic benefits. Therefore, I predict:

> **H1: In a neutral control condition, normally ovulating women in the highly fertile ovulatory phase will prefer a physically attractive mate more than will women who are in a non-fertile phase, especially for short-term sexual relationships.**

Research also indicates that the environment alters women's preferences. Specifically, women must often make a trade-off between a partner who possesses good genes and a partner who possesses good parenting skills. Depending on the environment, the costs and benefits of mating with a genetically fit versus high-investing partner shift. A pathogen-prevalent ecology favors mating with a genetically fit partner because having a high-investing partner carries diminishing marginal returns. Consistent with past correlational and experimental work, I also predict that:

> **H2: Increased pathogen threat will increase women's preference for a physically attractive mate, regardless of her fertility status**.

The first prediction (H1) aimed to replicate research on ovulatory shifts in mate preferences, whereas the second prediction (H2) aimed to replicate the preliminary experiments on environmentally contingent mate preferences expressed following a pathogen prime. However, combining these two lines of research provides a third and much more novel contribution. Although previous research finds that pathogen primes increase women's, but not men's, preference for and approach-behavior toward physically attractive mates, the underlying psychological mechanism and inferential information that physical attractiveness provides is unclear. There are three purported reasons why women might prefer physically attractive men as mates in a pathogen-prevalent ecology: (1) to avoid contagion, (2) to secure a disease-resistant partner who is more likely to survive, thrive, and invest in potential offspring, or (3) to secure a mate who possesses good genes that can be passed on to potential offspring. I propose that women prefer physically attractive mates in a pathogen-prevalent environment primarily because they want to extract genetic benefits from these men. If so, women should particularly desire these men as short-term sexual partners when they are most likely to become pregnant. Because the ovulatory phase of a woman's reproductive cycle presents a brief window of time when pregnancy is most likely, I predict that:

> **H3: Women in the highly fertile ovulatory phase of their cycle especially prioritize markers of genetic fitness and will prefer physically attractive men as short-term mates following a pathogen prime**.

This third prediction suggests an interaction between a woman's fertility status and a pathogen prime, such that the pathogen effect should be strongest for ovulating women.

This highly specific result would provide evidence that women's increased desire for physically attractive men following a pathogen prime is driven by their desire to extract genetic benefits for potential offspring, rather than by their desire to avoid disease or to secure a long-lived, investing partner.

Experiment Overview

In order to test these predictions, I recruited normally ovulating women (i.e., non-smoking women who are not on any form of hormonal birth control) to complete an online survey. Some of the women were exposed to a picture slideshow intended to increase the salience of disease in their local environment. Other women were exposed to a picture slideshow intended to increase negative arousal without the threat of pathogens or a neutral picture slideshow. Following this experimental manipulation, women viewed facial photographs of attractive men and then rated each man's general attractiveness and his desirability as a short-term and a long-term romantic partner. Participants also provided answers to an ovulation screening questionnaire, individual difference measures, and basic demographic information.

Method

Participants

584 normally ovulating women (e.g., not on hormonal contraception, non-smoking) between the ages of 18-40 were recruited through an online survey-hosting website (Amazon Mechanical Turk; mTurk). Participants completed the survey in exchange for $0.75 payment. Previous studies examining women's preferences and behaviors across the ovulatory cycle have used mTurk with reliable success and have replicated mTurk findings in laboratory studies (Durante et al., 2012; Durante, Rae, &

Griskevicius, 2013). All women reported being sexually attracted to men. Women who reported irregular menstrual cycle lengths (less than 24 days or greater than 35 days) or who were currently pregnant or breastfeeding were excluded from the analysis (N=182). A total of 402 women were included in the final data analysis reported below.

Procedure

Participants viewed an advertisement for a study on “visual processing and preferences” on the mTurk website. A web link included in the advertisement directed participants to the survey consent form. After reading about the study’s potential risks and benefits, participants indicated their consent by clicking a button that advanced to the next screen of the survey.

Priming Manipulation. After consenting to participate, participants were randomly assigned to a neutral control, negative arousal, or a pathogen prime condition. Each participant viewed a picture slideshow designed to elicit specific feelings (see Appendix B). Consistent with the cover story, the instructions informed participants that the study examined how individuals process and retain visual information, and that they should pay attention to the photographs in order to recall them later. In the Pathogen condition, participants saw 10 photographs that depicted individuals with obvious morphological or behavioral symptoms of infectious diseases. This set of stimuli has been used successfully in previous studies assessing the impact of perceived pathogen prevalence (see Schaller, Miller, Gervais, Yager, & Chen, 2010). In the Negative Arousal condition, the 10 photographs depicted angry individuals holding guns. In the Neutral Control condition, the 10 photographs depicted household cutlery (e.g., forks, spoons)[1].

Male Preference Measure. Immediately following the priming manipulation, participants saw three different male facial photographs selected[2] from a previous study examining facial attractiveness preferences (Park, Van Leeuwen, & Stephen, 2012; see Appendix C). For each photograph, participants were asked to imagine that they had just met the pictured man and that the two of them were "hitting it off." Participants then indicated their interest in each man by answering 9 questions in a randomized order.

As a measure of each man's general physical appearance, each woman reported how: (1) sexy and (2) attractive she found the man. As a measure of each man's desirability as a short-term mate, each woman reported how much she: (1) would like to go on a date with the man, (2) would like to have a short fling him, (3) would like to have sex with him, and (4) would like to start a short-term relationship with him. As a measure of each man's desirability as a long-term mate, each woman reported how much she: (1) would like to have a serious, committed relationship with the man, (2) would like to have a long-term relationship with the man, and (3) desired to marry him. All items were answered on 9-point scales that ranged from 1, *not at all*, to 9, *very much* (see Appendix D). The items were aggregated across the men to form a general physical appearance composite (α = .89), a short-term-mate-desirability composite (α = .92), and a long-term-mate-desirability composite (α = .92).

Fertility assessment. To ascertain fertility, participants provided the following information: (1) the start dates of their most recent menstrual period and their previous menstrual period, (2) the expected start date of their next menstrual period, and (3) the typical length of their menstrual cycle. I used the reverse cycle day (RCD) method to calculate the current cycle day for each participant. The RCD method is a reliable measure of fertility status (see DeBruine, Jones, & Perrett, 2005; Durante, Griskevicius, Hill, Perilloux, & Li, 2011; Gangestad & Thornhill, 1998; Haselton & Gangestad, 2006). This method calculates current cycle day by subtracting the start date of the most recent menstrual period from the date the participant took the survey. Cycle length is also calculated by subtracting the most recent period start date from the previous period start date.

The chances of becoming pregnant from one act of sexual intercourse increases substantially during the ovulatory phase of the cycle (see Wilcox, Dunson, Weinberg, Trussell, & Baird, 2001). Based on established methods using cycle day information, participants were divided into a high fertility group and a low fertility group. Following the conception probability curve, the high fertility group (n=110) consisted of women who had a conception probability above 5% (Cycle Days 9–17). The low fertility group (n=292) consisted of women who had a lower conception probability on the days leading up to ovulation (Cycle Days 1-8) and the days following ovulation (Cycle Days 18–29).

Individual Difference Measures. Participants also completed various individual difference measures, including sociosexual orientation (Simpson & Gangestad, 1991), disgust sensitivity (Tybur, Lieberman, & Griskevicius, 2009), perceived vulnerability to disease (Duncan, Schaller, & Park, 2009), and partner desirability and extrapair desires (if women reported being in dating relationships; see Appendix E). These measures were selected as potential moderators because previous research suggests that women who have unrestricted sociosexual orientations and follow a short-term mating strategy increase the importance they place on physical attractiveness in male mates (Buss & Schmitt, 1993; Simpson & Gangestad, 1990). Other research has found that women in relationships prefer attractive men if their current partner lacks indicators of genetic fitness (Little et al., 2002; Pillsworth & Haselton, 2006). Women who believe they are at a heightened risk of infection may also have an especially strong preference for physically attractive mates as a way to avoid contagion.

Results

Prediction 1: *In a non-pathogen environment, women at high compared to low fertility will show an increased preference for a physically attractive mate, especially as a short-term, sexual partner*.

The first prediction aimed to replicate past research on women's preferences for physically attractive mates across the ovulatory cycle. To do this, I examined the simple effects of fertility within the neutral control condition and the negative arousal condition for both short-term and long-term relationship contexts. In the neutral control condition, there was no simple effect of fertility on women's preference for physically attractive men as short-term (p = .236) or long-term (p = .169) relationship partners. In the negative arousal condition, there was no simple effect of fertility on women's preference for physically attractive men as short-term (p = .858) or long-term (p = .933) relationship partners. However, an inspection of the means suggested that there were directional trends. Without the threat of pathogens, women at high fertility preferred physically attractive men as short-term partners more than did women at low fertility.

Previous research has found that women who possess a more unrestricted sociosexual orientation increase the importance of physical attractiveness in a male partner (Buss & Schmitt, 1993; Simpson & Gangestad, 1990). Therefore, I chose to split the data into restricted (n = 191) and unrestricted (n = 200) women to analyze the simple effect of fertility in the neutral control condition[3]. For restricted women in the neutral control condition, there was no simple effect of fertility on preference for physically attractive men as short-term (p = .881) or long-term (p = .229) relationship partners. However, for unrestricted women in the neutral control condition, there was a marginally significant simple effect of fertility on their preference for physically attractive men as short-term partners, $F(1, 194) = 2.83$, $p = .094$ (see Figure 4). That is, women who tend to follow a short-term mating strategy prefer physically attractive men as short-term sexual partners when they are at high compared to low fertility. This simple effect did not emerge when unrestricted women rated the men as long-term partners (p = .381).

Prediction 2: *Pathogen threat will increase women's preference for a physically attractive mate, regardless of ovulatory status*.

The second prediction aimed to replicate and support the results from the preliminary experiments suggesting that women prefer more attractive men when pathogen threat is high. Consistent with these previous findings, a 3 (Condition: Neutral Control, Negative Arousal, Pathogen) x 2 (Fertility: Low, High) between-subjects ANOVA revealed a main effect of prime condition when women rated men as short-term partners, $F(2, 396) = 3.47$, $p = .032$, $\eta^2 = .017$ (see Figure 5). Further probing of this effect suggested that women in the pathogen prime condition differed significantly from women in the negative arousal condition, but not the neutral control condition. Regardless of fertility status, women in the pathogen condition rated men as more desirable short-term partners than did women in the negative arousal condition (p = .012), but not compared to women in the neutral control condition (p = .615). This pattern of effects did not hold when women rated men as long-term partners (p = .440) or when women rated men's general physical appearance (p = .352).

Prediction 3: *Following a pathogen prime, women at high fertility in particular will prefer physically attractive men as short-term mates.*

The last prediction aimed to test the proposed inferential mechanism for why women prefer physically attractive mates following a pathogen prime. As predicted, a 3 (Condition: Neutral Control, Negative Arousal, Pathogen) x 2 (Fertility: Low, High) between-subjects ANOVA revealed a marginally significant interaction on the short-term desirability composite, $F(2, 396) = 2.34$, $p = .098$, $\eta^2 = .012$ (see Figure 6). That is, the priming condition had a different effect on women depending on whether the women were at low or high fertility. Priming condition significantly influenced preferences for physically attractive men as short-term mates for women at high fertility, $F(2, 396) = 3.81$, $p = .023$, $\eta^2 = .019$, but it had no effect on women at low fertility (p = .783).

Further inspection of the pairwise comparisons within women at high fertility revealed that the pathogen condition differed marginally from the neutral control condition and differed significantly from the negative arousal condition. Compared to women in the neutral control condition, women in the pathogen condition marginally preferred physically attractive men as short-term sexual partners ($M_{\text{Neutral}} = 4.79$, SD = 1.72; $M_{\text{Pathogen}} = 5.64$, SD = 1.62; p = .057). Compared to women in the negative arousal condition, women in the pathogen condition significantly preferred physically attractive men as short-term sexual partners ($M_{\text{Negative}} = 4.54$, SD = 1.83; $M_{\text{Pathogen}} = 5.64$, SD = 1.62; p = .007).

A 3 (Condition: Neutral Control, Negative Arousal, Pathogen) x 2 (Fertility: Low, High) between-subjects ANOVA did not reveal a significant interaction when women rated men as long-term partners (p = .108) or when women rated the men's general physical appearance (p = .313).

Individual Difference Moderators

Finally, I examined potential moderators of the Condition x Fertility Status interaction. One alternative explanation for women's increased attraction to physically attractive male mates following a pathogen prime is a heightened fear of contagion. If women with higher scores on pathogen disgust sensitivity or perceived vulnerability to disease show an increased preference for physically attractive men following a pathogen prime, a desire to avoid contagion might also explain the pattern of effects. However, pathogen disgust sensitivity did not moderate the Condition x Fertility Status interaction of the general physical appearance composite (p = .843), the short-term desirability composite (p = .358), or the long-term desirability composite (p = .963).

Perceived vulnerability to disease also did not moderate the Condition x Fertility Status interaction of the long-term desirability composite (p = .631), but it did marginally moderate the interaction of the general physical appearance composite (p = .051) and the short-term desirability composite (p = .055). An inspection of the means revealed that the effects reported above were stronger for women with higher perceived vulnerability to disease. This moderation might suggest that women's preference for physically attractive mates is partially driven by a desire to avoid disease contagion. However, the precise pattern of effects for only the short-term desirability composite and the general physical appearance composite still support the hypothesis that preference is driven by women's desire to extract genetic benefits from physically attractive men.

The current study demonstrated how perceived pathogen prevalence leads women at different points in their ovulatory cycle to prefer more physically attractive mates. I failed to replicate past work that finds women at high (relative to low) fertility prefer physically attractive men, specifically as short-term sexual partners. However, I found additional support for the preliminary experiments and demonstrated that experimentally manipulated pathogen prevalence increased women's preference for physically attractive men. Contrary to the preliminary experiments, this effect only emerged when comparing the pathogen condition to the negative arousal condition and not when comparing to the neutral control condition. Lastly, the results suggested that women at high fertility who experienced a temporary increase in pathogen salience preferred physically attractive men as short-term partners more than did women at low fertility and women in non-pathogen threat environments. Taken together, these findings offer preliminary support that the heightened preference for physically attractive men is driven by an underlying concern for the genetic fitness of women's potential offspring.

General Discussion

Pathogens, disease, and infection have plagued humans throughout history. As a result, humans have evolved not only physiological immune systems to cope with disease threat, but also psychological mechanisms and a *behavioral* immune system to avoid contagion. The current research extends previous work by showing how pathogen threat influences specific approach behaviors.

In the current study, I found preliminary support that women show an increased preference for physically attractive men following a pathogen prime, especially when fertility is high and conception is likely. This result is consistent with hypotheses deduced from the strategic pluralism model of human mating (Gangestad & Simpson, 2000). Drawing on the evolutionary implications of differential minimal parental investment, this model predicts that women should be especially likely to prefer mates who might produce offspring endowed with a high degree of immunocompetence, and that this preference should be exaggerated under conditions of high pathogen prevalence (within which immunocompetence should be especially beneficial to reproductive fitness; Kaplan, 1996). In ancestral environments, prior to recent medical advances, the most pathogen-resistant offspring were more likely to survive to reproductive age. This would have been the case especially within ecological circumstances characterized by high levels of pathogen prevalence. Given that mate choices often involve trade-offs between desirable traits (e.g., physically attractive men may not be the most caring partners or dependable parents; Gangestad et al., 2007), female reproductive fitness would have been increased by a strategically flexible, context-contingent tendency to show relatively stronger preference for physically attractive mates in pathogen prevalent ecologies, especially when conception probability is high.

Limitations

Contrary to past research, I failed to demonstrate that women at high (relative to low) fertility prefer physically attractive men, specifically as short-term sexual partners. Previous studies documenting ovulatory shifts in mate preferences typically sample undergraduate women between the ages of 18-24, whereas the current sample contained women whose ages ranged from 18-40 with a mean of 28.1 years. This slightly older and more varied sample could possibly explain why I failed to replicate past work.

A recent meta-analysis of ovulatory shifts in female mate preferences also suggests that the most robust effects emerge when women are rating photos of body masculinity or male social dominance (Gildersleeve, Haselton, & Fales, in press). Effects examining female preference for facial traits, including general attractiveness, masculinity, symmetry, and averageness, is weaker. Therefore, the current study was limited by restricting women's ratings to preferences for facial attractiveness. Using full-body photographs as target stimuli might strengthen future studies.

Three preliminary experiments demonstrated that a pathogen prime led women, but not men, to increase their preference for physically attractive mates. Experiments 1 used a neutral control condition as the comparison group, Experiment 2 used a blank control, and Experiment 3 used a negative arousal condition. In the current study, I failed to replicate the effects found in Experiments 1 and 2, suggesting that compared a neutral or blank control condition, a pathogen prime increased women's preference for physically attractive male mates. One possible explanation is that the current study used a picture slideshow to prime the threat of pathogens as opposed to news stories or a disclaimer. Both of these primes are self-relevant and require participants to imagine or feel like they are in the threatening environment. In contrast, the picture slideshow contained pictures of possibly infected others that may have been less threatening to participants. Although previous studies have successfully documented pathogen effects using the slideshow manipulation (see Murray, Jones, & Schaller, 2013; Schaller, Miller, Gervais, Yager, & Chen, 2010), no study has used the slideshow manipulation to document changes in mate preferences.

Despite the aforementioned limitations, the results offer preliminary and marginal support that women prefer physically attractive men following a pathogen prime. If women use a man's physical attractiveness as a heuristic cue signaling his genetic fitness, an additional question arises: Does perceived pathogen prevalence lead women to respond especially favorably to men whose physical appearance implies "good genes," or especially aversively to men whose appearance may imply "bad genes," or both? Some researchers have proposed an “avoid unfit” hypothesis, finding that individuals with higher levels of pathogen disgust rate unattractive targets as especially unattractive (Park, van Leeuwen, & Stephen, 2012). The current study provides more evidence for an “approach fit” hypothesis, suggesting that female preference effects are mainly driven by approach-oriented responses to men who appear to have “good genes.” One limitation of the current study is that I did not directly compare women’s responses to relatively unattractive men. Future research needs to examine how perceived pathogen prevalence influences women’s potentially aversive and avoidant responses to unattractive men at various points of their ovulatory cycle. One might expect that, just as women are attracted to attractive men when conception is likely, women are repulsed by unattractive men when fertility is high (see Garver-Apgar, Gangestad, & Simpson, 2007).

Additional Implications and Future Directions

If perceived pathogen prevalence amplifies women's implicit concern with offspring immunocompetence, its effects may not be limited to preferences pertaining to facial attractiveness. It may also amplify preferences for other traits that are diagnostic of heritable immunocompetence or of "good genes" more generally. Lee and Zeitsch (2011) provide some preliminary evidence consistent with this speculation, showing that perceived pathogen prevalence leads women to place higher overall value on a broad collection of traits that may signal genetic fitness. But effects on additional specific traits need to be tested. One possible candidate is bodily symmetry ("fluctuating asymmetry"; Gangestad et al., 1994). Just as facial symmetry appears to be diagnostic of genetic fitness, so too is the bilateral symmetry of an organism's whole body. A man's fluctuating asymmetry is not easily perceptible directly, but there is abundant evidence that women's preferences are sensitive to other variables that correlate highly with it. These variables include body odor (Gangestad, Thornhill, & Garver-Apgar, 2005) and social dominance (Simpson et al., 1999). Thus, it is plausible that perceived pathogen prevalence might also lead to exaggerated preferences for men who have the scent of symmetry or who are more socially dominant in general.

It might also be worthwhile to test whether pathogen prevalence influences the priority that women place on a man's intelligence and creativity. Although results Experiment 1 offered no evidence for such an effect, other research implies that women may use a man's intelligence and creativity as inferential indicators of genetic fitness (Haselton & Miller, 2006; Miller & Todd, 1998). Furthermore, cross-cultural correlations reveal that, just as actual ecological variation in pathogen prevalence predicts preferences for mates who are healthier and more attractive, it also predicts preferences for mates who are more intelligent (Gangestad et al., 2006). However, if it turns out that there is no causal influence of pathogen prevalence on preference for creatively intelligent mates, this non-effect could reflect a developmental trade-off between immunocompetence and psychological traits such as intelligence and creativity. Immune systems are energetically expensive to build, and so are the cortical structures underlying intelligence and creativity. In harsh environments characterized by limited caloric resources, developmental investment in immunocompetence may be accompanied by lower levels of specific psychological traits, particularly reduced cognitive capacities of the sort that characterize intelligence (Curno, Reader, McEligott, Behnke, & Barnard, 2011; Eppig, Fincher, & Thornhill, 2010). Thus, intelligence and creativity may signal “good genes,” but they may also serve as heuristic harbingers of poor health (especially in ecologies characterized by resource scarcity and pathogen prevalence). In any case, it remains for future research to more directly assess whether perceived pathogen prevalence actually impacts mate preferences pertaining to intelligence, creativity, and other psychological traits diagnostic of good genes.

Additional directions for future research are also implicated by the current results. One important question is the extent to which objective reality actually corresponds to the inferential “link” between physical attractiveness and good genes: Just how much of an immunological advantage do physically attractive men pass onto their offspring? Although many studies have addressed a related question about individuals' physical attractiveness and their own health outcomes (Weeden & Sabini, 2005), additional trans-generational longitudinal studies are required to assess the extent to which individuals' physical attractiveness predicts the immunocompetence, health, and reproductive fitness of their offspring.

It will also be interesting to consider the collateral implications that strategically flexible female mate preferences might have for male behavior. Male mating strategies tend to be calibrated to female mate preferences (Kenrick, Li, & Butner, 2003). This has implications for a wide range of behaviors that men engage in strategically as a means of distinguishing themselves from other potential mates (e.g., Griskevicius, Cialdini, & Kenrick, 2006; Griskevicius, Goldstein, Mortensen, Cialdini, & Kenrick, D. T., 2006; Sundie, Kenrick, Griskevicius, Tybur, Vohs, & Beal, 2011). Because women's mate preferences change in response to perceived pathogen prevalence, men may adjust their behavior accordingly. For example, perceived pathogen prevalence may lead physically attractive men to more strenuously engage in behaviors that draw attention to their physical appearance, and may lead relatively unattractive men to more strenuously attempt to master—and conspicuously display—behaviors that might serve as additional signals of good genes (e.g., social dominance). Alternatively, for men who cannot easily exhibit traits connoting genetic fitness, perceived pathogen prevalence may motivate conspicuous displays of traits that connote their ability to be caring romantic partners and high-investing parents (see Gangestad & Simpson, 2000). Effects such as these might be observed not only at an individual level of analysis, but at a population level as well—as cultural differences predicted by actual ecological variation in pathogen prevalence. More generally, because of its immediate effects on female mate preferences, pathogen prevalence may also have indirect consequences on the psychology of men, as they strategically vary their behavior in order to compete most successfully in the mating game.

In conclusion, the current research adds to a growing literature on how perceived pathogen prevalence does not always lead to avoidance-oriented responses of the sort found in most previous work on the behavioral immune system (Schaller, 2011; White, Kenrick, & Neuberg, 2013). Although interpersonal avoidance (and behavioral inhibition more broadly) may be a generally adaptive response to the perceived threat of pathogen transmission, there are specific domains of interpersonal behavior in which this general strategy may be mitigated by additional strategies with separate implications for reproductive fitness. Mating is one such domain.

Footnotes

1. The picture slideshows were adapted from Schaller, Miller, Gervais, Yager, & Chen (2010) and have also been successfully used by Murray, Jones, and Schaller (2013). Mood assessments conducted after the slideshow by Schaller et al. (2010) revealed that self-reported stress was lower following the disease slideshow compared to the guns slideshow.
2. Target photographs were subsamples taken from a set of 5 photographs of Caucasian male models with neutral facial expressions, pre-rated for physical attractiveness (see Park, van Leeuwen, & Stephen, 2012). The three men were selected for being rated as highly sexy (M = 7.08), attractive (M = 7.44), dominant (M = 6.11), muscular (M = 6.03), and masculine (M = 6.42).
3. Results are only presented for the neutral control condition because no significant effects emerged within the negative arousal condition.

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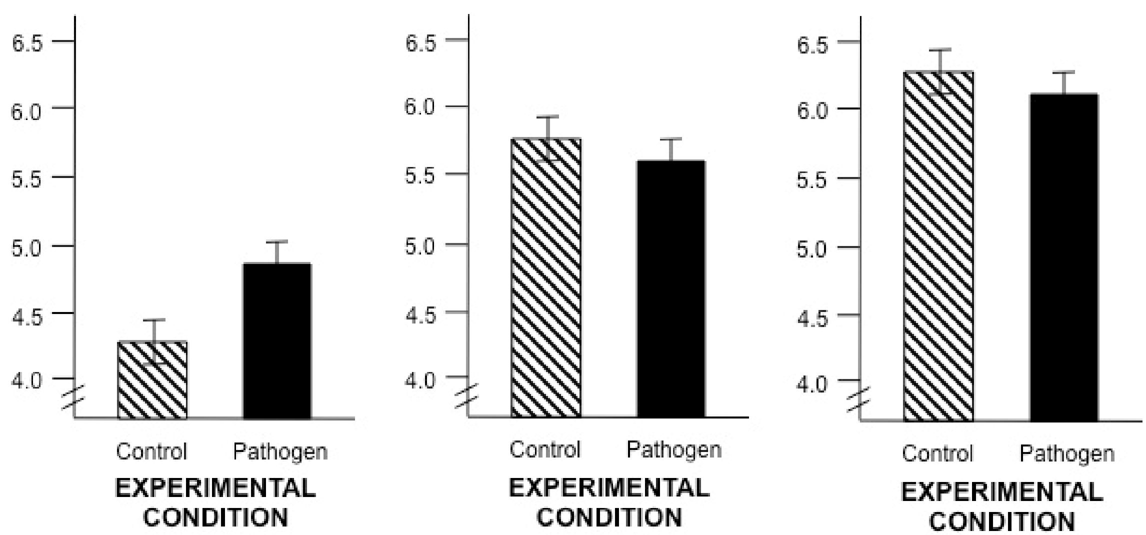
Appendix A

Figures for the preliminary experiments and the main analyses of the dissertation are included in this appendix.

Figure 1. Results from Experiment 1: Effect of the experimental manipulation of perceived pathogen prevalence on the importance that women and men place on specific traits in a mate.

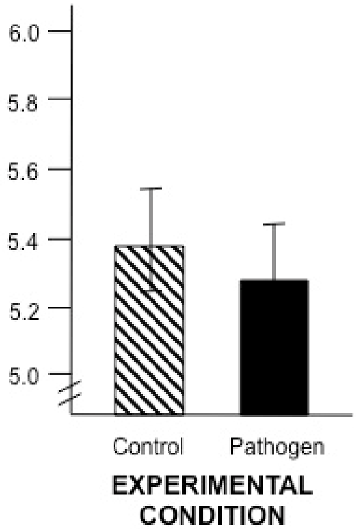
FEMALE PARTICIPANTS RATING MEN

Attractive & Sexy | **Reliable & Dependable** | **Intelligent & Creative**

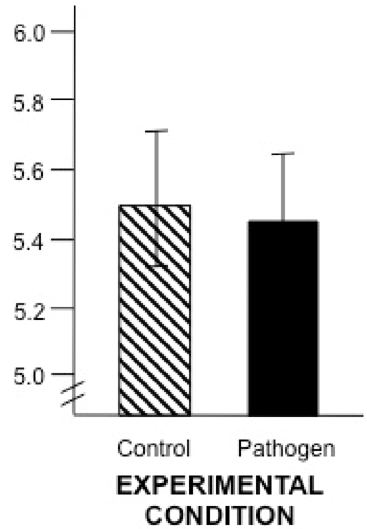


MALE PARTICIPANTS RATING WOMEN

Attractive & Sexy



Reliable & Dependable



Intelligent & Creative

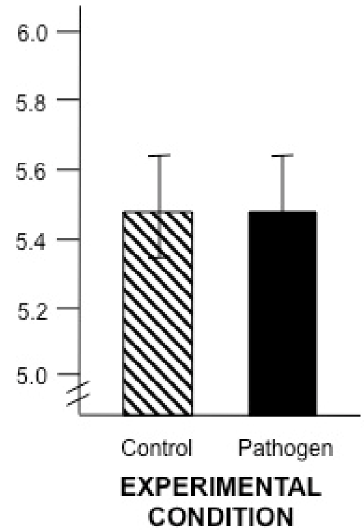
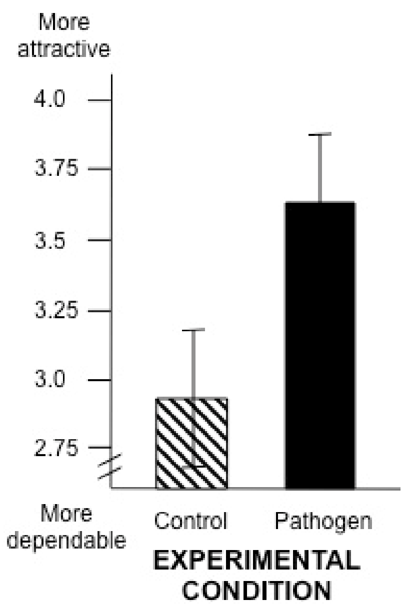


Figure 2. Results from Experiment 2: Effect of the experimental manipulation of perceived pathogen prevalence on women's and men's choices to go on a date with a person who is highly physically attractive versus dependable.

FEMALE PARTICIPANTS CHOOSING BETWEEN MEN



MALE PARTICIPANTS CHOOSING BETWEEN WOMEN

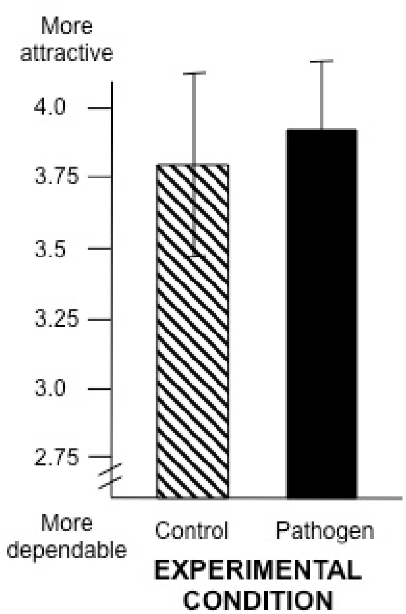
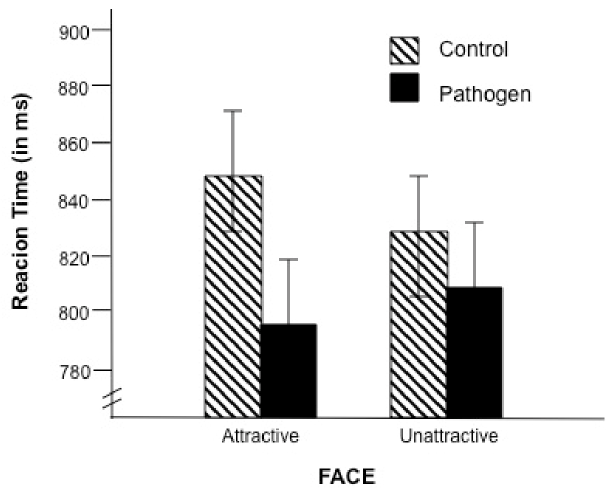


Figure 3. Results from Experiment 3: Effect of the experimental manipulation of perceived pathogen prevalence on the speed with which women and men make approach movements in response to relatively attractive and relatively unattractive opposite-sex faces.

FEMALE PARTICIPANTS VIEWING MEN



MALE PARTICIPANTS VIEWING WOMEN

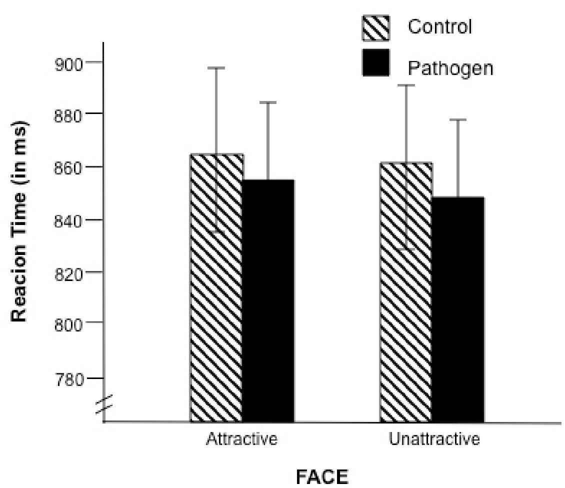


Figure 4. Mean ratings of physically attractive men as short-term relationship partners for women in the neutral control condition as a function of fertility status and sociosexual orientation.

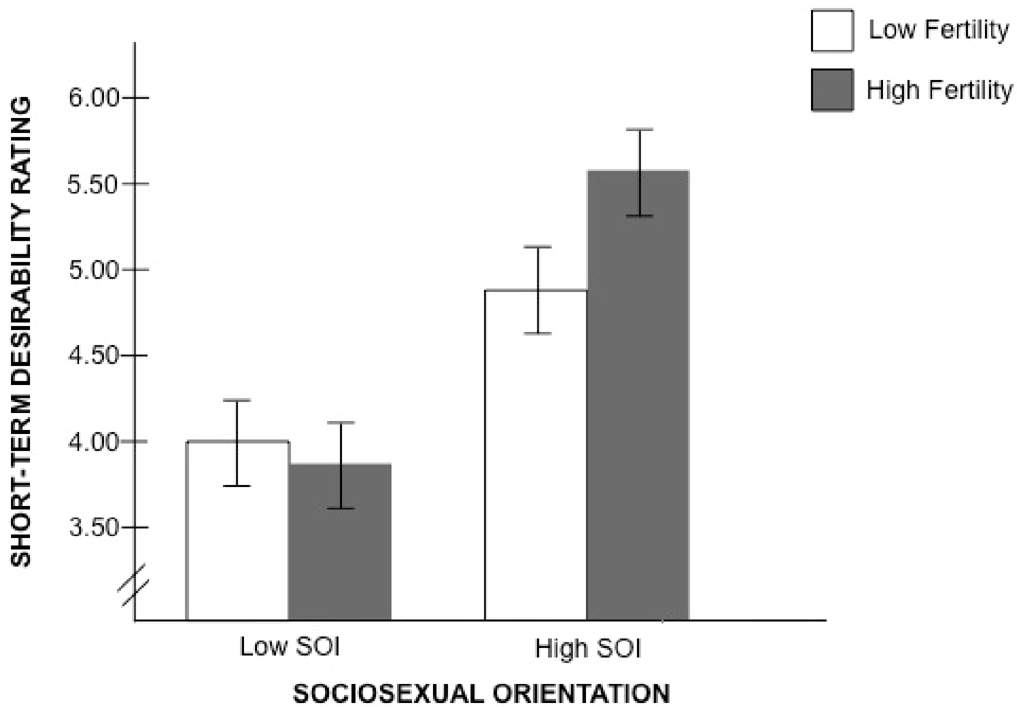


Figure 5. Mean ratings of physically attractive men as desirable short-term partners as a function of the pathogen prime compared to the neutral control and negative arousal conditions.

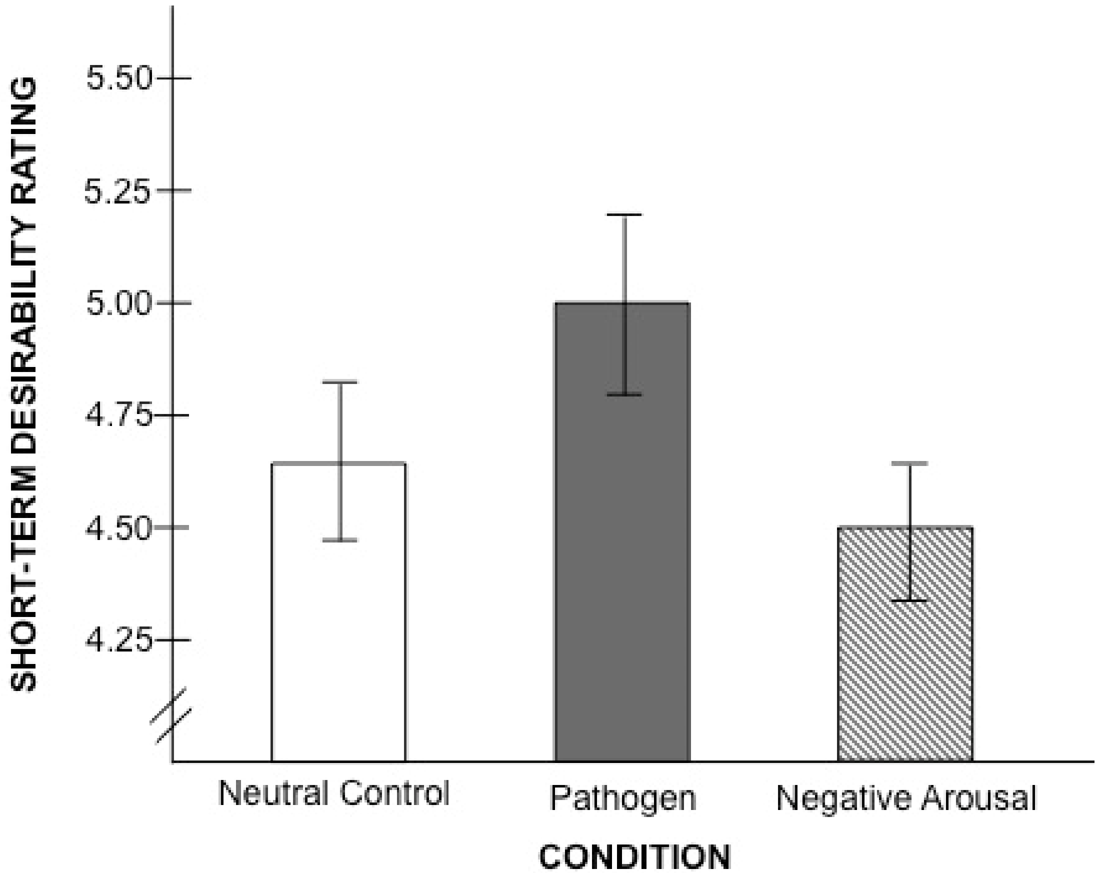
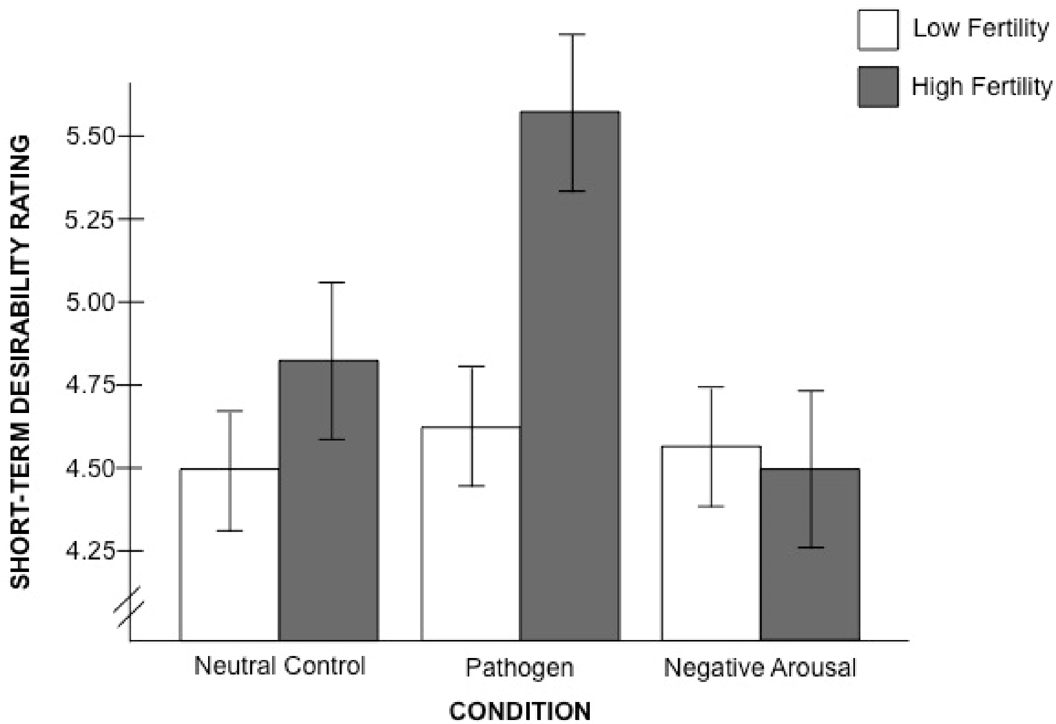


Figure 6. Mean ratings of physically attractive men as short-term relationship partners as a function of experimental condition and fertility status.



Appendix B
Pictures used for priming manipulation

<u>Neutral Control Condition</u>

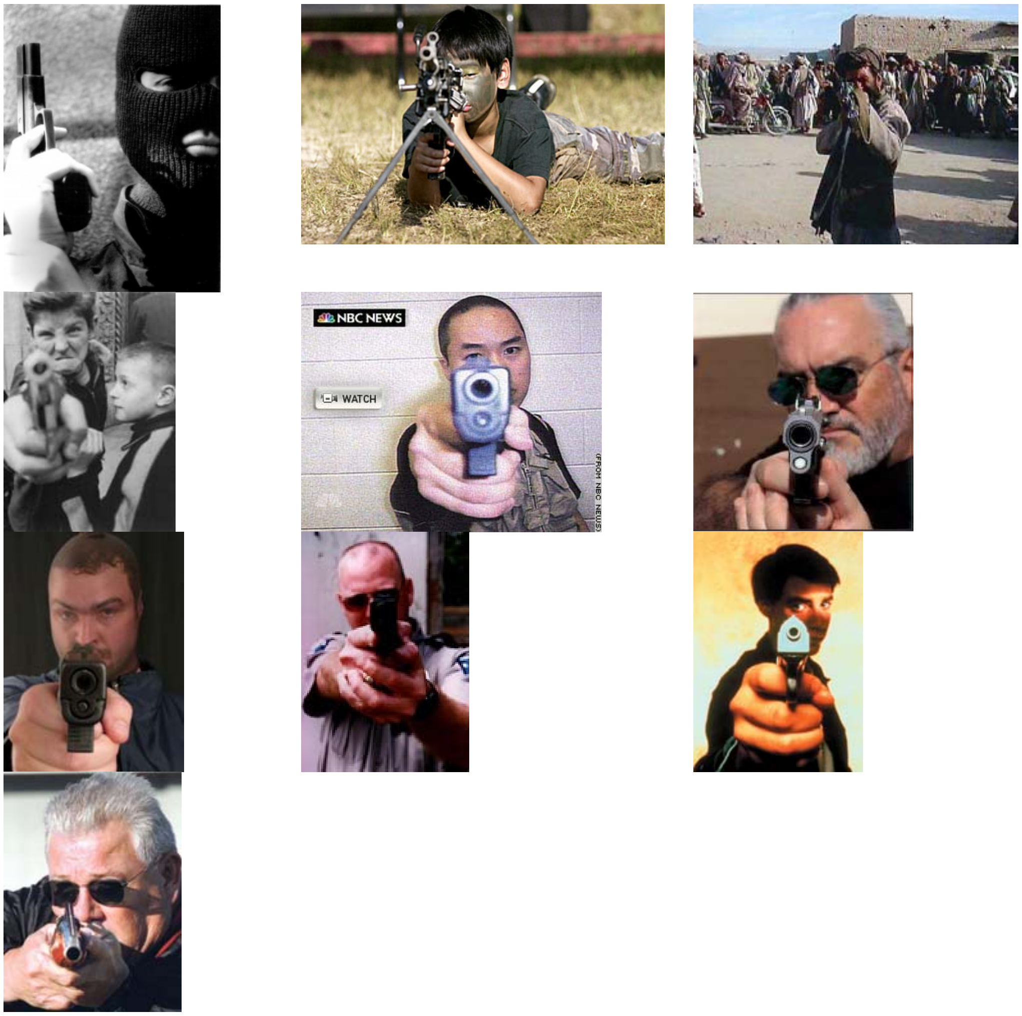









Negative Arousal Condition



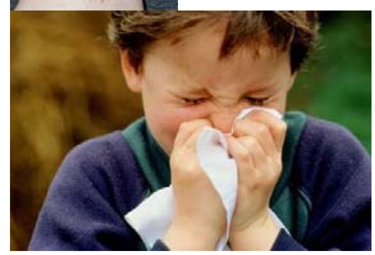
Pathogen Prime Condition



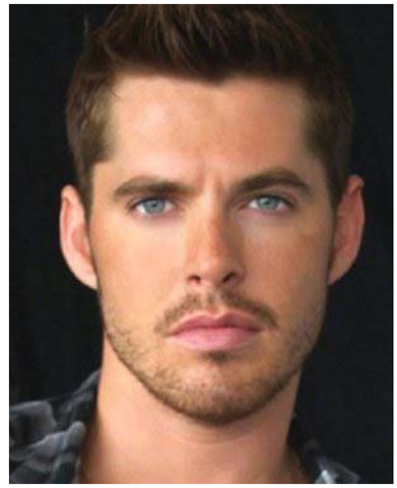









Appendix C
Attractive Male Photographs



Appendix D
Male Desirability Ratings for Various Relationship Contexts

Instructions: “Imagine you are getting to know this man and the two of you are hitting it off. Compared to most men…”

1. How much would you like to go on a date with him? (Short-term)
2. How sexy is the man? (General Physical Appearance)
3. How much would you like to have a short fling with him? (Short-term)
4. How much would you like to have a serious, committed relationship with him? (Long-term)
5. How attractive is this man? (General Physical Appearance)
6. How much would you like to have sex with him? (Short-term)
7. How much would you like to have a long-term relationship with him? (Long-term)
8. How much would you like to have a casual, short-term relationship with him? (Short-term)
9. How much would you like to marry him? (Long-term)

Appendix E
Individual Difference Questionnaires

Three-Domain Disgust Scale (Tybur, Lieberman, & Griskevicius, 2009):

1. Shoplifting a candy bar from a convenience store
2. Hearing two strangers having sex
3. Stepping on dog poop*
4. Stealing from a neighbor
5. Performing oral sex
6. Sitting next to someone who has red sores on their arms*
7. A student cheating to get good grades
8. Watching a pornographic video
9. Shaking hands with a stranger who has sweaty palms*
10. Deceiving a friend
11. Finding out that someone you don't like has sexual fantasies about you
12. Seeing some mold on old leftovers in your refrigerator*
13. Forging someone's signature on a legal document
14. Bringing someone you just met back to your room to have sex
15. Standing close to a person who has body odor*
16. Cutting to the front of a line to purchase the last few tickets to a show
17. A stranger of the opposite sex intentionally rubbing your thigh in an elevator
18. Seeing a cockroach run across the floor*
19. Intentionally lying during a business transaction
20. Having anal sex with someone of the opposite sex
21. Accidentally touching a person's bloody cut*

* indicates item scored in calculation for pathogen disgust sensitivity

Perceived Vulnerability to Disease (Duncan, Schaller, & Park, 2009):

1. It really bothers me when people sneeze without covering their mouths.
2. If an illness is "going around," I will get it
3. I am comfortable sharing a water bottle with a friend*
4. I do not like to write with a pencil someone else has obviously chewed on
5. My past experiences make me believe I am not likely to get sick even when my friends are sick*
6. I have a history of susceptibility to infectious disease
7. I prefer to wash my hands pretty soon after shaking someone's hand
8. In general, I am very susceptible to colds, flu, and other infectious diseases
9. I dislike wearing used clothes because you do not know what the last person who wore it was like
10. I am more likely than the people around me to catch an infectious disease
11. My hands do not feel dirty after touching money*
12. I am unlikely to catch a cold, flu, or other illness, even if it is "going around."
13. It does not make me anxious to be around sick people*
14. My immune system protects me from most illnesses that other people get*
15. I avoid using public telephones because of the risk that I may catch something from the previous user

* indicates reverse-scored item

Sociosexual Orientation Inventory (Simpson & Gangestad, 1991):

1. Sex without love is OK
2. I can imagine myself being comfortable and enjoying “casual” sex with different partners
3. I do not want to have sex with a person until I am sure that we have a long-term, serious relationship.
4. With how many different partners have you had sex with in the past 12 months?
5. With how many different partners have you had sexual intercourse on one and only one occasion?
6. With how many different partners have you had sexual intercourse without having an interest in a long-term committed relationship with the person?

Partner Desirability:

1. How would you judge your partner’s physical attractiveness compared to your own attractiveness?
2. How would you rate your partner's desirability as a short-term mate (e.g., a partner in a one-night sexual encounter or brief affair) compared to your own desirability as a short-term mate?

<u>Extrapair Desires:</u>

1. How much have you flirted with men other than your partner?
2. How much interest would you have in having a date with someone other than your partner, if someone you found interesting asked you out on a date?
3. How much interest would you have in having sex with someone other than your partner if you met someone you were very attracted to and who was also very attracted to you?
4. How much have you desired to have sexual intercourse with your partner?*
5. How sexually attracted to your partner have you been?*

* indicates reverse-scored item