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The Ecology and Evolution of Human Reproductive Behavior

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THE ECOLOGY AND EVOLUTION OF HUMAN REPRODUCTIVE BEHAVIOR

DISSERTATION

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Arts and Sciences
at the University of Kentucky

By
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2022

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ABSTRACT OF DISSERTATION

THE ECOLOGY AND EVOLUTION OF HUMAN REPRODUCTIVE BEHAVIOR

The complexity of human reproductive behavior has necessitated its examination through a variety of scientific disciplines, each focusing on specific elements of our biology, behavior, and society. However, this complexity also necessitates that we reintegrate the information learned from each discipline into a single framework, one rooted in the evolutionary principles that have shaped the development of all life on earth. In this dissertation, I use this framework to explore human reproductive behavior, with a particular focus on sexual coercion and fertility-mediated sexual behavior.

In Chapter 1, I introduce the approach taken in this document, identify several key limitations, and outline the general structure. In Chapter 2, I conduct a comprehensive and interdisciplinary review that includes the fundamentals of sexual conflict and reproductive strategies; the evolution of human reproductive characteristics in response to socio-cognitive demands; the aspects of human sociality expected to influence reproductive behavior; the identified trends in human mating behavior; the proposed pressures behind concealed ovulation in primates; the essentials of the menstrual cycle; and the existing evidence for behavioral fertility in humans. In Chapter 3, I use a game-theory model to investigate the emergence of sexually coercive behavior across a variety of species, including humans, in which male coercion is a non-developmentally-determined reproductive strategy to identify several ecological and behavioral characteristics that predict the emergence of coercive behavior generally consistent with observed trends. In Chapter 4, I use face-trait research to investigate the degree to which women recognize and discriminate between images of men with personality traits associated with different male reproductive strategies as well as how these preferences might be mediated by her relationship and fertility status. In Chapter 5, explore the intersection of fertility, fertility belief, and sexuality, specifically testing the hypothesis that a woman's sexual interest shifts in response to her fertility while taking into consideration her beliefs regarding her fertility. Finally, in Chapter 6, I review the primary take-home messages of this work and recommend that future research take these into consideration as they move forward.

By taking an interdisciplinary approach rooted in evolutionary biology, this work reveals the need for an understanding of human reproductive behavior that incorporates a wider view of reproductive ecology. In doing so, we can gain a more accurate, comprehensive, and nuanced understanding of human reproductive behavior.

KEYWORDS: Human Reproductive Behavior, Fertility, Human Evolution, Sexual Coercion, Mate Choice Preferences

Kaylynne M. Glover

06/14/2022

Date

THE ECOLOGY AND EVOLUTION OF HUMAN REPRODUCTIVE BEHAVIOR

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DEDICATION

This work is dedicated to Rosalind Franklin.
And to Hedy Lamar,
and to Lise Meitner, Alice Ball, Chien-Shiung Wu, and Trotula of Salerno,
and to every other woman whose credit for their work has been stolen by men.

It is dedicated to every victim of sexual violence,
and to every woman who has been told to smile.
To every person who has had to put their dreams on hold to make way for the dreams of men,
and to everyone who has been punished for saying enough.

It is dedicated to every disabled person,
and gender identity and sexual orientation,
and person of color and ethnic minority,
who has been neglected, exploited, and abused by researchers,
whose experiences have been ignored, minimized, and dismissed by physicians,
and whose every step forward has been impeded by those who benefit from the systems that oppress them.

It is dedicated to every woman who dares to be a parent and a professional,
and to every young girl dreaming of changing the world.

It is dedicated to bossy women everywhere.

Long may we reign.

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Joining a research lab is like joining an academic family, and they say that it takes a village to raise a child. So please allow me to introduce you to the village that has helped raise me.

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You also get academic siblings (lab mates) to fight with for this time and attention. And like real siblings, they also provide much needed perspective, assistance, and community (but thankfully, no noogies this time around). I'm very grateful for all of those who shared this space with me and for the support they gave over the years. I would like to give special thanks to Aviv Brokman, whose statistical aid has been invaluable, and to the three undergraduate students without whom this work would have surely suffered– Sarah Robbins, Ejehi Erewele, and especially Madison von Deylen. It has been an honor to have played a role in your own lives, and I'm so stinkin' proud of each of you. And finally, I would like to thank my many research participants who volunteered their time and effort (and specimens), literally making this work possible. While you were not official lab members, you(r contributions) were definitely part of the lab, and it really does mean a lot to me, and to scientists everywhere.

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graduate student representative and advocate at the university, state, and national level. This work was enthusiastically supported and funded by the Graduate School, the Office of the University President, and the Office of the Provost. I am deeply grateful for this, not only on my behalf, but on behalf of the students nationwide. There are serious systemic problems in graduate education, and these issues cannot be addressed without concerted attention and investment.

The stress of graduate school can do a number on your body, and it left its mark on mine. For a time, I was sure my body was going to collapse in on itself like a condemned building, but my department worked hard to ensure that I would have the financial support and flexibility needed to get through it. I'm very grateful to those who worked to make that possible, namely Drs. David Weisrock, Pete Mirabito, and Jessica Santollo. I would like to give extra thanks to Pete Mirabito who allowed me to be his teaching assistant and thereby ensured that I would have the flexibility necessary to navigate the chaos. Pete, thank you for never treating me like I was not doing enough or giving enough during that time. Your kindness and support helped counter the voices in my head that plagued me constantly.

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CHAPTER 1. INTRODUCTION

Humans are a product of 3.5 billion years of evolutionary forces. While the cognitive and technological advances of today seem to suggest we are largely decoupled from the biological influences of our ancestors, it is only within the last 100,000 years that we have been capable of the symbolic thought processes indicative of modern cognition (d'Errico et al. 2005, Henshilwood et al. 2006, d'Errico and Stringer 2011).

We must therefore consider the possibility that there are aspects of our daily lives that are influenced by evolutionary pressures. Certainly, several aspects are clearly biological and are tightly linked to our evolutionary history, such as physiological patterns of fertility, fecundity, and physical maturation. However, other aspects of our lives appear wholly independent of our biology and seem to emerge from a combination of social influences and rational decision-making, such as what to wear or who to date. And yet, sociality is not unique to humans. Indeed, the pattern of human evolution points to a coevolutionary dynamic between social complexity and cognition that has lasted for at least 5 million years and that has driven the emergence of uniquely human reproductive characteristics and demands – demands that are no less significant today. Thus, understanding these dynamics is crucial to understanding our behavior.

Resistance to exploring evolutionary or biological explanations for human behavior often comes from a misunderstanding of what this would mean for our behavior. “Biological” is often interpreted as “inevitable” – as though there is a single gene that codes for “kindness.” But biology is not deterministic. Biology is plastic. It provides a flexible framework upon which environmental and social conditions act and that allows for behaviors to emerge in response – behaviors that would likely be adaptive under those conditions. These conditions are the human condition – the experiences we have and the beliefs we adopt when we are young – and they interact with the existing underlying biological framework, both that which exists in our genetic makeup and those that are shaped by our fetal environment. Ultimately, the behaviors that emerge may be “adaptive” or “non-adaptive” based in their environment, but they may also be considered “good” or “bad” by society, two types of designation wholly separate from each other.

Accepting the adaptiveness of behavior does not excuse or mitigate it, and accepting a biological explanation for harmful behavior neither precludes its extermination nor excuses its existence. We must not resign ourselves to their continuation or acceptance. We must, instead, be realistic about what it may take to combat them. In the case of sexual violence, failure to recognize its reproductive aspects is not only unnecessary but unwise. Focusing exclusively on non-evolutionary causes will undoubtedly result in our failure to eradicate it.

Evolutionary approaches to behavior focus on identifying universal patterns. Identifying the degree to which a trait is consistent and predictable both within and across species is key in identifying the presence of evolutionary forces. Thus, even though human behavior is extraordinarily complex, with variation at the individual, population, cultural, and temporal levels, using an approach that focuses on identifying universal patterns allows us to identify traits shaped by evolution. When patterns are consistent with what we find in other species, this is evidence for a common origin for the trait; when they are inconsistent, this is evidence for a human-specific adaptation; when there is no universal pattern, this is evidence for the influence of independent local and cultural factors.

The complexity of human behavior requires that any authentic attempt to understand it include work from a wide range of disciplines. In this dissertation, I rely on a foundation of evolutionary principles rooted in behavioral ecology, namely those associated with sexual conflict, social dynamics, and mating behavior. I then incorporate findings from other scientific disciplines and subdisciplines including those from medicine, psychology, sociology, anthropology, and primatology, relying primarily on recent reviews, meta-analyses, and cross-cultural work, with the aim of presenting the most widely accepted position of the current experts of the field. Importantly, I will often discuss traits at multiple levels of analysis – explanations that are mechanistic, ontological, adaptive, and phylogenetic (Tinbergen 1963). This is not only in recognition of the fact that multiple levels of analysis are necessary to understand a trait, but also that levels of analysis may be intertwined. For example, one trait may not have current adaptive significance, having emerged when and how it did because it shares mechanistic roots with a different trait which, in contrast, *was* under active positive selection due to the specific conditions in its phylogenetic history. This is an inherent complexity of evolutionary exploration.

There are some unavoidable limitations to this work, and many of them center around the need for simplification. One area of simplification is in the degree of complexity I have allowed for each topic explored. The breadth of disciplines, while necessary, has placed constraints on the depth reasonably possible in this document, and while I have strived to do my due diligence to these topics, I have undoubtedly come up short in many regards. One specific area of limited investigation is with regards to sexual coercion, which I have focused on as a male-specific reproductive strategy. This approach should not be taken as an intention to downplay sexual violence committed for other reasons or by female perpetrators. It is merely that a broader approach is outside of the scope of this dissertation.

Another area of simplification is in the language that I have used. Because an evolutionary approach focuses on patterns of behavior, it necessitates the use of language that can allow for cross-species comparisons. Yet this language is insufficient to capture the complexities of sex determination and differentiation that occur across species as well as the diversity of identities within the human condition, particularly with regards to sex, sexuality, and gender. Thus, throughout this document, my language reflects the conventional usage of these terms, using the biological definitions of male and female – the male producing the small gametes, and the female producing the large gametes – to discuss non-human species and man and woman to discuss humans specifically. In doing so, however, I recognize that no single aspect of human biology can perfectly determine an individual's ultimate sexual or gender phenotype, nor can it encapsulate the social and cultural expectations associated with it. If the reader struggles with the usage of these terms, perhaps the simplest terminological approach is to associate my usage of the word "woman" with the individual who would invest the most in a single reproductive event, as it is this dynamic that tends to have the greatest influence on reproductive choices across species. Similarly, I use language reflective of mate choice preferences associated with heterosexuality, given the specific focus on the asymmetric nature of the costs associated with reproductive choices. I hope that future approaches will be able to explore human reproductive dynamics using a more nuanced understanding of the factors that influence sex, sexuality, and gender and thus can take both a more inclusive and a more comprehensive approach to understanding the evolution of human reproductive behavior.

The first official chapter of this dissertation (Chapter 2) is a comprehensive and interdisciplinary review of the evolution of human reproductive behavior. This provides much of the foundational work for the chapters that follow. It includes an overview of sexual conflict and mating behavior across species; a walk-through of human evolution, with special attention paid to the emergence of uniquely human reproductive characteristics; the relevant and critical components of human sociality, namely those associated with social status, competition, and developmentally plastic social strategies; trends in human mating behavior, including universal, sex-specific, and strategy-specific patterns in preferences and behaviors; a critique of the hypotheses on the evolution of concealed ovulation; the fundamentals of the human menstrual cycle and the unique complications of behavioral fertility research; and an analysis of the thus-far identified trends associated with the menstrual cycle, specifically those associated with attractiveness, male response, mood, sexual partner preferences, sexuality, and social behavior. By using an interdisciplinary approach, this review identifies several notable patterns whose importance have been overlooked in much of the recent work regarding human mating behavior including the importance of intrasexual competition among women for social status and resources, the role of alloparental care and multigenerational female bonds for resource provisioning and assisted birth, menstrual cycle-related patterns that emerge as a byproduct of pregnancy-maintenance, and the effect of confirmation bias on reported trends in behavioral fertility research.

The next chapter (Chapter 3) is a game theory model exploring male mating strategies in a female mate choice system. In response to female evaluation, males can choose to mate and invest in offspring, mate and withhold offspring investment, or engage in coercive mating. We explore the conditions under which each of these strategies emerge and persist using the criterion of evolutionary stability. We also explore the effect of female resistance, social policing, and extra-pair paternity. Further, we apply this model to six focal species in which male coercion appears as a true strategy. In chimpanzees, guppies, Japanese water striders, and scorpionflies, males making the highest investment in each reproductive event were the sole persisting type; in mallard ducks, an evolutionarily stable mixture of investing and coercing males prevailed; and in humans, a stable mixture of investing and non-investing types persisted. The factors that influence the emergence of coercion for each system is discussed.

In the following chapter (Chapter 4), I investigate the possibility that the existence of shared biosocial developmental factors between facial structure and behavioral tendencies allows for women to use male facial cues to make reproductive decisions. Women rated images that had been generated at the extreme ends of seven characteristics that are associated with female mate preferences, including facial attractiveness, short- and long-term relationship potential, and four forms of antisociality, including general antisociality and the Dark Triad. Images were judged on four types of ratings. The ratings, type of rating, the woman's fertility, and the woman's interest in a new sexual partner were incorporated into the analyses. Results indicated that for most image types, women show preferences in the expected direction, though women showed unexpected preferences for "poor" long-term partners and "high" psychopathy. Further, while the results were heavily moderated by the woman's interest in new sexual partners, they were generally not influenced by the menstrual cycle. The findings suggest that women may use male facial cues as a proxy for behavioral traits associated with reproductive strategies, suggest a potential for confirmation bias in fertility-based research, and suggest several avenues of exploration.

In the final chapter (Chapter 5), I investigate the intersection of fertility, fertility belief, and sexuality. I review the literature on fertility and sexuality, and I identify chronological trends in the findings that suggest the possibility that fertility belief and confirmation bias may be influencing contemporary trends in results. I then explore (1) the degree to which fertility influences a woman's sexuality when controlling for fertility belief, (2) the degree to which women are able to predict their fertility accurately, and (3) the degree to which methodology – particularly the method of determining the fertile and comparison window – influences the results. For at least one menstrual cycle, participants collected daily urine samples and completed daily journal responses on their sexual desire, hypothetical sexual behavior, happiness, and fertility belief. Results suggested that fertility had no influence on sexuality. Instead, happiness predicted sexual desire, and sexual desire predicted hypothetical sexual response. Further, even though participants were well-informed about the menstrual cycle, they were unable to predict it accurately; instead, their predicted fertility was primarily influenced by high sexual desire. Finally, I explored the effect that using estimated methods of fertility determination would have on these findings. A total of 36 estimated fertile/non-fertile pairings resulted in significant relationships between fertility and sexual desire 89% of the time, sexual response 78% of the time, and fertile belief 69% of the time – compared to 17%, 0%, and 0% using hormonal methods, respectively. These results suggest that fertility belief, not fertility itself, may be driving some of the documented fertility-associated shifts and that the use of proper controls for fertility belief and confirmation bias is needed in future research.

CHAPTER 2. THE ECOLOGY OF HUMAN REPRODUCTIVE BEHAVIOR: AN INTERDISCIPLINARY AND INTEGRATIVE REVIEW

2.1 ABSTRACT

Human reproductive behavior has been examined through a range of scientific disciplines and subdisciplines. This review pulls from a variety of them including those from biology, anthropology, medicine, psychology, and sociology. It includes an overview of sexual conflict and mating behavior across species; a walk-through of human evolution, with special attention paid to the emergence of uniquely human reproductive characteristics; the relevant and critical components of human sociality, namely those associated with social status, competition, and developmentally plastic social strategies; trends in human mating behavior, including universal, sex-specific, and strategy-specific patterns in preferences and behaviors; a critique of the hypotheses on the evolution of concealed ovulation; the fundamentals of the human menstrual cycle and the unique complications of behavioral fertility research; and an analysis of the thus-far identified trends associated with the menstrual cycle, specifically those associated with attractiveness, male response, mood, sexual partner preferences, sexuality and social behavior. By using an interdisciplinary approach, this review identifies several important patterns whose importance has been generally neglected in recent empirical work regarding human mating behavior. These patterns include the importance of intrasexual competition among women, the role of alloparental care and multigenerational female bonds for resource provisioning and assisted birth, menstrual-cycle-related patterns that emerge as a byproduct of pregnancy-maintenance, and the effect of confirmation bias on modern research in behavioral fertility research.

2.2 REPRODUCTIVE BEHAVIOR

Because humans are the product of the same evolutionary pressures that have shaped all life on earth, we must be willing to explore the possibility that these forces continue to influence our behavior, particularly when the behavior is related to reproduction. Understanding the evolutionary pressures that have shaped human reproductive behavior requires us to first understand those that have shaped all life on earth. Of particular concern are those associated with the dynamics of sexual conflict and how they lead to the emergence of structures – such as primary and secondary traits – and behaviors – such as those involved in mating persistence and resistance, which are involved in reproduction. It also requires understanding the factors that influence mate choice preferences and strategies, including differential reproductive investment, potential direct and indirect benefits, and the various life history-related variables that influence overall fitness.

2.2.1 Sexual Conflict, Mate Choice, and Reproductive Strategies

Sexual reproduction is often a process of conflict. The source of this conflict lies in the differences between the evolutionary interests of the sexes, interests originating at the genetic level and often manifesting as a variety of behaviors (Trivers 1972 [review], Parker 1979, Rice 1984, Andersson 1994 [review], Rice and Holland 1997, Parker and Partridge 1998, Gavrilets et al. 2001, Chapman et al. 2003, Arnqvist and Rowe 2013 [review], Clutton-Brock 2019 [review]). Sexual conflict can be categorized by how the trait in question manifests in and interacts with the sexes in question. One way it can be categorized is through genetic terms. The trait can be intralocus or interlocus, with intralocal conflict occurring when a single gene is expressed differently in each sex and interlocal conflict occurring when different sexes express different genes (Parker and Partridge 1998). Another way it can be categorized is through selection theory terms according to the fitness effects of the trait. The trait can manifest as sexually discordant selection, which occurs when the trait exists in both sexes but its fitness effects are dependent on the sex in which it is being expressed (and is thus similar to intralocal conflict). The trait can also manifest as sex-based social selection, which occurs when a trait, regardless of whether it exists in the other sex, has a negative fitness impact on the other sex. One notable benefit of conceptualizing sexual conflict in selection theory terms is that it allows both types of conflicts to exist simultaneously, as documented in a variety of species (Westneat and Sih 2009).

In addition to the kind of conflict present, we also must understand the kind of trait involved. Reproduction-related traits can be categorized as either primary or secondary sexual traits (Darwin 1871). Primary sexual traits appear at birth and are the internal and external genitalia directly involved in the reproductive act (e.g., uterus or baculum). Secondary sexual traits develop at sexual maturity, and though they distinguish between the sexes and may be necessary for reproduction, they are not directly involved in copulation (e.g., bright plumage or antlers). The degree of distinguishable difference between males and females due to primary and secondary traits is known as sexual dimorphism. The evolution of primary and secondary sexual characteristics is generally attributed to natural and sexual selection, respectively. However, evidence continues to emerge that the phenotypic expression of any particular trait has been shaped by a combination of these forces (Darwin 1871, Eberhard 1991, 1996, Andersson 1994 [review], Arnqvist 1998).

Sexual selection is a special form of natural selection in which traits are selected for due to their impact on their ability to find a mate and successfully conceive. There are two general kinds of sexual selection: intrasexual and intersexual selection. Intrasexual selection occurs when the conflict exists as a competition between members of the same sex for mating opportunities with the other sex. In contrast, intersexual selection occurs when members of one sex advertises themselves directly to members of the other sex, with the choosers directly selecting mates (Darwin 1871). Some patterns have emerged with regards to these types of selection. Intrasexual selection has been considered a primarily male behavior that includes both pre-mating (e.g., dominance displays and aggressive confrontations, often establishing a male-hierarchy) and post-mating behaviors (e.g., mate-guarding, mating plugs, toxic semen). Further, females tend to be the choosier sex (see below), and because of this, intersexual selection often manifests with males engaging in an elaborate display or ritual to advertise themselves to females (Clutton-Brock and Parker 1989 [review], Arnqvist and Rowe 1995, Andersson 1994 [review], Geary et al. 2004 [review]). However, not only are the boundaries between intra- and intersexual selection debated (Arnqvist and Rowe 1995, Berglund et al. 1996, Wiley and Poston 1996, Birkhead

1998, Pitnick and Brown 2000), but sex role reversals and partial reversals are common (Gwynne 1991 [review], Bonduriansky 2001 [review], Clutton-Brock 2007 [review]). Additionally, evidence continues to emerge that female intrasexual selection is more common than has previously been reported (LeBas 2006, Clutton-Brock 2007, Clutton-Brock 2009, Edward and Chapman 2011 [review]), and increased female-female competition then increases intersexual selective pressures for males to discern between and mate with successfully competitive females. This sex-reversed intersexual selective pressure may be responsible for some female secondary sexual characteristics (Andersson 1994 [review], Kraaijeveld et al. 2007, LeBas 2006, Clutton-Brock 2007, Clutton-Brock 2009), such as those fertility signals linked to reproductive value (Funk and Tallamy 2000, Amundsen and Forsgren 2001, Domb and Pagel 2001).

The prevalence of male competition and female choice has been recognized for nearly 150 years (Darwin 1871, Trivers 1972 [review], Andersson 1994 [review], Sargent et al. 1998), and the evolutionary pressures for this prevalence has been under investigation since. Almost a century after Darwin, Williams (1966) and Trivers (1972) identified parental investment – which can be viewed as a trade-off between investing in current and future reproduction (Stearns 1989 [review], 2000 [review]) – as a cost disproportionately paid by the sexes and thus as a source of sexual conflict. One of the more fundamental ways that this disproportionate investment emerges is in differential gamete size and number, with males investing in a higher quantity and females in a higher quality. Other potential investments, and thus contributors of conflict, include gestation, lactation, and direct parental care. Notably, while these investments are often higher in females, this is not always the case; the trade-off between investing in parenting behavior or mating behavior is influenced by other factors including the intensity of the presence of sex-biased environmental and social competition (Kokko and Jennions 2008).

Disproportionate reproductive investment is reflected in a species' operational sex ratio. Operational sex ratio (OSR) is the ratio of males to females in the mating pool, and it reflects the limits on the total number of offspring each sex can have per capita in their lifetime (Emlen and Oring 1977, Simmons 1995, Clutton-Brock and Parker 1992, Ahnesjö et al. 2001). OSR incorporates not only investment in gametes, but also in gestation, lactation, and direct care. When investment is higher in females, as it often is, this results in a higher, male-biased OSRs (Clutton-Brock 1989, Clutton-Brock and Vincent 1991, Clutton-Brock and Parker 1992, Geary et al. 2004 [review], Mills et al. 2007). A specie's or population's OSR can have substantial impacts on the kind and intensity of mate competition and, when combined with measures of sexual dimorphism, can act as a quantitative measure of sexual selection pressures (Owens and Thompson 1994, Mitani et al. 1996, Weir et al. 2011) – though it should be used with caution as it can over-estimate the strength of sexual selection (Klug et al. 2010). Further, there are other costs of mating that are not reflected in the OSR and that disproportionately affect females, including but not limited to fertilizing a costly egg with the sperm of a male that may be of relatively low quality and of resisting mating attempts, which can be aggressive and sometimes fatal (Daly 1978, Arnqvist and Rowe 2013 [review]). It is thus no surprise that sexually reproducing species are largely female-choice systems. Indeed, reversals of this pattern, and more balanced OSRs, are found where females have a faster rate of reproduction, either through favorable ecological circumstances or behavioral and physiological adaptations (Reynolds and Szekely 1997, Amundsen 2000).

Parental investment is one among many traits that helps shape an organism's life history. Life history (LH) is the general pattern of their life and is associated with various physiological and behavioral trends that include body size, maturation rate, offspring number, lifespan, and senescence (Lack 1947, Medawar 1952, Williams 1957, Stearns 2000 [review]). Life histories exist on a fast-slow continuum, in which faster organisms typically have shorter lifespans and engage in reproductive behaviors that prioritize mating effort over parental effort (Charnov and Schaffer 1973, Bell 1980, Bielby et al. 2007 [review], Dobson and Oli 2007 [review], Salguero-Gomez et al. 2016 [review]), and they can be used in both across- and within-species comparisons as well as both across- and within-sex comparisons. LH patterns are often developmentally plastic, emerging in response to a variety of interacting biological and environmental factors, in ways that strategically optimize the organisms' fitness (Figueredo et al. 2006, Wolf et al. 2007, Biro and Stamps 2008, Stamps and Groothuis 2010, Duckworth 2010, Réale et al. 2010, Trillmich et al. 2018, Del Giudice 2018, 2020).

Males and females tend to engage in different LH strategies. In general, male strategies are faster, particularly with regards to developmental-based life history traits such as growth rate (Tarka et al. 2018). They also tend to demonstrate greater variability in per-individual number of offspring and prioritize mating effort over parenting effort, pursing primarily mating persistence behaviors as opposed to the strategy of resistance more commonly found in females. These factors intensify male intrasexual competition over the relatively fewer sexually receptive females and drives the evolution of female discrimination and preference (Andersson 1994 [review], Arnold and Duvall 1994, Kingsolver et al. 2001).

As females exert choice over potential mates, predictable patterns of preferences emerge, often in context of the kind of benefit – direct or indirect – that they convey (Trivers 1972 [review], Clutton-Brock and Vincent 1991, Clutton-Brock 2007). Direct benefits are material contributions that positively contribute to the welfare of the offspring and/or mother (e.g., male parental care, territory defense, nuptial gifts – Price et al. 1993) and/or those that help to minimize the costs of mating (e.g., low parasite low, sexual aggression – Parker 1979, Arak and Enquist 1995, Holland and Rice 1998, Gavrilets et al. 2001) which, when high, often manifests as high female mating resistance (Chapman et al. 2003). Indirect benefits, in contrast, are the genetic contributions that go directly to the offspring and may include high survivability (good genes process) and/or increased attractiveness (the sexy son hypothesis, Fisher process) (Kirkpatrick and Ryan 1991). In response to female preferences, males evolve traits to advertise the benefits that they can convey. These traits may initially emerge through natural selection or through intrasexual sexual selection, but as they become associated with female preference, intersexual selection pressures may cause these traits to trend toward extreme displays that would otherwise be selected against under natural selection alone (Darwin 1871, Fisher 1930, Andersson 1994 [review], Berglund et al. 1996, Pomiankowski et al. 199, Iwasa et al. 1991, Iwasa and Pomiankowski 1999, Gavrilets et al. 2001, Kokko et al. 2002, Kokko et al. 2003, Kokko et al. 2006 [review]).

In some circumstances, males may evolve the ability to circumvent female choice and their resistance to mating (Rowe 1994, Thornhill and Palmer 2001 [review], Muller and Wrangham 2009 [review], Arnqvist and Rowe 2013 [review]). These abilities can take many forms and vary with regards to the intensity of sexual coercion involved. One form is the presence of behaviors that prioritize mating with females when they are particularly vulnerable and thus unable to resist (e.g., Tidemann 1982, Slooten and Lambert 1983, Brower 1997, Markow 2000). A more common form is the presence of mating persistence behaviors, in which males repeatedly, and often violently, engage in mating attempts (e.g., ducks – Mineau et al. 1983 [review]; pinnipeds – Campagna et al. 1988, Le Boeuf and Mesnick 1991, Galimberti et al. 2000; poecilids – Magurran 2001 [review], Bisazza et al. 2001; panorpa – Thornhill 1980(b); primates – van Schaik et al. 2004 [review], Muller and Wrangham 2009 [review], Baniel et al. 2017). Another form is the presence of guarding behaviors, in which males sequester females from mating with other males (Parker 1974; crustaceans – Jormalainen 1998; crayfish – Berrill and Arsenault 1984; scorpion flies – Thornhill 1984), or punish or threaten females who mate with other males. These behaviors often include violence or infanticide (primates – Smuts and Smuts 1993 [review], van Schaik et al. 2004 [review], Muller and Wrangham 2009 [review]; water striders – Han and Jablosnki 2010). A similar form emerges with some instances of high male-male competition. Threats of punishment by the dominant male may prevent a subservient, but preferred, male from mating with a female (Trivers 1972 [review]). All of these forms can be accompanied by physiological structures to aid in the behavior, many acting to immobilize females, and often include toxins, stings, and/or grasping structures (e.g., toxins in funnel-web spiders – Singer et al. 2000; sexual stings in some scorpions – Lira et al. 2018; grasping structures in water striders – Arnqvist 1989; grasping structures in insects – Darwin 1871, Eberhard 1991, 1996, Arnqvist 1997, Thornhill 1980(b), 1984, Thornhill and Sauer 1991, Sakaluk et al. 1995; grasping structures in Crustaceans – Conlan 1991; grasping structures in elasmobranchs – Kajiura et al. 2000, Pratt and Carrier 2001; grasping structures in Amphibians – Shine 1979 [review], Epstein and Blackburn 1997). These structures may serve to prevent a female from escaping or to prevent her from being mated by another male. In at least some species, the development of these structures is regulated by androgens (Shine 1979 [review], Epstein and Blackburn 1997, Jungfer and Hodl 2002).

Females have evolved counteradaptations in response to male persistence and coercive behavior (Smuts and Smuts 1993 [review], Clutton-Brock and Parker 1995(b) [review], Muller and Wrangham 2009 [review]). Documented counteradaptations include avoiding areas prone to harassment (primates – Smuts and Smuts 1993 [review], Muller and Wrangham 2009 [review]), thickened patches of skins to avoid costs from biting and stings (elasmobranchs – Pratt and Carrier 2001), spines to impede grasping structures (water striders – Arnqvist and Rowe 1995, Andersen 1997, Arnqvist and Rowe 2002; diving beetles – Bergsten et al. 2001), playing dead (robber flies – Dennis and Lavigne 1976; dragonflies – Khelifa 2017), fleeing or hiding (dragonflies – Wildermuth et al. 2019), having female andromorphs that mimic males of the same species (damselflies and butterflies – Johnson 1964, 1966, Robertson 1985, Cordero 1990, Cook et al. 1994, Andrés and Cordero 1999; lizards – Galán 2000; fiddler crabs – Burford et al. 2001), and engaging in convenience polyandry, in which females acquiesce to mating, often occurring when the costs of resistance are high and/or the costs of mating low (primates – Van Schaik et al. 2004 [review], Muller and Wrangham 2009; insects – Thornhill and Alcock 2013 [review]; crustaceans – Jormalainen 1998, Thiel and Hinojosa 2003; birds – Mineau et al. 1983, Westneat and Stewart 2003 [review]; primates – Smuts and Smuts 1993 [review], Muller and Wrangham 2009; other mammals – Clutton-Brock and Parker 1995(b); but see Boulton et al. 2018).

2.2.2 The Evolution of Human Sociality and Reproduction

The dynamics of sexual conflict and the factors that influence mate choice have also shaped primate, and thus human, evolution. The coevolution of cognition and social complexity has placed particular demand on the evolution of fetal and infant growth – and, in turn, the mothers responsible for their development in utero and during lactation. In many primates, these pressures seem to have resulted in particularly high degrees of female intrasexual competition, and in humans, several additional physical and social adaptations. These include structural changes necessary to give birth to infants with large craniums (e.g., wider pelvises, secondary altriciality, rotational birth), physical changes that increase the infants' access to high quality milk (e.g., larger female body size, gluteal-femoral fat deposition), and social structure changes necessary to ensure the mother and infant have the resources necessary for pregnancy, childbirth, and extended lactation (e.g., cooperative breeding, assisted birth).

2.2.2.1 Human Social, Cognitive, and Reproductive Evolution

At least 160 million years ago, pre-mammalian mothers evolved the ability to secrete milk from apocrine-like glands. This ability, most likely providing either hydration for eggs or immunological protection to hatchlings, was the origin of lactation, an adaptation crucial to the success of mammals. The ability of mothers to store energy and nutrients allowed for their dispersion into unpredictable environments that were otherwise inhospitable to offspring due to limited readily-available food sources. It also allowed for the specialization of the food source of the infant, increasing both the efficiency of their digestion and providing nutrients customized to the needs of the species. Finally, it allowed offspring to become increasingly altricial, allowing for increased maternal care and socialization (Oftedal 2002, Hinde and Milligan 2011 [review]).

Primates began diverging from other mammals over 80 million years ago (Tavaré et al. 2002), and many of the morphological and physiological characteristics unique to primates emerged as adaptations to arboreal living. In addition to favoring prehensile hands and feet, acute vision, and a generalized diet, evidence suggests that the more complex nature of an arboreal environment demanded increased cognitive skills (Tomasello 2000 [review]). It has been proposed that it was this resulting increase in cognitive ability that allowed primates to not only begin to group together, which may decrease predation risk (Hamilton 1971, Turner and Pitcher 1986), but to engage in social behavior. Social living conveys a variety of benefits, including resource partitioning, cooperative hunting and grooming, and reduced predation and parasite risk. However, it also carries costs, most notably those associated with maintaining and navigating social hierarchies; for example, engaging in dominance interactions can be physiologically taxing, and low-status individuals will often have limited access to resources and restricted reproductive opportunities (Alexander 1974 [review], Earley and Dugatkin 2010, Clutton-Brock and Huchard 2013 [review]). These costs of social living may have acted as a selection pressure for increased cognitive skills that would allow optimal maneuver in an increasingly complex system, including skills for developing methods of communication, navigating interpersonal relationships, and maintaining social contracts (Dunbar 1998(a)(b) [review]).

The coevolutionary relationship between cognition and sociality may be one of the key forces driving primate evolution. Several unique aspects of primate physiology and society are related to the enormous energy demands of high cognition, specifically those needed during the early phases of fetal development. The demands of cognition increase with group complexity and are particularly high for ape species in highly dynamic fission-fusion social systems in which the size and composition of groups change frequently (Dunbar 1998(a)(b) [review], Dunbar and Schultz 2007, Street et al. 2017).

The demands for cognition may manifest most clearly in primate reproductive ecology. Even though primate offspring have the longest relative gestation periods, they are also born moderately altricial and require exceptionally lengthy periods of lactation and care (Derrickson 1992, Hinde and Milligan 2011 [review]). Female primates spend nearly their entire adult lives pregnant, lactating, and/or caring for offspring (Thompson 2013 [review]), and the resulting mother-offspring bond thus forms the core social unit of primate societies (Broad et al. 2006 [review]). Lactation, more energetically expensive even than gestation (Thompson 2013 [review]), conveys a multitude of benefits including both immunological support and the provision of secure, balanced, and easily-digestible nutrition. For monkey and ape species with high cognitive demands, lactation provides key fatty acids necessary for rapid early brain growth and accessible only from animal sources. Extended lactation and late weaning are associated with rapid brain growth (Humphrey 2010 [review], Thompson 2013) and may facilitate social learning and increase safety and foraging skills, particularly in dangerous environments (Hayssen 1993). Thus, the length of time spent lactating represents a trade-off between its costly energy demands, the direct benefits provided to the offspring, and the mediating influence of various environmental and social factors, such as the availability of food in the local environment and the mother's social context (Humphrey 2010 [review], Hinde and Milligan 2011 [review]).

The need for increased energetically-expensive lactation may have been a key factor in the evolution of primate physiology and sociality. It has been proposed as one of the selection pressures favoring reduced sexual dimorphism, selecting for larger females more capable of handling the additional energy costs (Ralls 1976 [review], Myers 1978, Kappeler 1990, Mitani et al. 1996, Plavcan 2012 [review]). It may also contribute to the unique form and degree of female intrasexual competition found in many primates. Not only do females engage in direct contests for high-quality food resources, but they are uncommonly and intensely aggressive with other females (Stockley and Campbell 2013 [review]). Targets seem chosen for their likelihood of bearing future competitors of their offspring (Huchard and Cowlishaw 2011, Stockley and Campbell 2013 [review]); infanticide is common (Stockley and Campbell 2013 [review]), and pregnant females target estrus ones, causing extended infertility and future miscarriages (Huchard and Cowlishaw 2011, Beehner and Lu 2013).

To maintain group cohesion in such a highly competitive environment, primates engage in numerous complex affiliate and prosocial behaviors that impose further cognitive demands (Dunbar 1998(a)(b) [review], Dunbar and Schultz 2007, Jaeggi and Gurven 2013 [review]). Coalition- and alliance-forming behavior in primates can form lifelong interpersonal relationships, and they rely heavily on physical contact, both sexual and nonsexual, to build and maintain them. Notably, adult food sharing is relatively rare in primates – particularly in females – though it has been documented as a means of building social alliances, namely in captivity (Jaeggi and Gurven 2013 [review]).

Because humans are primates, we retain many of the same adaptations distinctive to other primates. However, the shift to bipedalism that occurred 5-8 Mya initiated a chain of evolutionary changes that accelerated divergence from our primate relatives (Glazko and Nei 2003, Park et al. 2007, Pavličev et al. 2020; see Figure 2.1). Importantly, these changes included the evolution of hairlessness that appeared in the hominin line around 6 Mya (Sutou 2012) and structural changes to the pelvis that were near complete by 4 Mya (Lovejoy 1981 [review], Gruss and Schmitt 2015 [review], Pavličev et al. 2020 [review]). Even still, the hominin pelvis continued to widen for another 2 ½ My, due not to demands of bipedalism (Gruss and Schmitt 2015 [review], Pavličev et al. 2020 [review]), but instead to the demands of birthing children with exceptionally large craniums and greater cognitive abilities (Schoenemann 2006 [review]). Australopithecus infant craniums were so large that, even with hips wider than any other hominin before or since, they would have posed a risk in childbirth (Gruss and Schmitt 2015 [review], Pavličev et al. 2020 [review]). However, differences in overall size sexual dimorphisms remained fairly constant during this time (Plavcan 2018 [review]), suggesting that any species-wide shift toward monogamous, multimale kin groups, as has been proposed (Larsen 2003), did not have a significant evolutionary effect.

Even though infant craniums continued to enlarge throughout Homo, the width of the pelvis did not (stabilizing approximately 1.5 Mya). This suggests the existence of an opposing selection pressure acting against further pelvic widening. It was initially proposed that bipedalism was the primary constraint against a further widening pelvis (Washburn 1960); however, recent evidence from biomechanical and kinematic research indicate this to unlikely be the case (Warrener et al. 2015, Warrener 2017, Whitcome et al. 2017). Thermoregulatory constraints in sub-Sahara Africa likely contributed to pelvic width constraints (Gruss and Schmitt 2015 [review]), but a review of pelvic floor-related disorders indicates that the need for strong pelvic floor musculature was also likely critical (Pavličev et al. 2020 [review]). For women, the benefits of a wider pelvis for childbirth are weighed against those of a narrower pelvis for maintaining pregnancy: women with wider pelvises are more likely to be diagnosed with pelvic floor disorders associated with the strain of carrying a fetus to term. The structural inability of a wide pelvis to maintain strong pelvic floor musculature is consistent in men and women, with wider pelvises being linked to pelvic floor disorders and injuries in both. For men, weak pelvic floor muscles are also associated with erectile dysfunction, the importance of which may have increased with the loss of a baculum in the hominin line (Pavličev et al. 2020 [review]).

Thus, large hominin brains and constricted hip widths may have acted as selective pressures for the emergence of several unique reproductive characteristics associated with the genus Homo (3 Mya) and Homo erectus (2 Mya) specifically. It is likely that one of the first adaptations to emerge was cooperative breeding, a socio-reproductive adaptation in which helpers, or alloparents, assist in caring for the offspring of others. When present, alloparental care conveys a variety of benefits, including allowing for both slower maturation and early sociocognitive development for the infant and for early care-giving practice for the helpers, who are often non-reproductive females, both former and likely to be future mothers (Hrdy 2007 [review]).

Cooperative breeding has played a crucial role in human evolution, and it has been recognized as one of the defining aspects of human society (Kennedy 2003, Hrdy 2007 [review], Fernandez-Duque et al. 2009 [review], Kramer and Russell 2014 [review]). Evidence suggests that cooperative breeding may be related to socio-cognitive development in primates in general (Burkart and Van Schaik 2010; see also Thornton and McAuliffe 2015, Burkart and Van Schaik 2016, and Thornton et al. 2016). Indeed, it seems to have had a ratcheting effect on human cognition, further increasing the selective pressures for cognition, as having additional caregivers would select for offspring with the ability to remember the characteristics of – and perceive the intentions and emotions of – many different people at very young ages (Barrett et al. 2002 [review], Hrdy 2007 [review], 2009 [review], Burkart et al. 2009). It Is proposed to have been the primary selection pressure for both the sexually dimorphic, hormone-mediated behavioral responses to infant-related stimuli (Campbell 2013 [review], Archer 2019 [review]) and early female reproductive senescence in the form of menopause ("The grandmother hypothesis": Williams 1957, see 2001, Dawkins 1976, Alexander 1979, 1990, Hill and Hurtado 1991, Pavelka and Fedigan 1991, Peccei 1995, Hawkes et al. 1998, Hawkes and O'Connell 1999, Shanley and Kirkwood 2001). Indeed, available data from modern families indicates that alloparental care from a grandparent instead of a father results in equal or better child outcomes than those associated with a nuclear family (DeLeire and Kalil 2002). Cooperative breeding is likely responsible for the predominant social pattern found throughout human social systems – which is that of intergenerational groups of relatives engaging in alloparental, and specifically, allomaternal, care – and has been recognized as a major cause of the general success of humans (Hrdy 2007 [review], Schacht and Kramer 2019 [review, cross-cultural]).

Other shifts in reproductive characteristics began to emerge in the Homo lineage, likely as adaptive responses to the selective pressures for increased cognition. Prior to around 2 million years ago, there had been little change in body size sexual dimorphism. However, a substantial shift occurred between H. erectus (2 Mya) and H. heidelbergensis (800,000 ya) that was accompanied by an increase in brain size (DeSilva et al. 2021). Importantly, this shift was driven primarily by an increase in female body size (Plavcan 2012 [review], Plavcan 2018 [review], Grabowski et al. 2018) – a pattern that has been recognized as a sign of increased lactational demands in other species. Thus, this is proposed to be the case in Homo evolution (Dufour and Sauther 2002 [review], Plavcan 2012 [review]), given the benefits of lactation over pregnancy for offspring growth, particularly for neurocognitive development (Innis 2007, Thompson 2013).

The unique pattern of gluteal-femoral fat (GFF) deposition found in women is another characteristic unique to humans that may have emerged with increased body size. This pattern of fat deposition is absent in other primates, and it has been proposed to be an adaptative response to meet demands for cognitive growth. There are several lines of evidence to support this. Fetal neurocognitive development is dependent upon milk that is high in specific types of fatty acids (Innis 2007 [review]), and GFF stores high concentrations of these fatty acids (Lauritzen and Carlson 2011, Karastergiou et al. 2012, White et al. 2014). Further, this fat depot is regulated by estrogen, is more lipolytically active than other types of adipose tissue (Lauritzen and Carlson 2011, Karastergiou et al. 2012, White et al. 2014), and serves as a primary energy reserve consumed during both pregnancy and lactation (Lassek and Gaulin 2006, Thompson 2013). Further, fat deposition in this area specifically may be crucial in providing the balance necessary for bipedal locomotion during pregnancy and lactation (Pawowski 2001). Thus, it seems likely that this sexually dimorphic feature evolved during a point in our evolutionary history in which there was exceptional pressure on lactation for infant growth.

Finally, it may have been accompanied by the emergence of another uniquely human, sexually-dimorphic characteristic. Permanently enlarged breasts are absent in other primates, and their adaptive significance in humans have long been debated. Many have proposed that they must have emerged as a mate attraction signal, as they serve no clear reproductive purpose, a hypothesis I discuss below (e.g., Cant 1981, Gallup 1982, Low et al 1987, Szalay and Costello 1991, Barber 1995, Marlowe 1998, Puts 2010 [review], Puts 2016 [review]). However, it is also possible that breast enlargement is a by-product of the selective pressures for GFF deposition (Mascia-Lees 1986). Both GFF deposition and breast remodeling occur in response to estrogen and shift during puberty, pregnancy, and lactation (Breast: Javed and Lteif 2013 [review], GFF: Lauritzen and Carlson 2011, Karastergiou et al. 2012, White et al. 2014), and there would have been minimal selective pressures constraining breast enlargement. Further, larger breasts (and hips) may have aided in lactation through a more functional means. Unlike other primates whose offspring can cling to chest hair while nursing (Anderson 1988), hairlessness in hominin began as early as 6 Mya and was already established in the Homo lineage when lactational demands increased (Jablonski 2004 [review]). Thus, mothers who could carry their offspring on their hips while nursing – a behavior that continues in modern humans, particularly in Indigenous cultures or those that lack breastfeeding taboos (Anderson 1988, Liamputton 2011 [review]) – would have a fitness advantage, and larger, flaccid, lactating breasts may have been selected for (Anderson 1988).

At around the same time that pelvic widths stabilized in the Homo lineage, around 1.5 million years ago, the earliest indications of another reproductive characteristic – secondary altriciality – began to emerge (Rosenberg 1992 [review]). Secondary altriciality, a phenomenon in which offspring are born exceptionally premature, is recognized as a unique characteristic of humans. It is likely to have emerged as an adaptation for easier childbirth when bearing children with increasingly large craniums, particularly since pelvic widths stabilized at the same time they it began to appear, seemingly having reached their physiological constraints. Importantly, the emergence of secondary altriciality corresponded with another substantial shift in brain size (DeSilva et al. 2021) as well as the use of stone tools and social hunting (Garcia et al. 2021 [review]). Secondary altriciality likely had another ratcheting effect on cognition: increasingly altricial, vulnerable offspring would require more caregivers and thus larger groups; larger groups would add selection pressures for increased cognition, which would then select for increased altriciality. Further, the shift to growth outside of the womb not only provides access to the more nutrient-rich milk but also to complex socio-cognitive conditions, which may have added additional selective pressures for increased cognition (Alexander 1990). Secondary altriciality seems to have stabilized in the Homo lineage around 500,000 years ago, having seemingly reached the trade-off limit of survivability (Wittman and Wall 2007 [review], Gruss and Schmitt 2015 [review]).

The final reproductive adaptation to emerge in Homo is the "twisted" female pelvis and rotational birth process. Changes to the pelvis that reflect this birthing process – and the first increase in pelvic sexual dimorphism in the Homo lineage – began to appear around 500,000 years ago (Gruss and Schmitt 2015 [review]), and it corresponded with the first evidence of linguistic capabilities (Barney et al. 2012, Krause et al. 2007, Dediu and Levinson 2013). This rotational birth requires the continual adjustment of the fetal head as it progresses through the birth canal, allowing infants to be born with larger craniums without a larger pelvis. Because of this process, the modern human pelvis is the most sexually dimorphic skeletal feature of modern humans, characterized by internal anatomical features tied to these childbirth demands (Fischer and Mitteroecker 2017). As a result, childbirth in modern humans is both complicated and dangerous. Birthing assistance is near-universal in human society (Khan et al. 2006 [review], Wittman and Wall 2007 [review]); childbirth without training or access to modern medical care – conditions which might most closely resemble those of our ancestors – is associated with a 1 in 16 lifetime mortality risk due to pregnancy and childbirth-related complications (Boama and Arulkumaran 2009). The need for obligate midwifery likely increased selective pressures for a system of strong multigenerational female relationships. The evolution of the rotational birthing process seems to have stabilized around 200,000 – 300,000 years ago (Gruss and Schmitt 2015 [review]) along with the cognitive skills necessary for rudimentary story-telling (Konner 2016 [review]) – an adaptation critical for modern society (Barrett et al. 2002 [review]) – and that corresponds with the emergence of the modern human species. Still, our cognitive capabilities continued to develop: the earliest evidence of a capacity for culture points to approximately 170,000 years ago (Lind et al. 2013), and it has only been within the last 100,000 years that there is any evidence of symbolic thought and behavior, adaptations considered to be the hallmark of modern cognition (Thought: 75,000-1000,000 – d'Errico et al. 2005, Henshilwood et al. 2006, d’Errico and Stringer 2011; Behavior: 50,000-60,000 years – McBrearty and Brooks 2000, Deino and McBrearty 2002, Conrad 2010, Tylén et al. 2020).

2.2.2.2 Human Sociality

Human social behavior is complex, and many aspects of it are relevant to reproduction. Across species, the structure of the social hierarchy determines the distribution of resources, with high status individuals controlling a greater access of resources. Position in the social hierarchy is navigated primarily through social conflicts and dominance displays, and thus dominance behaviors – and the biological components that influence them – are central to social behavior. We should expect to find the same biological underpinnings that influence non-human dominance behaviors influencing human ones. We should also find evidence of strong selective pressures for navigating complex social dynamics, including the presence of the ability to detect crucial aspects of personalities, particularly dominant and/or dangerous ones, at early ages. Finally, we should see high female intrasexual competition reflective of the same sex hierarchy seen in other primates with high demands of lactation.

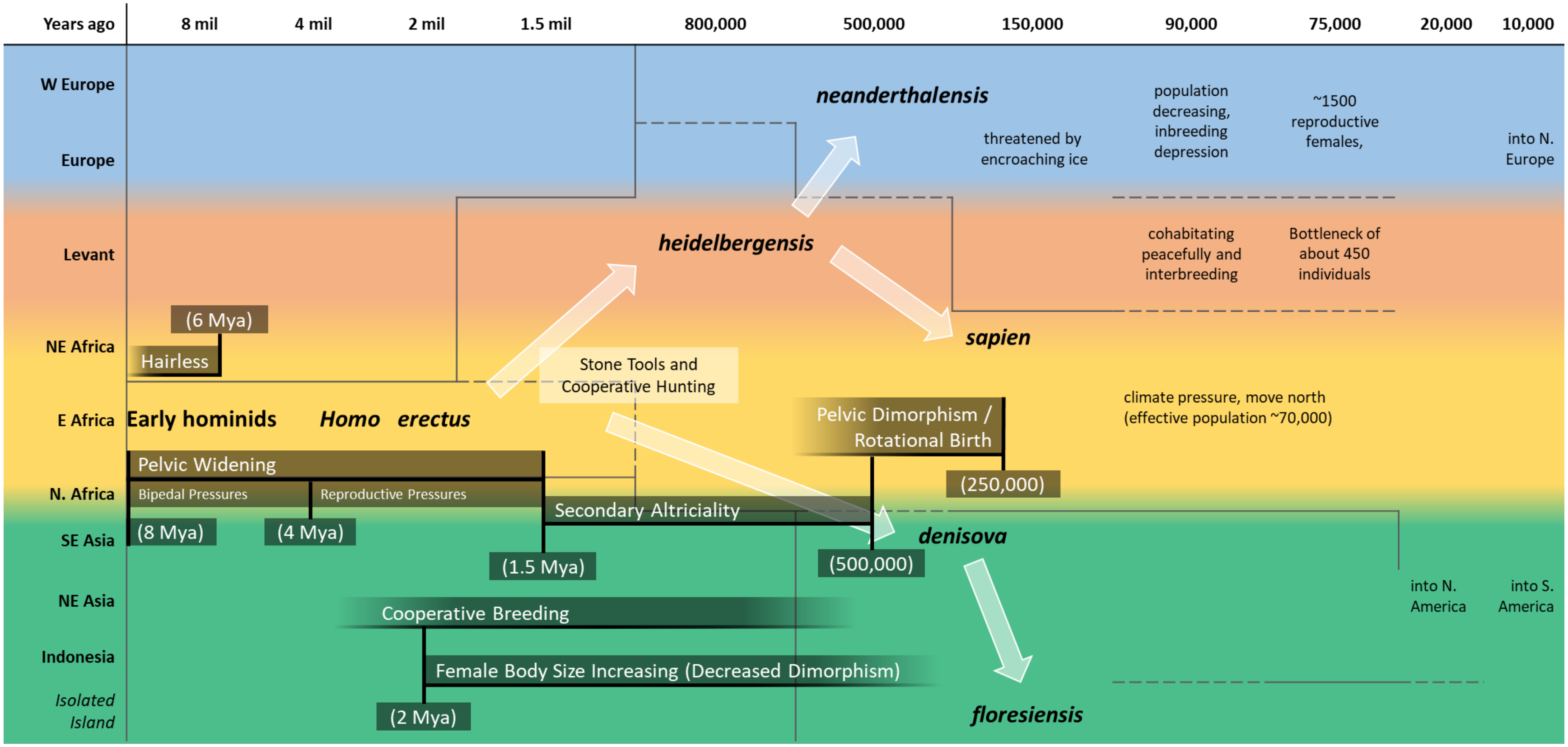


Figure 2.1. Geographical timeline of hominin evolution with accompanying reproductive-related adaptations .evidence.

2.2.2.2.1 DOMINANCE AND PROSOCIAL-ANTISOCIAL BEHAVIOR

Dominance behaviors are used in group-living species to establish and maintain social hierarchies. During social conflicts, competitive interactions are often resolved through the use of dominance behaviors instead of aggressive ones because they minimize the risk of physical harm (Mazur 1985). These conflicts, which can present as diverse types of displays, result in the subservient "loser" retreating, and in primates, these conflicts are usually face-to-face interactions in which eye contact is critical (Mazur 1985, Van Honk et al. 2014 [review]). This "winner-loser" dynamic allows us to conceptualize dominance behaviors as existing along a continuum of being socially vigilant – a dominant, approach-biased defense of status – and socially avoidant – a submissive, withdraw-biased anxiety (Terburg and van Honk 2013 [review], Van Honk et al. 2014 [review]).

Dominance interactions are heavily regulated by testosterone. Testosterone is perhaps most commonly known for its effect on male-typical sexual dimorphisms (T'Sjoen et al. 2019 [review]), including a low-pitch voice (Puts et al. 2006); a low waist-to-hip ratio (Svartberg et al. 2003) and abdominal fat deposition (Santosa et al. 2017); and broad facial features (Fink and Penton-Voak 2002, Bulygina et al. 2006, Thordarson et al. 2006, Weston et al. 2007, Toma et al. 2008, Marečková et al. 2011, Whitehouse et al. 2011). However, its influence on dominance is such that many have proposed that it be most appropriately be conceptualized as a strategic status-seeking hormone (Hirschenhauser and Oliveira 2006 [review], Eisenegger et al. 2011 [review], Terburg and van Honk 2013 [review], Van Honk et al. 2014 [review], Geniole and Carré 2018 [review]). Notably, the relationship between dominance and testosterone is bidirectional, with levels of testosterone influencing status-seeking behavior, and the outcomes of social contests influencing testosterone levels. Evidence seems to indicate that testosterone's effect is highly adaptive, acting strategically in coordination with higher order reasoning to engage in selective status-seeking behavior (Van Honk et al. 2014 [review]). For example, high testosterone is associated with low-status individuals engaging in subservient behavior in response to a conflict with a high-status person (Inoue et al. 2017), in making normally trusting people (but not untrusting people) suspicious during a conflict (Bos et al. 2010), and in increasing aggression during times of social instability (Wingfield et al. 1990, Wingfield 2017 [review]).

Dominance behaviors are often conceptualized as antisocial, usually as various forms of aggression, hostility, and violence. However, they can also be prosocial, with those in high status positions engaging in the kinds of leadership behaviors that are crucial in maintaining large, complex social groups. For example, engaging in prosocial behavior is associated with success in navigating conflicts, negotiating social norms, forming long-term bonds, and managing free-riders in large groups (Smith 2004 [review], Jaeggi and Gurven 2013). Prosociality is associated with high social status: prosocial individuals have greater social influence (Hardy and Van Vugt 2006, Willer 2009), are preferred for cooperative tasks (Hardy and Van Vugt 2006, Willer 2009), are more likely to receive gifts (Willer 2009), and have a better reputation (Milinski et al. 2002, Hawkes and Bird 2002, Jaeggi and Gurven 2013). Perceptions of group generosity are associated with social rank (Smith 2004 [review], von Rueden et al. 2008, Gurven and Hill 2009), and displays of generosity (Harbaugh 1998, Hawkes and Bird 2002, Anderson and Kilduff 2009), along with commitment and competence (Hawkes and Bird 2002, Anderson and Kilduff 2009) are often employed in social contests.

Testosterone's influence on dominance behaviors, including both the emergence of prosociality and antisociality, is reflective of behaviors associated with slow and fast life history strategies (Figueredo et al. 2006, Del Giudice 2018, 2020). Indeed, testosterone concentration seems to play a critical role in moderating the degree of behavioral plasticity possible, which in humans seems attuned to the unique demands of human sociality (Ponzi et al. 2020). Higher levels of testosterone are associated with a greater degree of phenotypic variation, particularly in traits for which males show higher levels of variation than females (Del Giudice 2018). High testosterone seems to increase the effect of stress on emergent physiological and behavioral patterns. The life history patterns identified in humans emerge in large part due to the effect of socioenvironmental conditions on the hormonal pathways responsible for reproduction and stress-response: the hypothalamus-pituitary-gonadal axis (HPG) and the hypothalamus-pituitary-adrenal axis (HPA), respectively (Del Giudice 2018, Ponzi et al. 2020). Indeed, this may be responsible for the sex-specific effects that high maternal stress has on negative male fetal outcomes (Rosa et al. 2019). Overall, these socioenvironmental conditions seem to communicate the need for a faster LH strategy optimized toward a harsh and unpredictable environment; in addition to various the biological components, the emergence of antisociality is associated with chronic stress, parental rejection, and childhood trauma. These factors are summarized below, with a complete list of references in Table 2.1.

Understanding the mechanistic developmental underpinnings of prosocial and antisocial behavior may allow us to understand their adaptive potential and limitations. What follows is an abbreviated review of some of the key factors associated with the development of antisociality, specifically those associated with testosterone and dominance behaviors. As indicated, a fundamental differentiation between prosocial and antisocial behaviors seems to primarily occur as the result of the testosterone- (HPG) and cortisol- (HPA) related factors. Dominance behaviors in general manifest as a tendency to engage in approach-biased behavior in response to stimuli. This is the result of testosterone acting on the amygdala, triggering an increased sensitivity to reward in response to potential threats. Thus, elevated levels of testosterone are associated with "approach" behavioral responses. However, the effect of testosterone is balanced by the effect of cortisol which also acts on the amygdala. Cortisol is released in response to stress and acts to return the body to homeostasis, and it increases punishment sensitivity. Thus, the balance of testosterone to cortisol – of "approach" and "fear" – shapes the ultimate response. High testosterone combined with low cortisol result in the "fearless dominance" we associate with aggression.

The interactions of testosterone- and cortisol-related factors, particularly given specific socioenvironmental conditions, seem responsible for the emergence of other aspects of antisociality. One factor seems to be the production of vasopressin. Vasopressin is one of the neurohormones used to stimulate cortisol production, and it is associated with increased aggression, both in response to its concentration and in response to the presence of certain vasopressin receptors. Importantly, vasopressin production increases in response to conditions of chronic stress. Another factor is sensitivity to androgen. Androgen sensitivity is influenced by the number of androgen receptors available which in turn is genetically determined. Decreased androgen sensitivity is associated with increased violence, potentially due to the formation of a link between violence and pleasure regulation. Another factor is how reactive the amygdala is to threats. As discussed, the type of amygdala response is influenced by the interactions of testosterone and cortisol, but the intensity of that response is influenced by how reactive the amygdala is. The amygdala is regulated by the prefrontal cortex (PFC), and the strength of this regulatory pathway determines how responsive the amygdala is to threats: a stronger pathway indicates a more well-regulated amygdala that is less reactive, and vice versa. Thus, aggression (high T / low C) can be associated with proactive, or instrumental, aggression when the pathway is strong, or it can be associated with reactive, or explosive, aggression when the pathway is weak. Importantly, one way to weaken this pathway is through long-term exposure to high concentrations of testosterone, thus helping to explain the association between reactive aggression and long-term exposure to high testosterone. Two other factors seem to influence the emergence of general antisociality: the presence of parental rejection, and the concentration of the sex hormone binding globulin (SHBG). SHBG is responsible for transporting testosterone, suggesting a role for heightened testosterone sensitivity.

The influence of testosterone-related factors on the emergence of two other antisocial behaviors has been explored, and both types of behavior seem to have little to do with testosterone. Evidence for a connection to criminal behavior is weak, apart from the aforementioned behaviors and tendencies that are also associated with criminal behavior. Instead, the development of criminal behavior seems largely influenced by the presence of childhood trauma. Evidence for a connection to sexual offending is similarly weak. While testosterone is related to both sexual activity and violence independently, there seems to be no particularly unique effect of testosterone, nor does there appear to be an interaction effect between them (though see section on male reproductive strategies for more details on sexual coercion).

There are several specific types of personality disorders characterized by unique patterns of antisocial behavior. Three of these – narcissism, Machiavellianism, and psychopathy – are collectively referred to as the Dark Triad. These “Dark personalities” share the use of aggressive, callous, and manipulative means to achieve self-advancing goals (Paulhus and Williams 2002, Furnham et al. 2013 [review], Jonason et al. 2013, Lee and Ashton 2014 [review], Semenyna and Honey 2015, Muris et al. 2017 [review], Koehn et al. 2019 [review], Jonason and Sherman 2020, Schreiber and Marcus 2020 [review], Truhan et al. 2021). While they share much in common, these Dark personalities have distinctive characteristics: Machiavellianism is characterized by subtle and cunning manipulation, narcissism with extreme self-preoccupation, and psychopathy with egocentric hostility. They also differ in their patterns of aggression: Machiavellianism is associated with both proactive and reactive aggression (van Lier 2015), narcissism with reactive aggression exclusively (Bobadilla et al. 2012, van Lier 2015), and psychopathy with a pattern sharply distinct from the other two. There are two intersecting aspects to psychopathy: callous-unemotionality (CU) and impulsivity-antisociality (IA). Each aspect is characterized by proactive and reactive aggression, respectively, and because of this, they have historically been referred to as primary and secondary psychopathy (or sociopathy). However, as there are individuals with characteristics of both dampened emotionality and impaired self-control, conceptualizing these as intersecting spectrums is more accurate (Skeem et al. 2007, Bobadilla et al. 2012, van Lier 2015, Yildirim and Derksen 2015(a), Neumann et al. 2015, Porter et al. 2018, Bronchain et al. 2020, Harrison 2021).

Table 2.1. Biosocial developmental factors associated with dominance in humans.

Characteristic	**Factor**	**Citations**
Dominance	Testosterone	Puts 2010 [review], van Honk et al. 2011, Montoya et al. 2012 [review], Geniole et al. 2013, Terburg and van Honk 2013 [review], van Honk et al. 2014, Carré and Olmstead 2015 [review], Carré et al. 2017 [review], Geniole et al. 2017 [review], Gray et al. 2020 [review]
	Prenatal	Swaddle and Reierson 2002, Carré et al. 2009 [review], Wong et al. 2011, Geniole et al. 2015 [review]
	Circulating	Gladue et al. 1989, Mazur and Booth 1998, Penton-Voak and Chen 2004, van Bokhoven et al. 2006, Eisenegger et al. 2011 [review], Reimers and Diekhof 2015, Dreher et al. 2016, Kandrik 2017, Carré et al. 2017 [review], Carré and Archer 2018 [review]
Prosocial	Testosterone	
	Prenatal	Stirrat and Perrett 2012
	Circulating	Eisenegger et al. 2010, van Honk et al. 2011, Reimers and Diekhof 2015, Dreher et al. 2016, Probst et al. 2018 [review]
	Interaction Effect	Carré and Archer 2018
Antisocial	Testosterone	
	Prenatal	Stirrat and Perrett 2010, Haselhuhn and Wong 2012, Hehman et al. 2013, Jia et al. 2014, Geniole et al. 2015 [review]
	Circulating	Dabbs and Morris 1990, Mazur and Booth 1998, Stålenheim et al. 1998, Aromäki et al. 1999, Chance et al. 2000, van Bokhoven et al. 2006
	Interaction Effect	Carré and Archer 2018
	SHBG	Stålenheim et al. 1998
	Heritability	Choy et al. 2018 [review]
	Parental Rejection	Woeckener et al. 2018
Aggression	Testosterone	van Bokhoven et al. 2006, Carré et al. 2017 [review]
Reactive-Proactive	Testosterone	Carré and Olmstead 2015 [review], Probst 2018
	Amygdala Responsiveness	Mehta and Beer 2010, Volman et al. 2011, Yildirim and Derksen 2012(a) [review], Van Honk et al. 2014 [review], Peters et al. 2015, Spielberg et al. 2015, Volman et al. 2016
	Cortisol	Terburg et al. 2009, Barzman et al. 2010, Batrinos 2012 [review], Montoya et al. 2012 [review], Romero-Martínez et al. 2013, Vaeroy et al. 2019 [review]
	Vasopressin	
	Receptors	Meyer-Lindberg et al. 2011 [review], Zai et al. 2012, Vollebregt et al. 2021
	Chronic Stress	Scott et al. 1998, Thompson et al. 2004
	Heritability	Choy et al. 2018 [review]

Table 2.1. (continued)

Characteristic	**Factor**	**Citations**
Violence	Testosterone	
	Prenatal	Carré and McCormick 2008
	Circulating	Dabbs and Morris 1990, Windle 1994, Aromäki et al. 1999, Carré et al. 2017 [review]
	Lifetime	Hoskin and Ellis 2021
	Androgen Sensitivity	Rajender et al. 2008, Vermeersch et al. 2010, Batrinos 2012 [review], Geniole et al. 2020 [review]
Sex-related	Testosterone	No effect: Rada et al. 1983, Rada et al. 1976, Dabbs et al. 1995. Effect: Giotakos et al. 2004. Correlate of sexual activity: Aromäki et al. 2002.
Criminality	Testosterone	Ellis and Hoskin 2015(b)
	Prenatal	Present: Ellis and Hoskin 2015(a) [review] Mixed: Yildirim and Derksen 2012(a) [review], Gotby et al. 2015
	Circulating	Dabbs and Morris 1990, Banks and Dabbs 1996, van Bokhoven et al. 2006, Yildirim and Derksen 2012(a) [review], Gotby et al. 2015
	Lifetime	Hoskin and Ellis 2021
	Childhood Trauma	Cima et al. 2018

These Dark personalities develop from a mix of biological and environmental factors. Heritability analyses have demonstrated that Machiavellianism is the least genetically influenced (Additive genetic effects: 0.31, Shared environmental effects: 0.39, Non-shared environmental effects: 0.30 – Vernon et al. 2018; Onley et al. 2013, Schermer and Jones 2020), though the biological mechanisms at play are not well identified beyond some unique task-related fluctuations in testosterone and cortisol (Pfattheicher 2016, Dane et al. 2018). Narcissism has a stronger genetic association (Additive genetic effects: 0.59, Non-shared environmental effects: 0.41 – Vernon et al. 2018; Heritability: 53 to 64% – Konrath and Bonadonna 2014 [review]; Onley et al. 2013, Schermer and Jones 2020), and evidence suggests its development is related both to testosterone (Pfattheicher 2016, Dane et al. 2018, Borraz-Leon et al. 2019) and cortisol. Indeed, cortisol seems to be a crucial component to narcissism (Konrath and Bonadonna 2014 [review], Pfattheicher 2016, Dane et al. 2018). Narcissism also shows a unique dopamine receptor bias, one that demonstrates a high priority for punishment-avoidance behaviors (D1<D2) (Yildirim and Derksen 2015(b), Miles et al. 2019). Finally, narcissism shows unique neuroanatomical patterns that indicate decreased activity in structures associated with empathy and a dysfunctional salience network. This dysfunctionality causes both a hyper-fixation on self-reflection and a strong, painful alarm response upon doing so, in addition to social rejection (Jankowiak-Siuda and Zajkowski 2013, Olsson 2014, Konrath and Bonadonna 2014 [review], Feng et al. 2018, Jauk and Kanske 2021 [review]).

Psychopathy's association with violence, aggression, and criminal behavior has made it of particular research interest. It has a strong genetic component (Additive genetic effects: 0.64, Shared environmental effects: 0.04, Non-shared environmental effects: 0.32

– Vernon et al. 2018; Onley et al. 2013, Schermer and Jones 2020), particularly for men (Tuvblad and Beaver 2013) and for the traits associated with callousness and unemotionality (Viding and McCrory 2018 [review]). The development of psychopathic traits has been associated with several important biological components. These are summarized below, with references in Table 2.2. Psychopathy has a strong association with elevated levels of testosterone, both prenatally and, importantly, during key developmental phases. It also has a unique association with estradiol: high prenatal estradiol levels are associated with CU in male psychopaths and both CU and impulsive-antisocial traits in female psychopaths, and fluctuating estradiol shows reactivity patterns similar to testosterone in various social tasks. Unsurprisingly, psychopathy is also associated with cortisol, with the two aspects of psychopathy showing the predicted corresponding levels: CU is associated with high cortisol concentration and low cortisol reactivity; IA with low concentration and high reactivity. Surprisingly, however, female psychopaths show no association with cortisol.

Several neuroendocrinological factors play important roles in psychopathy, including the development of CU and IA traits. One of these is serotonin, a neurohormone responsible for homeostatic regulation; it helps to establish the boundaries of what is considered "stable." For both aspects of psychopathy, the activity of the serotonin transporter molecule seems to help mediate violence and life-course offending, with low activity being associated with more violent behavior (Table 2.2). But other aspects of serotonin – specifically serotonin concentration, functionality, and receptor phenotype (Table 2.3) – influence the divergence of CU and IA traits. One of its primary impacts is in the development of the characteristic hyporesponsivity associated with CU traits, even in the presence of elevated testosterone which would be expected to result in hyperresponsivity. High levels of serotonin and exceptionally high serotonin functionality is associated with high behavioral stability and thus with CU traits, whereas the inverse is associated with low behavioral stability and IA traits. Another serotonergic difference between CU and IA traits is in the phenotype of the serotonin receptors, specifically the degree to which the receptors are "rigid" or "plastic". This range of rigidity-plasticity helps to determine the degree to which social interaction is necessary for the maintenance of homeostasis. Rigid phenotypes do not require social interaction for homeostatic maintenance – they boundaries of homeostasis are well-maintained – whereas plastic ones do. Thus, rigid phenotypes are associated with CU traits, and a disinterest in social interactions, and plastic phenotypes are associated with IA traits, and a need for social interaction. Notably, plastic phenotypes are also associated with prosocial behavior. Whether plastic phenotypes diverge into pro- or antisocial behavior is shaped by early developmental experiences, specifically the presence of long-term states of acute stress during development. This seems to be detrimental in establishing homeostatic states which results in more IA-type traits.

Table 2.2. Biosocial factors related to the development of psychopathy.

Aspect	Factor	Citation
Psychopathy (General)		
	Testosterone	van Honk and Schutter 2006 [review], Montoya et al. 2012 [review]
	Sex Hormone Binding Globulin (SHBG)	Stålenheim et al. 1998
	Reactivity Pattern	Geniole et al. 2013, Dane et al. 2018, Harrison 2021
	Estrogen	
	Prenatal	Blanchard and Lyons 2010
	Reactivity Pattern	Harrison 2021
	Serotonin	
	Transporter	Choy et al. 2018 [review]
	Oxytocin	Donaldson and Young 2008, Meyer-Lindenberg et al. 2011 [review], Fragkaki et al. 2018 [review]
	Receptor	Brüne 2012 [review], Dadds et al. 2014
	Environmental	Harris et al. 2001, Donaldson and Young 2008, Meyer-Lindenberg et al. 2011 [review], Fragkaki et al. 2018 [review]
	Disordered Childhood Attachment	Yildirim and Derksen 2012(b) [review]
	Lack of Parental Protection	Gao et al. 2010, Brüne 2012 [review], Yildirim and Derksen 2015(a) [review], Blanchard et al. 2016(b)
Callous-Impulsive Aspect		
	Testosterone	Stålenheim et al. 1998, Loney et al. 2006, van Honk and Schutter 2006 [review], Barzman et al. 2010, Vaillancourt and Sunderani 2011, Yildirim and Derksen 2012(b) [review], Herpers et al. 2014 [review], Yildirim and Derksen 2015(a), Loomans et al. 2016, Cima et al. 2018, Harrison 2021
	Cortisol	Loney et al. 2006, van Honk and Schutter 2006 [review], Barzman et al. 2010, Vaillancourt and Sunderani 2011, Yildirim and Derksen 2012(b) [review], Montoya et al. 2012 [review], Herpers et al. 2014 [review], Loomans et al. 2016, Kimonis et al. 2017, Cima et al. 2018, Harrison 2021
	Reactivity Pattern	Glenn et al. 2011, Herpers et al. 2014 [review], Harrison 2021
Callous-Impulsive Aspect		
	Estrogen	
	Prenatal	Blanchard and Lyons 2010
	Dopamine	
	Receptors	Yildirim and Derksen 2012(b) [review], Yildirim and Derksen 2015(b)
	Serotonin	Montoya et al. 2012 [review], Yildirim and Derksen 2013 [review], Yildirim and Derksen 2015(a) [review]
	Dopamine / Serotonin Ratio	Soderstrom et al. 2003, Yildirim and Derksen 2013 [review], Yildirim and Derksen 2015(b) [review]

Table 2.2. (continued)

Aspect	Factor	Citation
	Oxytocin	Dadds et al. 2014, Fragkaki 2020
	Environmental	
	Parental Over-Control	Gao et al. 2010, Blanchard et al. 2016(b)
	Trauma	Cima et al. 2008, Yildirim and Derksen 2012(b) [review], Yildirim and Derksen 2015(a) [review], Fragkaki et al. 2018 [review]
	Social Rejection	Yildirim and Derksen 2012(b) [review], Yildirim and Derksen 2015(a) [review]
Sexual Dimorphic Effect		
	Testosterone	Welker et al. 2014
	Cortisol	Vaillancourt and Sunderani 2011, Welker et al. 2014, Herpers et al. 2014 [review]
	Estrogen	
	Prenatal	Blanchard and Lyons 2010

Table 2.3. Dopaminergic and serotonergic factors that differentiate the callous-unemotional (CU) and impulsive-antisocial traits associated with psychopathy.

Factors	**Callous-unemotionality**	**Impulsivity-antisociality**
Dopaminergic Factors		
Concentration	High	Exceptionally High
Functionality	High	Low
Regulation	High	Low
Receptor Phenotypes	D1>D2	D1=D2
Serotonergic Factors		
Concentration	High	Low
Functionality	Exceptionally High	Exceptionally Low
Receptor Phenotype	Rigid	Plastic

Dopamine also helps to explain key behavioral differences between the two aspects of psychopathy. Both are associated with high dopamine concentration (and for IA, pathologically so), but they differ in functionality, regulation, and receptor biases (Table 2.3). These differences help to explain two crucial differences between the aspects. One is the difference in goal-oriented (CU) vs. thrill-seeking (IA) motivation, and the second is the ability of those with CU traits, but not IA traits, to respond to social feedback and thus integrate socially. The D1>D2 receptor bias found in primary psychopathy can be amplified by the effects of testosterone, which downregulates D2 receptors. Finally, the functions of dopamine and serotonin interact in the regulation of aggressive impulses, such that the higher the ratio of dopamine to serotonin, the more disinhibited the impulses are.

Finally, oxytocin plays a vital role in the development of psychopathy, particularly for callous-unemotional traits. As a regulator of the stress response, acting on both cortisol and amygdala reactivity, oxytocin is a key hormone in the development of interpersonal relationships. Early environmental conditions affect oxytocin in three crucial ways. First, experiences act to attenuate the positive impact that oxytocin has on an individual. Specifically, the effect that oxytocin has is influenced by the intensity and type of early experiences that the person has. Second, experiences influence the amount of circulating oxytocin present, with negative childhood experiences resulting in lower levels of oxytocin and the development CU traits. Finally, experiences have epigenetic effects on the genes that code for the oxytocin receptor, with increased methylation being associated with CU traits. This final effect interacts with existing oxytocin receptor polymorphisms that vary in the degree to which the individual is susceptible to early environmental experiences, an effect that influences their social cognition, interpersonal attachment, and social network size.

It is thus unsurprising that early childhood experiences are crucial in the development of psychopathy. Negative childhood experiences result in disordered attachment, beginning with dysfunctional parental relationships and extending into social ones. Both CU and IA traits are associated with a lack of parental protective factors, or those behaviors associated with warmth, care, and undivided attention. They diverge with the addition of other behaviors: CU traits are associated with over-controlling parental behaviors and IA traits with abuse, trauma, and social rejection.

Biological and environmental factors combine to create unique neuroanatomical patterns for those with psychopathy. This is particularly true for the CU aspect, which demonstrates a dysfunctional ability to utilize emotional, autobiographical memories in decision-making. There are two specific areas that show poor activation: the pathway connecting emotional memory storage (striatum) to decision-making (dorsal and ventral areas of the medial frontal cortex), and the area responsible for emotional memory retrieval (posterior cingulate cortex and the precuneus complex) during moral decision-making scenarios (Sonderstrom et al. 2002, Yildirim and Derksen 2015(a), Pujol et al. 2019 [review]). That these differences are associated with weak functional connectivity between storage and decision-making suggests that this emerges from an early maturation of these pathways (Pujol et al. 2019 [review]), likely a result of disordered attachment.

As illustrated, the emergence of prosocial and specific antisocial behaviors is the result of complex developmental interactions. Genetic factors that influence neuroendocrine production, receptor polymorphisms, and transporter proteins can create a framework for behavior biased toward types of prosocial and antisocial behaviors. Whether those behaviors emerge is dependent upon early social and environmental experiences – most crucially those related to caregiving – that cue the individual to their environment and the kinds of behaviors that seem most adaptive for optimal fitness.

2.2.2.2.2 INTERPERSONAL COMMUNICATION THROUGH FACE-TRAITS

The complexity of human social behavior combined with having highly altricial offspring might be expected to select for sophisticated methods of interpersonal communication. Of particular priority might be the ability to identify potentially untrustworthy or threatening people, particularly while at young ages and through simple means. Because of the costs associated with trusting an untrustworthy person, any such ability would be expected to be both robust to deception and prone to false positives (i.e., false red flags) as opposed to false negatives (i.e., false green flags).

One potential method of doing this would be to associate static facial features with behavioral tendencies if they share underlying developmental factors. Indeed, there is evidence for this in humans and in chimpanzees, suggesting that complex social dynamics may have driven some of these relationships (Humans – Todorov et al. 2015 [review], Todorov 2017 [review], Todorov and Oh 2021 [review]; Chimpanzees – Kramer et al. 2011). Moreover, social judgments made based on these associations – known as face-traits – tend to be consistent, rapid, and accurate (Todorov et al. 2015 [review], Todorov 2017 [review], Todorov and Oh 2021 [review]), and are less variable than social judgments made based on dynamic features (Todorov and Porter 2014, Hehman et al. 2015).

In this discussion of face-traits, a few distinctions need to be made. The first distinction is a terminological one with regards to the use of the word "personality." Biologists use the term personality to describe consistent behavioral trends in animals, particularly when those trends are indicative of adaptive strategies. Psychologists, on the other hand, include cognitive and emotional elements in their definitions of personalities, which they diagnose through a variety of validated metrics that assess specific clusters of characteristics. Here, I will primarily be referring to personality in context of a set of behavioral trends, as it is behavior that would have the most relevance to social judgments. However, I may periodically reference personalities as defined by psychologists and assessed by specific metrics. The second distinction is in the use of the word "accuracy." Each of the studies discussed below that refers to accuracy does so by comparing judgments against documented behavior and/or scores on validated metrics (self- and/or acquaintance-rated) and by using a statistical standard of accuracy that may or may not correspond with the usage in other studies. This variability introduces a degree of uncertainty with regards to exactly how accurate the detection of any one trait may be. My focus in this paper is on the identification of general trends, and thus a discussion of the strengths and weaknesses of the different measures of accuracy used here is outside of the scope of this dissertation. The final distinction is that between social judgments of faces in general and the identification of face-traits. A face-trait is the term used to describe static facial characteristics that have been found to correlate accurately with behavior, that share developmental roots with that behavior, and for which judgments remain generally consistent. Social judgments of facial images, in contrast, are influenced by many factors. These include the context of the image itself, such as lighting, time of day, and where it was taken; variations in the individual whose image is being captured, such as head tilt, facial expression, and makeup; and variations on the part of the individual making the judgment, such as mood, prejudices, preexisting beliefs, and the context for which they are making the judgment. As a result, social judgments of faces in general, while rapid and consistent, do not appear to be accurate (Hassin and Trope 2000, Fiske et al. 2007 [review], Todorov et al. 2015 [review], Todorov 2017 [review]).

Research into face-traits began when researchers recognized the high degree of inter-rater consistency between social judgments of faces. They began to identify patterns between the personalities of the individuals, the social judgments being made, and specific facial cues, and these patterns that have eventually allowed for the identification of face-traits. Much of this research has relied on composite images, in which images of individuals who score similarly on a specific metric for a behavior or set of behaviors are merged into one image, or on computer-generated or -manipulated faces. The use of these techniques have allowed researchers to identify and isolate aspects of the face that are key in making accurate judgments – those that represent an actual face-trait. The cues that have been identified as being most important in the accuracy of social judgments of faces tend to be influenced by many of the same factors expected to predict behavior. These cues include muscle tone, skin tone and texture, masculinized facial features, and resemblance to facial expressions, which are all in turn influenced by environmental and social factors such as access to nutrition, sleep deprivation, environmental stressors, testosterone-related factors, and frequent repetition of facial expressions that become imprinted in the neutral expressions (Todorov 2017 [review]). Further, accuracy seems related to cues taken from the whole face (not specific facial features – Todorov et al. 2010), internal facial features (not area of the face outside of the features – Kramer and Ward 2010), and the right side of the face (as opposed to the left – Jones et al. 2012), and that accuracy in judgments are generally robust to the effects of attractiveness and age of the target (Penton-Voak et al. 2006, Little and Perrett 2007, Kramer and Ward 2010, but see Sutherland et al. 2013).Additionally, accurate judgments are made very rapidly, with consensus being reached in less than 50 ms (as low as 39 ms) with no improvement made on the judgment after 150 ms (Bar et al. 2006, Ballew and Todorov 2007, Borkenau et al. 2009). In fact, asking participants to take their time and make deliberate judgments can cause their accuracy to decrease (Ballew and Todorov 2007). In fact, the effects of these judgments have been detected even when presented at a rate below objective awareness, such as in priming images (Todorov et al. 2009).

To determine the degree to which face-traits aid in the communication of general personality tendencies, many researchers have explored the degree to which "Big Five"-related face-traits might exist, and the results indicate that some aspects of personality are more closely related to face-traits than others. The Big Five is the term used to describe a five-factor personality structure that broadly encompasses a variety of personality characteristics, and it includes extraversion, neuroticism, agreeableness, conscientiousness, and openness to experience (presented in order of accuracy; Norman 1963, Goldberg 1993 [review], John and Srivastava 1999 [review]). The most accurately identified Big Five dimension is extraversion (e.g., gregariousness, activity, warmth), judgments of which seem consistent for both sexes (Penton-Voak et al. 2006, Little and Perrett 2007, Borkenau et al. 2009, Kramer and Ward 2010, Todorov et al. 2013, female only – Alper et al. 2021), using both real (individuals) (Penton-Voak et al. 2006, Borkenau et al. 2009, Todorov et al. 2013) and composite images (Penton-Voak et al. 2006, Little and Perrett 2007, Kramer and Ward 2010, Alper et al. 2021). This trait has also emerged from computational models that generated faces from manipulating face shape and skin quality (Todorov et al. 2013). In particular, Borkenau et al. (2009) determined that the components of "excitement-seeking" and "positive emotions" were more strongly detected than "warmth" and "activity" when using real, non-neutral (expressive) faces. Also fairly accurate is the dimension of neuroticism (e.g., anxiety, irritability, impulsivity). However, it may be accurate only in women (Little and Perrett 2007, Kramer and Ward 2010, Jones et al. 2012), though one study has detected it in men instead of women (Penton-Voak et al. 2006). These studies used individual images, both 2D (Penton-Voak et al. 2006, Kramer and Ward 2010) and 3D facial scans (Jones et al. 2012), and composite images (Penton-Voak et al. 2006, Little and Perrett 2007, Kramer and Ward 2010). However, it has also been identified as being accurately and reliably identified using machine learning (specifically an end-to-end convolutional neural network generated from a dataset of faces and personality traits – Zhang et al. 2017). Less accurate may be agreeableness (e.g., trustworthy, altruism, modesty), which seems more easily detected in female faces and using composite images only (Little and Perrett 2007, Kramer and Ward 2010, Jones et al. 2012, Alper et al. 2021). Perhaps one of the least accurate dimensions is conscientiousness (e.g., competent, dutiful, deliberate), having been identified using composite images only (Little and Perrett 2007, Alper et al. 2021), with one study finding it women only (Little and Perrett 2007) and another in both sexes (Alper et al. 2021), though it has also been identified as being accurately and reliably identified using machine learning (specifically an end-to-end convolutional neural network generated from a dataset of faces and personality traits – Zhang et al. 2017). Finally, seemingly the least accurate dimension is openness to experience (e.g., imaginative, excitable, curious). It has been detected in two studies, though inconsistently: one study accurately detected it in individual male faces (but not in composites, and not in female faces – Penton-Voak et al. 2006), and whereas another found it in composite female faces (but only using "internal" facial features [cropping the face into a "T" that includes the eyes, nose, and mouth], and not in male faces – Kramer and Ward 2010). Interestingly, both neuroticism and contentiousness have been identified as being accurately and reliably identified using machine learning (specifically an end-to-end convolutional neural network generated from a dataset of faces and personality traits – Zhang et al. 2017).

Face-traits that are most accurately identifiable seem to be those related to dominance and trustworthiness, which is unsurprising given the importance of these characteristics in social contests and for the survival of altricial young. Indeed, 80% of social judgments seem to be made along these two dimensions (Oosterhof and Todorov 2008, Sutherland et al. 2013, Walker and Vetter 2016, Messer and Fausser 2019, Todorov and Oh 2021 [review]), in ways that are cross-culturally and interracially reliable (Walker et al. 2011, Short et al. 2012, Ma et al. 2015, Sutherland et al. 2018, Todorov and Oh 2021 [review]). Dimensions of these two traits have been mapped onto 2D and 3D faces to generate models that have been independently validated to reliably represent varying degrees of the dimensions (Oosterhof and Todorov 2008, Todorov et al. 2013, Walker and Vetter 2016, Todorov and Oh 2021 [review]). The importance of face-to-face dominance contests in primates may be the primary selection pressure for the emergence of dominance-related face-traits, and the need to identify potentially untrustworthy people at a young age for trust-related ones. Trustworthiness has been one of the more extensively studied dimensions, having been recognized as one of the traits that can be identified most accurately and reliably (Todorov et al. 2009, Todorov et al. 2010, Stirrat and Perrett 2010, Todorov et al. 2013, Rule et al. 2013). Todorov et al. has examined trustworthiness judgments in a variety of ways, including the amount of time it takes to make accurate and reliable judgments (below the threshold of objective awareness, 2009) and trends when using partial or whole faces (initial judgments are based on holistic faces, 2010). Stirrat and Perrett (2010) examined trustworthiness using actual behavior and found patterns in facial structure that accurately predicted a man's likeliness to either collaborate or exploit partners in trust games as well as the likelihood of his partners to trust him (particularly subordinate women).

In fact, it seems as though the primary driving force behind identifiable face-traits is threat-detection (Oosterhof and Todorov 2008, Walker and Vetter 2016), a relationship that may be mediated in part by the influence of testosterone. As discussed, testosterone and testosterone-related factors influence dominance behaviors – and especially antisocial ones. They also influence the development of male-typical facial dimorphisms, having a broadening effect on the forehead, chin, jaw, and nose (Fink and Penton-Voak 2002, Bulygina et al. 2006, Thordarson et al. 2006, Weston et al. 2007, Toma et al. 2008, Marečková et al. 2011, Whitehouse et al. 2011). Thus, it is unsurprising that a systematic review and meta-analysis has found that facial width-to-height ratio (fWHR) is associated with dominance behavior in both sexes (Geniole et al. 2015 [review, meta-analysis]). fWHR has also been associated with several threat-related behavioral tendencies that have also been reliably and accurately identifiable from facial images. These traits include threat potential and behavior (Identification – Oosterhof and Todorov 2008, Todorov et al. 2013; fWHR – Geniole et al. 2015 [review, meta-analysis]); aggression (Identification – Carré et al. 2009; fWHR – Carré et al. 2009, Carré and McCormick 2008, Geniole and McCormick 2015, Haselhuhn et al. 2015 [meta-analysis]); and likelihood of holding explicitly racially prejudiced beliefs, a characteristic that seems more rapidly identifiable by minority groups than others (Hehman et al. 2013).

There is also evidence that this threat detection-related ability might include traits associated with the Dark Triad. In fact, Dark Triad-related images seem to be more reliably and accurately detectable than the Big Five personality traits (Alper et al. 2021), again suggesting that threat-detection is the primary driving force behind face-trait detection. Much of this work has come from the use of composite images created by Holtzman (2011) that represent the extreme ends of the Dark personalities. These images were generated by (1) scoring volunteers on self- and acquaintance-reported metrics that included (but were not limited to) the Mach-IV (for Machiavellianism), the Narcissistic Personality Inventory-40 (NPI), and the Self-Report Psychopathy Scale (SRP-III) (Holtzman 2011); and (2) morphing the facial images of the 10 highest and lowest scoring individuals into one image. The images were then validated by presenting the high/low pairs, along with a description of the associated personality, to non-acquaintance participants for judgment. The participant was asked to indicate which image represented that characteristic and their confidence in their assessment (scale from -5 to +5, with -5 indicating high confidence for the image on the left, and +5 high confidence for image on the right). The Holtzman composites have been used in numerous other studies with results that support the ability to discriminate between high and low scorers in predictable ways. These images have been used to explore mating preferences with regards to Dark personalities, in forced-choice designs, with results that indicate preferences against those with these personalities (e.g., Lyons et al. 2015, Marcinkowska et al. 2015, 2016, Lyons and Blanchard 2016, Lyons and Simeonov 2016). Some studies have morphed Holtzman composites with other unique faces to create new composites that vary along these characteristics. The results of these studies, also forced-choice, similarly suggest an ability to discriminate between Dark Triad images in predictable ways (Mating preferences – Brown et al. 2017, Brewer et al. 2018, Brewer et al. 2019, Alper et al. 2021; Boss preferences – McElroy et al. 2020). Other studies have sought to replicate this using novel images. Gordan and Platek (2009) photographed volunteers who completed the aforementioned Dark Triad metrics and the trustworthiness questions from the General Social Survey (modeled in Glaeser et al. 2000) and then displayed these images to participants while in an fMRI. Images associated with high psychopathy, Machiavellianism, and trusting behavior – but not narcissism – resulted in high amygdala activation. Shiramizu et al. (2019) also generated their own composite images, though they used the "Dirty Dozen" metric to assess for the Dark Triad (Jonason and Webster 2010). They found that participants were able to identify narcissism in male and female faces and psychopathy in male faces, but were not able to identify Machiavellianism. Giacomin and Rule (2018) studied narcissism specifically using the NPI and real images of participants. They presented faces, cropped to display different parts of the face, to participants and asked them to rate their perceived degree of narcissism, which allowed them to identify the eyebrows as being the cue most accurately associated with narcissism.

It is important to note a few important aspects of the Dark Triad studies using the Holtzman images. The first is the limitations of relying on forced-choice designs. While this does validate the differences between high/low images, it does not represent a "real world" scenario, as it is highly unlikely that someone will be given the chance to identify a potentially threatening individual by directly comparing them to their polar opposite. Further, these images were validated only with respect to the high/low aspect of the characteristic for which they were created. There is no evidence that participants would be able to assign the associated Dark personality to each image and thus be able to spontaneously identify the traits in question. Finally, it is highly probable that any "identification" of the Dark Triad from faces is driven more by an underlying association between the Dark personalities and their overall threat-potential than by an ability to detect these specific personalities. This underlying relationship, on its own, would predict that participants would show an aversion to Dark Triad-related faces, even if participants were not detecting the Dark Triad itself. Indeed, this may partly explain the inconsistency in the detection of the Dark Triad from faces.

In addition to the facial features indicated above, accuracy of face-trait identification is heavily dependent upon how the association between facial characteristics and behavioral tendencies is formed. Evidence suggests that face-trait detection is learned in development, potentially as a kind of "mapping" that connects behavioral traits to face-spaces (Over and Cook 2018). The ability to identify face-traits seems to begin to emerge early: children as young as 7 months old can identify trustworthiness from facial cues (Jessen and Grossmann 2016), and by between 10 and 15 months, they begin to identify and predict the outcomes of dominance dynamics (Thomsen et al. 2013, Mascaro and Csibra 2014). Child-adult agreement in judgments seem to begin to converge by around 3-4 years old (Cogsdill et al. 2014, Cogsdill and Banaji 2015, Charlesworth et al. 2019) and become consistent by 5-6 (Cogsdill et al. 2014), with evidence suggesting they use the same facial features to make their judgments (Ma et al. 2015). The judgments made by children have been found accurate using the faces of adults, other children, and rhesus macaques, suggesting a universality of these traits and abilities at least somewhat independent of cultural factors (Cogsdill and Banaji 2015). However, unlike for adults, it does appear as though there is an influence of facial attractiveness for children (Ma et al. 2015), particularly for female raters (Ma et al. 2016).

Importantly, repeated interactions with diverse kinds of faces seems to affect accuracy (Freeman and Ambady 2011, Freeman et al. 2020). Specifically, accuracy seems dependent upon how much detail can be extracted from the facial information (Charbonneau et al. 2020), and detail extraction seems related to the quality of experience had in extracting information from various faces (Freeman and Ambady 2011). It has been proposed that this ability to extract detail from other-race faces may be one of the mechanisms by which stereotypes and prejudices emerge (Over and Cook 2018). Indeed, evidence continues to emerge that a crucial factor in the development of implicit bias in children is the cognitive inability to process and evaluate individual other-race faces, an ability that develops early in childhood (Lee et al. 2017, Qian et al. 2017). This may help explain several race-related trends: why the ability of a perceiver to accurately assess face-traits seems to be influenced by the racial group identity of perceiver (Hugenberg and Bodenhausen 2003, Xie et al. 2019) as well as the degree to which the perceiver has had interracial contact during development (Furl et al. 2002); why judgment accuracy of other-race faces degrades over time in comparison to same-race faces (Strachan et al. 2017); why implicit (but not explicit) biases increases the perception of negative emotions and traits in other-race faces (Hugenberg and Bodenhausen 2003, Dotsch et al. 2008, Stanley et al. 2011, Charbonneau et al. 2020); why the cross-generational decrease in explicit racism has been accompanied by no change in implicit racism (Baron and Banaji 2006); and why majority-race persons often say that those of other races "look the same" (MacLin and Malpass 2001) – individuals with a poor ability to extract detailed information from other-race faces because they lacked quality interracial interactions in development may utilize a cognitive default categorization process that perceives other-race faces as being a potential threat (see Kubota et al. 2012 [review] for differential neurological responses with regards to implicit and explicit racism).

Finally, other kinds of beliefs and processes can affect accuracy. Preconceptions regarding the traits in question, such as its association with other traits (e.g., correlating intelligence and trustworthiness in an individual – Stolier et al. 2018, Putz et al. 2018, Kocsor et al. 2019) or the context in which they are making the assessment (e.g., for online dating, job application – Todorov and Porter 2014) can influence the results. Priming effects can likewise bias face-trait judgments (e.g., "these individuals are auditioning for a movie villain" or "are professional bankers" – Todorov and Porter 2014) and may act to form stereotypical beliefs about the faces with which they are associated (Kocsor and Bereczkei 2017). Further, once beliefs are formed by stereotypes, this then may result in a self-fulling prophesy; those of a specific race may be consistently depicted negatively in media, and as a result, an individual of that race may be treated negatively by others, which in turn may cause them to begin to behave negatively (Snyder et al. 1977, Darley and Fazio 1980, Chen and Bargh 1997, Todorov 2017 [review]).

Overall, the evidence suggests that the use of face-traits in social decision-making is a complex process that involves several biological and cultural factors. Evolutionary pressures to identify and avoid untrustworthy people, including the ability to discriminate between prosocial and antisocial personalities, seems to have selected for the ability to extract and evaluate detail from faces, an ability shaped by their social environment. This may have acted as a type of "in-group identification mechanism" by which out-group people, for whom they have little ability to extract facial details, are automatically categorized as a potential threat. Thus, this may result in the overgeneralization of facial information to create a spontaneous, subjective judgment that prioritizes the identification of potential sources of harm over complete accuracy.

2.2.2.2.3 FEMALE INTRASEXUAL COMPETITION

The degree of intrasexual competition found in non-human primates is uncommonly high, and it seems driven by the need for resources to support the high demand for energetically-expensive lactation. As a result, primate social structures include two separate social hierarchies, and for the female hierarchy, social status is associated with reproductive success, a relationship maintained both by access to resources and the ability to suppress the reproduction of other females. Humans demonstrate similar social characteristics. Women and men have separate same-sex hierarchies, and they demonstrate comparable levels of both aggression and competition (Balliet et al. 2011 [review]).

However, there are sex differences in our competitive behavior (Vaillancourt 2013 [review], Campbell 2013 [review], Stockley and Campbell 2013 [review], Stanyon and Bigoni 2014 [review], Archer 2019 [review]). First, women are generally more intrasexually competitive than men. A metanalysis of 50 years of research has shown that, in comparison to men, women are more cooperative in mixed-sex groups but less cooperative with same-sex groups (Balliet et al. 2011 [review]). The second difference is that female intrasexual competition occurs primarily over reproductive resources and varies predictably with sexual maturity, the local OSR, and resource availability (Campbell 2013 [review], Stockley and Campbell 2013 [review], Archer 2019 [review]). Finally, women show a preferential use of indirect aggression over all other forms of aggression (Vaillancourt 2013 [review]); instead of physical violence, women use interpersonal social dynamics to assert dominance. This may be a contributing factor behind the female-biased behavioral dimorphisms with regards to social interests and social skills (Campbell 2013 [review], Stockley and Campbell 2013 [review], Archer 2019 [review]) that are reflected in sexually dimorphic neuroanatomy (Stanyon and Bigoni 2014 [review]).

This preference for the use of indirect aggression may have arisen through strong selective pressures to preserve the mother's safety. Given the importance of lactation and the mother-child bond, it is unsurprising that maternal mortality has a stronger negative impact on child survivability than paternal mortality (Campbell 2013 [review]), a pattern we see in non-human primates as well (Marlowe 2007 [review]). This may also be supported through neuroanatomical evidence which shows sexually-dimorphic limbic effects. Not only do women show stronger and more pronounced responses to general threats than men, but they show opposite responses to oxytocin: increased oxytocin results in increased, not decreased, fear. This effect of oxytocin, a key hormone in interpersonal bonding and group identity, may act to promote infant protection and maternal survival, enhancing instincts of defense in a woman with a strong attachment to an infant (Campbell 2013 [review], Stockley and Campbell 2013 [review], Stanyon and Bigoni 2014 [review]).

2.2.3 Modern Human Mating Behavior

As we have seen, human evolution has been shaped in part by sexual conflict and life history dynamics. These dynamics, not the least of which are those associated with differential reproductive investment, are at least partly responsible for a series of evolutionary events from which several unique aspects of modern human biology and society have emerged. These include increased socio-cognitive complexity, cooperative breeding practices, unique female-female aggressions, substantial changes to the female body, a risky childbirth process, dominance dynamics that emerge from biosocial developmental interactions, and the ability to detect, at very young ages, aspects of personality from facial structure. We might thus expect other aspects of our behavior, particularly those associated with mating, to reflect the influence of sexual conflict and life history dynamics.

2.2.3.1 The Human Mating System

Men and women show reproductive differences indicative of a female choice system. Women invest more into each offspring than men (OSR 8.6-11.7, Marlowe and Berbesque 2012), and men have a marginally higher reproductive variance (Labuda et al. 2010), suggesting that they would be the choosier sex. Men and women should then engage in mating behaviors respective of this system, including the use of strategies that align with fast/slow life histories and preferences for sexual partners that indicate a priority on reproductive capability/resource provisioning, respectively.

Indeed, men do tend to engage in behavior associated with a faster reproductive strategy. Compared to women, men prefer a greater number of sexual partners and demonstrate a tendency toward unrestricted sexuality: they engage in sex earlier, more frequently, and with a greater number of lifetime partners. Men also demonstrate a greater willingness to pursue short-term sexual relationships, to engage in sexual activity early in a relationship, and to lower their standards with regards to potential short-term mates. They are more likely to regret investing in relationships that did not result in sex and to overperceive a woman's sexual intent, and they are less likely to regret sexual acts and to be repulsed by sexually disgusting scenarios. Men and women also show reversed tendencies with regards to relationship deception: men are more likely to deceive women with regards to their interest in long-term commitment, whereas women are more likely to deceive men about their sexual availability. Furthermore, men are more likely to be angry when deceived regarding sexual availability, whereas women are more likely to be angry when deceived regarding emotional investment (Schmitt et al. 2001 [review], Schmitt 2005 [cross-cultural], Shackelford et al. 2005 [cross-cultural], Penke and Asendorpf 2008, Valentine and Li 2012 [review], Schmitt and Jonason 2015 [cross-cultural], Buss and Schmitt 2016 [review], Buss 2016 [review], 2017 [review], Csajbók and Berkics 2017, Buss and Schmitt 2019 [review], Walter et al. 2020 [cross-cultural], Thomas et al. 2020 [cross-cultural]).

As expected, men and women show patterns of mate preferences that align strongly with their reproductive priorities, patterns that are consistent across cultures and throughout history. They do share some consistencies for preferences for long-term mates, namely those of reliability, dependability, kindness, and agreeableness. However, there are some notable, and predictable, differences that emerge for both long- and short-term mating situations. Women show a highly consistent preference for men with social status and financial security, a preference that also tends to correlate with male age (e.g., Buss 1989, Kenrick et al. 1990, 1993, Singh 1995(b), Li et al. 2002, Shackelford et al. 2005 [cross-cultural], Li and Kenrick 2006, Helle et al. 2008, Walter et al. 2020 [cross-cultural], Thomas et al. 2020 [cross-cultural]). Men, in turn, prefer women with features that are associated with reproductive capability, namely those at the intersection of sexual maturity and youth (Valentine and Li 2012 [review], Pisanski and Feinberg 2013 [review, cross-cultural], Buss and Schmitt 2016 [review], Buss 2016 [review], Buss and Schmitt 2019 [review]). These differences in mate preferences are remarkably universal and consistent, so much so that knowing an individual's preferences can accurately classify their sex with 92% accuracy (Conroy-Beam et al. 2015). Notably, however, differences between male and female preferences have been decreasing slightly in the last 20-25 years (Oliver and Hyde 1993, Hyde 2007), particularly in cultures that have adopted more egalitarian approaches to sexuality (Muggleton and Fincher 2017), although with no effect as the result of greater general gender equality (Zhang et al. 2019, Walter et al. 2020 [cross-cultural]).

Even though multigenerational groups of kin are the dominant social pattern in humans, social serial monogamy is the dominant mating pattern. The reason for this pattern is under debate, and will be addressed to some degree at various points below, but there is little doubt that, even though humans show high variation in their mating pattern – with polyandrous, polygynous, and promiscuous mating patterns appearing both across and within societies – monogamy is the primary pattern within any one group (Marlowe 2000, Brown et al. 2009, Fortunato 2018, Schacht and Kramer 2019 [review, cross-cultural]). The specific pattern that has been identified is that of sexually-exclusive pairbonds residing with each other for extended periods of time (Labuda et al. 2010, Schacht and Kramer 2019 [review, cross-cultural]). Aspects of this system that seem particularly universal is the relative stability of relationships, the ways in which fathers invest in their offspring, and the prevalence of the residential pair-bond (Schacht and Kramer 2019 [review, cross-cultural]). Indeed, even though infidelity may occur, the rate of extrapair paternity in humans is relatively lower than that of many other socially monogamous species (~1.7-3.3%, cross-cultural meta-analysis – Anderson 2006, but see Scelza et al. 2011, 2020 for case studies in Indigenous populations; Larmuseau et al. 2016 [review]). Further, evidence indicates that this monogamous behavior has been influenced by evolutionary forces. Biological indicators of sperm competition – including testes volume, rate of sperm production and ejaculation, ejaculate composition, and penis morphology – all suggest that humans engage in levels of sperm competition and rates of male extrapair sex most comparable to primates with little to no sperm competition (e.g., solitary male orangutans, monogamous gibbons – Lovejoy et al. 2009 [review]). Also, genetic indicators for the potential for polygyny suggest that the polygyny rate is relatively low, with a ratio of Xchromosome-to-autosome genetic recombination rates between 1.1 to 1.4 (1 = equal effective population size for males and females– Labuda et al. 2010).

The patterns of human mating behavior suggest that our system is influenced by at least two primary factors. One factor would act to allow the documented variation in the mating system to emerge. Evidence suggests that this is resource availability, as the current variety in mating systems is strongly associated with the local access to resources (Marlowe 2000, Brown et al. 2009, Fortunato 2018, Schacht and Kramer 2019 [review, cross-cultural]). The second factor would be one that acts as an evolutionary pressure to maintain the prevalence of serial, social monogamy. It has often been assumed that this is maintained by the female reliance on male provisioning. However, the dominance of cooperative breeding in both modern society and human evolutionary history would indicate that this is a historically strong need. Thus, this suggests the existence of another strong biological selective pressure, external to resource acquisition, that has influenced the dominance of this mating system.

2.2.3.1 Female Mating Behavior

We would expect female relationship preferences to show a pattern of trade-off decisions that maximize her access to reproductive resources (Gangestad and Simpson 2000 [review], Geary et al. 2004 [review], Valentine and Li 2012 [review], Buss and Schmitt 2019 [review]). In particular, we expect her to take into consideration the socioenvironmental factors that influence the availability of resources, the type of relationship she is pursuing, and the potential direct and indirect benefits that the men might provide – including whether the benefits come with any costs and whether she can discern those costs and benefits in the first place.

A great deal of research interest has focused on identifying the exact direct and indirect benefits that men might confer. Direct benefits should primarily include two potentially-overlapping categories: the ability to acquire resources and the ability to invest those or other resources (e.g., time, energy, education, etc.) in offspring. Indirect benefits should be those related to a man's genetic quality that he could pass down to his offspring. It has been proposed that male-typical sexual dimorphisms may be a signal of good genes on the pretext that testosterone may have immunosuppressing effects (Folstad and Karter 1992, Wedekind and Folstad 1994, Hillgarth et al. 1997). However, current evidence suggests that testosterone does not have immunosuppressing effects in humans (Nowak et al. 2018).

It may be that testosterone acts as a signal of both direct and indirect benefits through its relationship to social dominance. Testosterone influences both masculinized features and dominance behaviors, and dominance is associated with reproductive success in both Indigenous and Western cultures (Kaplan and Hill 1985, Mulder 1987, Hawkes et al. 2001, Smith 2004 [review], Gurven and Von Rueden 2006 [review], Hopcroft 2006, Von Rueden et al. 2011). In Western cultures specifically, it is related to wealth, income, and education, which are also associated with reproductive success in men: wealth and income are positively related to the amount of sex a man has (Hopcroft 2006), and, along with education, the number of children he has (Hopcroft 2006, Weeden et al. 2006, Fieder and Huber 2007, Nettle and Pollet 2008). Social status is also associated with increased intramarital fertility and lower infant mortality (Von Rueden et al. 2011). In contrast, these relationships are negative in women: wealth, income, and education in women is associated with fewer children (Weeden et al. 2006, Fieder and Huber 2007, Nettle and Pollet 2008), possibly due to delayed childbearing and thus decreasing fertility (Weeden et al. 2006, Fieder and Huber 2007), the difficulties balancing motherhood and careers (Fieder and Huber 2007), and/or a way of diverting resources from offspring quantity to offspring quality by investing more resources into the fewer offspring they have (Mace 2000, Penn et al. 2007). Interestingly, there is a negative relationship between intelligence and both frequency of sex and number of offspring for men and women (Hopcroft 2006).

However, as illustrated, dominance can come at a cost. In addition to the associations with general antisocial, aggressive, and violent behavior, cross-cultural evidence suggests that testosterone bidirectionally mediates the trade-off between mating effort and parental effort that mirrors its influence on status-seeking behavior: higher testosterone leads to a decrease in parental behaviors, and decreased parental behaviors leads to an increase in testosterone (Mazur and Michalek 1998, Archer 2006, Kuzawa et al. 2009, Alvergne et al. 2009, Gettler et al. 2011(b), Puts et al. 2015, Roney and Gettler 2015). Similarly, testosterone concentration is associated with early sexual experience (Mazur et al. 1994); a general aversion to long-term relationships (Booth and Dabbs 1993, Puts et al. 2015); and increased interest in multiple sexual partners (Mazur et al. 1994, Bogaert and Fisher 1995, Peters et al. 2008), even when in a committed relationship (McIntyre et al. 2006, Edelstein et al. 2011, Pollet et al. 2011, Polo et al. 2019, Klimas et al. 2019). Further, in context of within-relationship behaviors, testosterone is negatively associated with long-term relationships (Gray et al. 2002, Alvergne et al. 2009, Polo et al. 2019), engagement in relationship and partnership maintenance behaviors (Gray et al. 2002), and investment in relationship quality (Booth and Dabbs 1993, Das and Sawin 2016, Gray et al. 2017) and is positively associated with infidelity (Booth and Dabbs 1993, Fisher et al. 2009, Klimas et al. 2019) and relationship violence (Booth and Dabbs 1993). Finally, in context of long-term parenting roles, testosterone is associated with having fewer children (Gray et al. 2002) and engaging in lower quality parenting behavior and effort (Storey et al. 2000, Fleming et al. 2002, Alvergne et al. 2009, Muller et al. 2009, Van Anders et al. 2012, Weisman et al. 2014). Importantly, and expectedly, these trends are mediated by other factors including cortisol (Gettler et al. 2011(a)), personality differences (Perini et al. 2012), sexual and parenting desires (McIntyre et al. 2006), and environmental and social factors (Goldey and van Anders 2015).

Thus, we would expect women to demonstrate mating preferences reflective of trade-off decisions related to the effects of testosterone. Women may choose to mate with non-dominant men for the direct benefits he may provide, primarily that of paternal care. Women may also choose to mate with dominant men for both the direct and indirect benefits that he may provide: direct benefits through the access to the resources that may come from his social dominance, and indirect benefits through her children's access to the biological factors that influence dominant behaviors. However, mating with dominant men may increase her risk of harm from the antisociality associated with it or the (currently unidentified) costs of an increased risk of a non-monogamous relationship. Thus, masculinity may be a signal of benefits but may not always be preferred, and women might be particularly selective about their choices regarding masculine men. Further, all of this should be mediated by her relationship priorities and access to resources, shifting toward masculinity in short-term contexts or when she has independent access to resources and/or alloparental care.

The complexity of predicted female mate choice preferences is supported by the available evidence. In general, male attractiveness tends to be variable (Penton-Voak and Perrett 2000(a) [review], Roberts and Little 2007 [review], Valentine and Li 2012 [review], Pisanski and Feinberg 2013 [review, cross-cultural], Buss and Schmitt 2019 [review]). However, as indicated above, there is one cross-cultural and historically-strong – and predictable – preference: social status and financial security, which tends to correlate with partner age (e.g., Buss 1989, Kenrick et al. 1990, 1993, Singh 1995(b), Li et al. 2002, Shackelford et al. 2005 [cross-cultural], Li and Kenrick 2006, Helle et al. 2008, Walter et al. 2020 [cross-cultural], Thomas et al. 2020 [cross-cultural]).

Other patterns of preferences further support the predictions. Women prefer men who demonstrate prosocial behaviors (Moore et al. 2013, Farrelly et al. 2016, Csajbók and Berkics 2017, Ehlebracht et al. 2018, Margana et al. 2019) and only find obviously dominating behaviors attractive when prosocial behaviors are present (Jensen-Campbell et al. 1995) and aggressive ones are absent (Sadalla 1987, Lyons and Blanchard 2016). Given the choice, they prefer men that have gained their social status through prestige over those use have gained it through dominance (Snyder et al. 2008), a distinction made based on the emphasis of earning respect through displaying knowledge and skills, a method of gaining social status that seems unique to humans (Maner 2017 [review]). Other features generally found attractive include signals of sexual maturity, expressiveness (Cunningham 1990), and general health, cued either through an average wait-to-hip ratio (Singh 1995(b)) or from skin color or tone (Scott et al. 2010, Vera Cruz 2018). There is some evidence that women find facial and body symmetry and/or averageness attractive, for which there may be some relationship to health (particularly in areas where health is generally poorer – Gangestad and Buss 1993, DeBruine et al. 2010 [cross-cultural], Tybur and Gangestad 2011, Lee and Zietsch 2011), but direct evidence linking health to symmetry is inconclusive (Van Dongen and Gangestad 2011, Van Dongen 2012, Graham and Özener 2016 [review], Walter et al. 2020 [review, cross-cultural]).

As expected, there does not appear to be a strong link between perceptions of facial attractiveness and masculinity. The results of some studies show a slight preference for masculinity (Johnston et al. 2001, DeBruine et al. 2006), especially between narcissistic women and narcissistic male faces (Lyons and Blanchard 2016); others show no preference for masculinity at all (Singh 1995(b), Swaddle and Reierson 2002, Penton-Voak and Chen 2004, Boothroyd et al. 2008, Scott et al. 2010, Kandrik 2017 [dissertation]), including when using facial or head hair as a proxy for masculinity (Muscarella and Cunningham 1996, Neave and Shields 2008); and still others show preferences for feminized faces (Perrett et al. 1998, Rhodes et al. 2000). Women do seem to perceive masculine faces as healthful (Rhodes et al. 2003), but they also associate masculine faces with being cold, unemotional, dishonest, uncooperative, and being a poor parent (Perrett et al. 1998), and both men and women associate them with being likely to prioritize mating effort over parental effort (Kruger 2006). Women also show a commitment skepticism bias in which they show suspicion of commitment signals that are easy to fake (Haselton and Buss 2000, Cyrus et al. 2011).

Women also show preferences attuned to – with intention to avoid – men on the Dark Triad. Women are likely to associate especially masculine faces with psychopathy and, particularly, narcissism (Lyons et al. 2015), and they show an aversion to both faces and behaviors associated with the Dark Triad (Faces, All dark personalities – Lyons et al.

2015, Lyons and Blanchard 2016, Brewer et al. 2019, but see Carter et al. 2014; Behaviors, Psychopathy – Rauthman and Kolar 2013, Blanchard et al. 2016(a); Behaviors, Narcissism and Machiavellianism – Rauthman and Kolar 2013). Interestingly, however, there is some evidence that sociosexually-unrestricted women show contraceptive-based variation, preferring narcissists while not on contraceptives and showing a marked aversion to Machiavellian faces while on contraceptives (Marcinkowska et al. 2015).

As expected, women demonstrate relationship-type context-dependent shifts in their preferences (Gangestad and Simpson 2000 [review], Valentine and Li 2012 [review], Buss and Schmitt 2016 [review], Buss and Schmitt 2019 [review]). For long-term mates, women place priority on partners demonstrating an ability to provide direct benefits through cues of prioritizing either partnership and paternal care or social status and resource provisioning. Evidence suggests that for long-term partners, women generally prefer the former, putting significant emphasis on men who are kind, dependable, intelligent, companionable, fond of children, hard-working, altruistic, trustworthy, and who engage in helping behavior (Buss 1989, Kenrick et al. 1990, 1993, Buss 1994, Hill and Hurtado 1996, Scheib 2001, Moore et al. 2013, Farrelly et al. 2016, Csajbók and Berkics 2017, Ehlebracht et al. 2018). Dominance is secondarily important, preferred only when accompanied by prosociality (Jensen-Campbell et al. 1995) or expressions of and behaviors associated with moral outrage (Brown et al. 2021). These preferences tend to hold true in real-world mating choices (Valentine and Li 2012 [review], Conroy-Beam and Buss 2016, but see Eastwick and Finkel 2008 for exceptions), even appearing in preferences for in-vitro sperm donors (Scheib 1994, Whyte et al. 2016).

Female preferences for short-term mates tend to align with their preferences for long-term mates, with some notable differences. Though women are less likely to pursue short-term mates, across cultures, women are more likely to engage in short-term relationships if they score high on the Big Five's score of Extraversion or if they have a more unrestricted sociosexuality (Schmitt and Shackelford 2008, but see Jonason and Buss 2012). They also often avoid long-term relationships by using physical, social, and emotional avoidance behaviors (Jonason and Buss 2012). For short-term relationships, women show many of the same preferences as they do for long-term ones (Ehlebracht et al. 2018). This is particularly true for sexually restricted women (Simpson and Gangestad 1992, Muggleton and Fincher 2017) who also seem to put a premium on agreeable male faces (Brown et al. 2019). However, there are some differences in the preferences for short-term partners. Specifically, they prefer men with greater masculinity (Little et al. 2002, Frederick and Haselton 2007), physical attractiveness (Scheib 2001, Li and Kenrick 2006), and dominance (Snyder et al. 2008, Penke and Asendorpf 2008, Valentine et al. 2014). Sexually unrestricted women show more marked preferences for these features (Simpson and Gangestad 1992, Gangestad and Simpson 2000 [review], Penke and Asendorpf 2008, Valentine and Li 2012 [review], Marcinkowska et al. 2015, Buss and Schmitt 2016 [review], Buss and Schmitt 2019 [review]), particularly for men with extraverted faces (Brown and Sacco 2017). However, the general aversion of men with Dark personalities holds true for short-term relationships (Lyons et al. 2015, Blanchard et al. 2016(a), Brewer et al. 2018, Brewer et al. 2019, but see Jonason et al. 2015), regardless of whether they are under the influence of alcohol (Brewer et al. 2019) or the woman's degree of sensation-seeking tendencies (Brewer et al. 2018, but see Aitken et al. 2013 for differences in

Machiavellian preferences), suggesting that this aversion is not based on externally-enforced social expectations.

The pattern of female preferences also seems to hold true for women's choices for extrapair relationships (Little et al. 2002). There have been several explanations proposed for why women would pursue extrapair relationships, which will not be reviewed in-depth here. However, the proposed hypotheses include the following: it may be an attempt to obtain indirect benefits through good-gene or variable-gene donations while continuing to receive direct benefits from their primary partner; it may be to provision resources or protection from multiple potential fathers; it may be to establish a "back-up" mate, potentially one of high status; it may be revenge to deter her partner's infidelity; or it may be as a genetic constraint (Greiling and Buss 2000 [review], Buss 2000 [review], Tregenza and Wedell 2000 [review], Scelza 2013 [review], Forstmeier et al. 2014 [review], Buss et al. 2017 [review]).

While women do generally prefer to avoid men on the Dark Triad, there may be evidence of assortative mating. Women with Dark personalities prefer men with Dark personalities (and vice versa) (Jonason et al. 2011, Jonason et al. 2015, Blanchard et al. 2016(a), Lyons and Blanchard 2016), even for long-term relationships (Jonason et al. 2015, Lyons and Blanchard 2016). This pattern may be particularly strong for those who score high for psychopathy (Jonason et al. 2011, Jonason et al. 2015, Blanchard et al. 2016(a)). This preference may have consequences on actual reproductive outcomes; women who prefer narcissistic faces tend to have more children than those who prefer other Dark personalities (Marcinkowska et al. 2016).

2.2.3.2 Male Mating Behavior

2.2.3.2.1 MALE MATE PREFERENCES

Even though men are generally less selective than women in choosing mates, men do show preferences that emerge cross-culturally. As indicated above, for both long- and short-term mates, men prefer women with features that are associated with reproductive capability (Valentine and Li 2012 [review], Pisanski and Feinberg 2013 [review, cross-cultural], Buss and Schmitt 2016 [review], Buss 2016 [review], Buss and Schmitt 2019 [review]). Reproductive capability, which can be measured using fertility and fecundity, has been associated with several estimable features. One feature is the presence of indications of reached sexual maturity. Thus, as expected, men show a preference for female-typical secondary sexual features that develop with puberty. These include the growth of breast tissue (Javed and Lteif 2013, Havlíček et al. 2015), the development of female-specific facial structures (Cunningham 1986, Johnston and Franklin 1993, Cunningham et al. 1995, Perrett et al. 1998, Verdonck et al. 1999, Penton-Voak and Perrett 2000(a) [review], Probst et al. 2016), and the uniquely-female pattern of gluteal-femoral fat deposition (Karastergiou et al. 2012, White et al. 2014) that results in a lower waist-to-hip ratio (Valentine and Li 2012 [review]). Another feature associated with reproductive capability is age, with younger women being more fertile and fecund than older women (Frank et al. 1994). Thus, we would also expect men to be attracted to women who demonstrate features associated with youthfulness. Indeed, men do show a preference for women with more neotenous features, including large eyes, small noses, and full lips (Cunningham 1986, Buss 1989, Jones and Hill 1993, Jones et al. 1995, Cunningham et al. 1995, Collins and Missing 2003, Walter et al. 2020 [cross-cultural]) and with a lesser degree of body and facial hair (Ferrante 1988, Cibula et al. 2000). Thus, we find that men generally prefer young, sexually mature women.

Some researchers have proposed the existence of female ornaments that have been primarily shaped by intersexual selection and the need to attract male mates. Their reasoning is that females, needing to attract resource-provisioning males, would signal their reproductive quality through the development of costly ornaments. The ornaments in question are those associated with the female-typical "hourglass" body shape, namely those of large breasts and hips/buttocks, which they propose signal to men their fertility and/or fecundity (e.g., Cant 1981, Gallup 1982, Low et al 1987, Parker 1987 [review], Szalay and Costello 1991, Barber 1995, Marlowe 1998, Miller 1998 [review], Puts 2010 [review], Stewart-Williams and Thomas 2013, Shackelford and Hansen 2015 [review], Sugiyama 2015 [review], Thornhill and Gangestad 2015 [review], Puts 2016 [review]). Proponents of this hypothesis often recognize that dimorphic hips likely originated under the lactation-related demands associated with increased cognition, but they argue that they are now primarily under mate attraction selective pressures. However, permanent breasts, in contrast , seem to have no other reproductive purpose and are particularly unique – permanently enlarging with puberty instead of temporarily with lactation, as in other primates – and thus most likely evolved primarily under mate attraction pressures. The potential for their having evolved under intrasexual selective pressures have been dismissed since breasts "do not increase fighting ability" and thus "do not appear designed for contest competition" (Puts 2010 [review], see also Puts 2016 [review]). Putting aside the fact that intrasexual competition in women is predominantly social, not physical, and thus the related pressures would not likely have resulted in weaponized physical characteristics, there are other concerns with this hypothesis, the foundations of which have been touched on above and will be elaborated on below.

One concern is that it presumes that females would need to attract males in a female choice system. Of course, it is possible that humans have not always been a female choice system. Perhaps at some point after our divergence from other primates 5-8 million years ago, we shifted to a male mate choice system, one with selective pressures strong enough to select for female ornaments. However, if a shift did occur, there is no evidence of it in the fossil record, suggesting that its effects would not likely have been particularly substantial. Further, it has since reversed, at least to such a degree that human society shows universal behavioral trends of a female mate choice system. Finally, this kind of shift is unprecedented; the majority of species on earth are female mate choice systems with no evidence of fluctuation within this kind of time span. Thus, while such a shift is possible, it is unlikely.

However, assuming that females did need to attract males, the reason that is often given – that they relied on males to provide resources – is also questionable. While the concept of a nuclear family dependent upon a single resource-provisioning male may be common in modern Western societies, this is a relatively new and local phenomenon, neither normal across cultures nor in our evolutionary history. Adult male-female resource-provisioning is absent in other primates (Jaeggi and Gurven 2013 [review]); instead, females compete intensely with other females for resources (Campbell 2013 [review], Stockley and Campbell 2013 [review], Archer 2019 [review]), a pattern that persists in modern humans (Campbell 2013 [review], Stockley and Campbell 2013 [review], Archer 2019 [review]). Additionally, our evolutionary history indicates a strong reliance on cooperative breeding support from non-reproductive female family members, not males (Hrdy 2007 [review], Fernandez-Duque et al. 2009 [review], Kramer and Russell 2014 [review], 2015 [review], Schacht and Kramer 2019 [review, cross-cultural]), a pattern powerful enough to persist in modern society and result in the dominant cross-cultural social system of an intergenerational group of relatives engaging in allomaternal care (Kennedy 2003, Hrdy 2007 [review], Schacht and Kramer 2019 [review, cross-cultural]). Its importance may be evidenced by current data that shows that children who grow up with a grandparent instead of a father are as successful, and often *more* successful, than those who grow up with a father (DeLeire and Kalil 2002). Thus, while it is of no doubt that resource acquisition has been one of the highest priorities for *Homo* females, the universal and historical pattern of non-reliance on males for resource acquisition would suggest that any selective pressures to attract men for resource-provisioning specifically would not likely have been strong enough to result in the emergence of costly female ornaments.

This hypothesis also assumes that the presence of attraction toward a trait is an indication of some adaptive significance of that trait. However, attraction is not necessarily static; indeed, plasticity in attraction parameters would be highly adaptive in fluctuating environments, allowing individuals to adopt preferences for behaviors and physical conditions based on the degree that those characteristics would be fit in that environment. Sexual conditioning, or the process in which standards of attraction are conditioned through experiences at key points in development, is a well-documented phenomenon, particularly in mammals (e.g., Crowley et al. 1973, Silberberg and Adler 1974, Zahorik and Johnston 1976, Johnston et al. 1978, Domjan et al. 1986, Pfaus and Wilkins 1995, Paredes and Alonso 1997, Kippin et al. 1998, Kippin and Pfaus 2001, Pfaus et al. 2013). It is also well-documented in humans, developing not only during key phases in development but in response to exposure to specific stimuli under certain conditions (Pfaus et al. 2001 [review], Pfaus et al. 2003 [review]). Thus, attraction preferences vary substantially at the cultural level (e.g., Tovée et al. 2006, Salska et al. 2008, Swami 2015) and the individual level, even shifting in response to laboratory experiments (e.g., Letourneau and O'Donohue 1997, Hoffman et al. 2004, Brom et al. 2014).

One way to determine the degree to which a characteristic has emerged under evolutionary pressures is to examine of the universality of it – in this case, the preference for large breasts and hips. Unsurprisingly, most of the research supporting this claim has been done in modern, heavily Western-influenced cultures in which this is the standard of attractive female forms. However, there is significant variation in preferences for these features, one that appears not only across cultures but within the same culture over relatively short periods of time (Douglas and Shepard 1998, Swami and Tovée 2005, Swami et al. 2010, Dixson et al. 2010, 2011(a)(b)). In fact, as would be predicted under a sexual conditioning model of attraction, the emergence of associations between a trait and a preference for that trait in human cultures seems related to culturally- and socially-defined factors of optimality for that specific region, including age of reproduction and indications of potential offspring quality (Grammer et al. 2003 [review]). Historical evidence regarding preferences for female body shape indicate that standards of female attractiveness is most strongly influenced by factors that affect the relative competition for resources, such as climate, food supply, and the value that is placed on women's work, and social dynamics, such as the relative dominance of women and the likelihood of negative consequences for adolescent girls expressing their sexuality (Anderson et al. 1992 [review], Smuts 1992).

Proponents of the female ornaments hypothesis have frequently argued that while the sexually-dimorphic nature of the female hip may have initially evolved in response to motherhood-related demands, it is now under direct mate selection pressures in the form of runaway sexual selection. However, there is little evidence for the presence of additional mate selection pressures. The sexually dimorphic aspects of the female pelvis are directly tied to pregnancy-, childbirth-, and childcare-related pressures (Fischer and Mitteroecker 2017), not with would-be expected pelvic widening, which has been dimorphically stable throughout hominin evolution (Gruss and Schmitt 2015 [review]). Instead, the changes that have occurred are primarily internal and are related specifically to the obstetric demands of pregnancy and childbirth (Fischer and Mitteroecker 2017), namely those associated with rotational birth. Further, these dimorphic changes only began emerging in the fossil record approximately 500,000 years ago, coinciding with substantially decreased overall sexual dimorphism and the stabilization of secondary altriciality (Gruss and Schmitt 2015 [review]). And while it is possible that the sexually dimorphic pattern of gluteal-femoral fat (GFF) deposition is currently under male selection pressures, there is no reason to suspect that the lactation-related demands would be any less significant than they have been in the past, particularly given the current degree of social complexity. Any association that has developed between these dimorphisms and male mate preferences seem to have emerged secondarily. Indeed, cross-cultural evidence indicates that a low waist-to-hip ratio, regardless of BMI, is nearly universally recognized as attractive, suggesting at least some association has been formed with the male preference. However, such an association would be expected – GFF deposition is associated with lactation and thus emerges at puberty, and men show a universal preference for all puberty-associated shifts as they indicate sexual maturity (Singh 1993(a)(b), 1995(a), Singh and Young 1995, Rilling et al. 2009, Singh et al. 2010 [cross-cultural], Bovet and Raymond 2015). Thus, there is little reason to invoke intersexual sexual selection as a primary driving force for either the emergence or maintenance of sexually dimorphic hips.

The primary focus for the female ornaments hypothesis is currently on the evolution of permanent breasts in humans. Proponents of the hypothesis that breasts evolved as a signal of mate attraction have put forth several mechanisms as potential explanations. Some of the earliest hypotheses proposed that breasts evolved as permanent estrus displays, claiming that the temporary fertility displays of swollen genitalia found in other primates would be difficult to maintain, and thus selected against, in a bipedal species (Gallup 1982, Szalay and Costello 1991, Stanyon and Bigoni 2014). This hypothesis was initially proposed when it was thought that humans were the only primate species without estrus displays, but research into the evolution of concealed ovulation no longer supports this idea (see below for more on concealed ovulation). The most commonly proposed mechanism today is that large breasts are an indication of reproductive value, either that of lactation success or overall fertility, and that it may or may not be under runaway sexual selection (e.g., Cant 1981, Low et al 1987, Barber 1995, Marlowe 1998, Miller 1998 [review], Puts 2010 [review], Thornhill and Gangestad 2015 [review], Puts 2016 [review]).

However, there is little evidence to support this. First, while there is a universal, cross-cultural preference for a low waist-to-hip ratio, there is no similar preference for breasts of any size. This suggests that, if there is an adaptive significance to breast size, it has yet to be tied in any substantial way to male preferences. It also suggests that male preferences for breasts are relatively weak and thus would be unlikely to drive any type of runaway sexual selection. Second, there does not appear to be an adaptive significance to breast size, measured either by lactation success or by general health or fitness outcomes. Lactation success is associated with glandular and lobular tissue, not the fatty tissue that is responsible for breast size, making lactation success independent of breast size. This finding has been replicated using measurements associated with pregnant, non-pregnant, lactating, and non-lactating women, and for measures of either milk quality or capacity (Geddes 2007 [review], Sriraman 2016 [review], Żelaźniewicz and Pawlowski 2019). Further, larger breasts are associated with numerous negative health and reproductive outcomes, some of which independently influence lactation success. Breast size is correlated with BMI and breast asymmetry, both of which are linked to poor lactation success (BMI – Mangel et al. 2019, Asymmetry – Arbour and Kessler 2013) and breast cancer (Size – Jansen et al. 2014 [review], Asymmetry – Scutt et al. 2006). Breast size is also associated with increased risk of reproductive disorders, infectious diseases (Kościński et al. 2020), and type 2 diabetes (Ray et al. 2008), and the correlated increased risk of asymmetry is also associated with a poor immune system (Locke and Arnocky 2021). Thus, if breast size was under sexual selection pressures, it would be strongly offset by those associated with fitness, and given the importance of lactation inhuman history, it would be highly unlikely for runaway sexual selection to develop.

In contrast to the hypothesis that having large breasts evolved to attract mates, there is at least one other explanation as to why having permanently enlarged (if not large) breasts may have evolved: that it is a by-product of gluteal-femoral fat deposition (Mascia-Lees 1986) that had adaptive qualities when in a location that aided in the functional demands of breast feeding when hairless. In non-human primates, offspring cling to their mothers' chest hair while nursing (Anderson 1988); however, hairlessness in hominin began as early as 6 Mya (Sutou 2012) and was already established in *Homo* (Jablonski 2004 [review]). Therefore, when the demands for lactation increased in *Homo* and selected for GFF deposition, it is likely that this acted non-selectively, increasing this unique kind of adipose tissue deposition anywhere that responds to the growth of estrogen, which includes breast tissue (Breast – Javed and Lteif 2013 [review]). This extra breast tissue would increase the degree of flexibility in nursing positions when hairless. Indeed, modern children are often nursed while being carried on their mother's hips, enabled by fatty breast tissue that becomes flaccid while lactating, and is particularly visible in cultures that lack breastfeeding taboos, including indigenous ones (Anderson 1988, Liamputton 2011 [review]). Thus, larger fatty breasts may have emerged primarily as a biproduct with the demands for GFF deposition that, when placed in breast tissue, aided in the functional demands of breastfeeding.

Instead of emerging in response to the need for females to attract resource-provisioning males, it is most likely that the "hourglass" figure associated with the female-typical body shape emerged in response to the selective pressures of other reproduction-related demands. As these features are associated with sexual maturity, it would not be surprising for them to be identified as attractive features since they signal reproductive capability. Shifts in the degree of this preference would likely emerge in response to local cultural, social, and environmental needs. In modern Western societies and with the emergence of socioeconomic systems that disrupt intergenerational allomaternal care patterns, the need to attract resources through male-provisioning may emerge, and large breasts and hips may emerge as a culturally-specific mate attraction signal. Thus, the dominance of the Western preference for large breasts/hips may have emerged through specific, unique cultural factors. Several Western practices during the 20th century have had direct impacts on breast-feeding practices – specifically those of increases in hospital births, the practice of twilight sleep, and the introduction of commercially-available infant formula (Trevathan 2010 [review], Wolf 2012). These have had direct impacts on the degree to which breastfeeding is socially acceptable which, in combination with the patterns associated with the emergence sexual preferences through sexual conditioning, may have resulted in a dominant pattern of attraction to breasts.

2.2.3.2.2 MALE REPRODUCTIVE STRATEGIES

In a female mate choice system, males can engage in different mating strategies to optimize their fitness. Mating strategies are often reflective of life history strategies and can be categorized as either investing primarily in parenting behavior (slow) or mating (fast) behavior (Figueredo et al. 2006, Del Giudice 2018). The precise manifestation of these strategies would depend upon the various biological, environmental, and social conditions in which he finds himself as well as the specific direct and indirect benefits that the females might prefer. In humans specifically, they can be conceptualized as existing along a continuum of behaviors associated with the primary pursuit of long-term relationships or short-term relationships, respectively.

There are patterns of preferences and behaviors that emerge at either end of the parenting-mating effort continuum. One pattern is the differences is in mate preferences. Men who prioritize mating effort value physical attractiveness (Valentine and Li 2012 [review]) whereas men who prioritize parenting effort value sexual inexperience and conservativeness (Buss 1989, Buss and Schmitt 1993, Buss 1994, 2000, 2006, Valentine and Li 2012 [review], Buss 2018 [review], Buss and Schmitt 2019 [review]). Another pattern is the difference is in their self-advertisement behavior. Those who prioritize mating effort (as opposed to parenting effort) attract women by displaying resource generosity (as opposed to long-term acquisition capability), engaging in dominance behaviors (as opposed to showing kindness and understanding), and derogating their competitors' lack of dominance (as opposed to their lack of relationship commitment) (Schmitt and Buss 1996). A final pattern is the differences is in how they maintain, or avoid, long-term relationships. Men who prioritize mating effort will use a variety of relationship avoidance behaviors including neglect, avoidance, emotional distancing, and interpersonal violence (Jonason and Buss 2012). In contrast, men who prioritize parenting effort use behaviors associated with mate-guarding and sexual jealousy (Buss 1989, Buss and Schmitt 1993, Buss 1994, 2000, 2006, Valentine and Li 2012 [review], Buss 2018 [review], Buss and Schmitt 2019 [review]).

Evidence suggests that the effect that testosterone has on dominance behaviors is reflected in mating behaviors. The patterns of behaviors associated with parenting effort and mating effort align predictably with testosterone-mediated submissive-dominant behaviors, such that high testosterone is associated with dominance (pro- and antisocial) and an investment in mating effort while low testosterone is associated with submissiveness and an investment in parenting effort (Booth and Dabbs 1993, Mazur et al. 1994, Bogaert and Fisher 1995, Storey et al. 2000, Fleming et al. 2002, Gray et al. 2002, McIntyre et al. 2006, Peters et al. 2008, Alvergne et al. 2009, Fisher et al. 2009, Muller et al. 2009, Edelstein et al. 2011, Pollet et al. 2011, Van Anders et al. 2012, Weisman et al. 2014, Puts et al. 2015, Das and Sawin 2016, Gray et al. 2017, Polo et al. 2019, Klimas et al. 2019). These mating strategies seem to be an adaptive response to early biosocial developmental cues that direct the individual toward fast strategies that would be adaptive in an unpredictable and dangerous environment (Del Giudice 2018).

The mating behavior indicative of the Dark personalities suggest that they might represent specialized fast strategies (Jonason et al. 2009, 2010, Jonason et al. 2016), particularly psychopathy (Jonason et al. 2010). In general, all three personalities are associated with tendencies toward high mating effort (Jonason et al. 2011, Furnham et al. 2013 [review], Westhead and Egan 2015, Jonason et al. 2017), though with some nuances: Machiavellianism is also associated with strategic long-term relationships, and psychopathy is associated with highly impulsive mating behavior (Furnham et al. 2013 [review]). Further, the Dark personalities tend to exhibit particularly low standards for mates, which may be a way of ensuring access to a sexual partner regardless of the environmental or social condition (Jonason et al. 2011), and their tendency to assortatively mate (Jonason et al. 2011, Jonason et al. 2015, Lyons and Blanchard 2016), a tendency particularly consistent for psychopaths (Jonason et al. 2011), may emerge from preferences for partners with similar life history strategies. That this specific preference emerges for long-term partners, when they show a general aversion to long-term relationships, is particularly notable.

As with dominance behaviors, testosterone modulates parenting-mating behavior bidirectionally and in real-time. Increased testosterone leads to a decrease in parental behaviors, and decreased parental behaviors leads to an increase in testosterone (Mazur and Michalek 1998, Archer 2006, Kuzawa et al. 2009, Alvergne et al. 2009, Gettler et al. 2011(b), Puts et al. 2015, Roney and Gettler 2015). This is true even for non-fathers with low testosterone, who respond in more caring ways to infant cries (Fleming et al. 2002). Fatherhood in general is associated with lower testosterone (Kuzawa et al. 2009, Perini et al. 2012, Gettler et al. 2015, Gray et al. 2017), an effect that is stronger for those who provide direct care and interact often with their children (Muller et al. 2009, Gettler et al. 2011(a)). The relationship between fatherhood and testosterone begins with pregnancy: expectant fathers experience a drop in testosterone throughout the pregnancy (Berg and Wynne-Edwards 2001, Saxbe et al. 2017), and the strength of that decline is associated with parenting behaviors after birth (Saxbe et al. 2017). It should be noted that there are other hormonal shifts associated with parenting behaviors in fathers as well (cortisol – Berg and Wynne-Edwards 2001, Gettler et al. 2011; estradiol – Berg and Wynne-Edwards 2001, Gettler et al. 2015; oxytocin, prolactin – Gettler et al. 2015).

Sexually coercive behavior appears in both human and non-human species as a predominantly male behavior. Its emergence, including how it develops and whether it has adaptive significance, has long been explored as a means to understand, and prevent, this behavior (e.g., Malamuth 1998 [review], Archer and Vaughan 2001 [review], Muller and

Wrangham 2009 [review], Ward and Beech 2016 [review]). Evidence to date suggests that sexually coercive behavior in humans emerges through various developmental pathways and under the influence of several different biosocial factors, and when it emerges, it can often be explained as an adaptive behavior given that specific biosocial context.

One way that sexual coercion may emerge is as a fast mating strategy (Thornhill 2004, Abbey et al. 2006, Gladden et al. 2008, Camilleri and Stiver 2014 [review]). Indeed, it often appears in men who have marked tendencies toward an unrestricted sociosexuality, an extensive sexual history, and strong preferences for both high partner variety and casual, impersonal sex (Kanin 1985, Malamuth et al. 1991, 1995, Lalumière and Quinsey 1996, Lalumière et al. 1996, Malamuth 1998 [review], Abbey et al. 2006, McKibbin et al. 2008 [review], Westerlund et al. 2010, Camilleri and Stiver 2014 [review]). It seems to emerge from a combination of biosocial developmental factors similar to those associated with high mating effort, though with some additional elements (Ellis 1998 [review], Westerlund et al. 2010, Camilleri 2012 [review], Ciardha and Ward 2013 [review], Tharp et al. 2013 [review], Camilleri and Stiver 2014 [review], Långström et al. 2015 [cross-cultural, longitudinal]). Identified developmental factors include genetics (20-25% – Westerlund et al. 2010, 51% – Barnes et al. 2013, 40% – Långström et al. 2015); unstable and traumatic childhoods (Malamuth et al. 1991, 1995, Malamuth 1998, Abbey et al. 2006, Ward and Beech 2016), particularly those that involved hypersexual social influences at a young age (Malamuth et al. 1991, 1995, Malamuth 1998, Abbey et al. 2006, Yost and Zurbriggen 2006); and social deviance and criminal behavior in adolescence (Malamuth 1998, Abbey et al. 2006). Interestingly, sexual coercive tendencies are also identifiable from face-traits (Pavlović et al. 2019). Perhaps unexpectedly, most evidence suggests that testosterone does not seem uniquely higher in sexual coercers when compared to those with a high mating effort or with general tendencies toward violence (Rada et al. 1983, 1976, Dabbs et al. 1995, Giotakos et al. 2005; but see Giotakos et al. 2004). Testosterone may, however, be a stronger correlate of sexual activity in sex offenders than in others (Aromäki et al. 2002), and a hyperactive hypothalamic-pituitary-gonadal (HPG) axis may be responsible for coercive behavior that emerges in response to tendencies toward novelty seeking (Giotakos et al. 2004).

The fairly strong relationship between sexual coercion and the Dark Triad is further evidence that both might represent specialized fast mating strategies (Reise and Wright 1996, Yost and Zurbriggen 2006, Mouilso and Calhoun 2012, Lee et al. 2013, Figueredo et al. 2015, Westhead and Egan 2015, Jonason et al. 2017, Koehn et al. 2019 [review], Jonason and Sherman 2020, Zeigler-Hill et al. 2016). This relationship is likely enabled by the Dark Triad's general reliance on exploitative social strategies and overall lack of empathy, which seems to have a buffering effect against sexual violence (Abbey et al. 2006). Both sexual coercers and Dark personalities show an acceptance of female-directed dominating and aggressive behavior, particularly in response to sexual rejection among coercers (Malamuth 1998; Coercers – Malamuth 1998, Abbey et al. 2006; Dark Triad – Schmitt et al. 2017, Brewer and Abell 2015). However, where the Dark personalities are associated with increased violence in general, coercers are associated only with increased sexual violence (Malamuth 1981, 1986, Malamuth et al. 1986, Rice et al. 1990, Prentky and Knight 1991, Lalumière and Quinsey 1996, Hare 1996, Brown and Forth 1997, Lisak and Roth 1988, Paulhus and Williams 2002, Camilleri et al. 2009, Woodworth et al. 2013, Lee et al. 2013, Brown et al. 2015, Westhead and Egan 2015). The relationship between sexual coercion and the Dark Triad appears strongest with psychopathy and weakest with narcissism (Psychopathy specific – Rice et al. 1990, Harris et al. 1991, Prentky and Knight 1991, Hare 1996, Serin 1996, Brown and Forth 1997, Hemphill et al. 1998, Camilleri et al. 2009, Woodworth et al. 2013, Brown et al. 2015; Narcissism specific – Schmitt et al. 2017).

Another way that sexual coercion may emerge is as a slow mating strategy. Engaging in a slow mating strategy carries the risk of cuckoldry, and sexual coercion may help to mitigate this risk. Men who invest in parenting behavior and whose partners are unfaithful not only miss other reproductive opportunities but also risk contributing extensive resources into offspring that are not theirs. Thus, men in long-term relationships tend to engage in a variety of behaviors that are associated with minimizing his risk of paternal uncertainty, with the types of behaviors shifting in response to the risk (Buss 1988, Thornhill and Palmer 2001 [review], Shackelford 2003 [review], Goetz et al. 2008(a) [review], McKibbin et al. 2008 [review], Kaighobadi et al. 2009 [review], Goetz 2010 [review], Buss and Duntley 2011 [review], Shackelford et al. 2014 [review], Albert and Arnocky 2016 [review], Buss 2016 [review], Shackelford et al. 2016 [review], James and Shackelford 2019 [review]). These behaviors often manifest as controlling his partner's access to other men, and these behaviors are thus often referred to as mate retention tactics (MRTs). These tactics employ varying forms of intimate partner violence (IPV), most notably sexual violence (SIPV), and may include, but are not limited to, stalking, social isolation, threats, physical violence, and sexual coercion. Sexual coercion in long-term relationships often includes emotional or relational manipulation as well as physical force (Shackelford and Goetz 2004), and it seems to be employed strategically when the likelihood of cuckoldry is exceptionally high. It has been proposed that it may be a form of sperm competition; by forcing copulation when the chances are high of another male's semen being present, a man may be able to displace that semen and decrease his chances of cuckoldry (Gallup et al. 2003, Gallup and Burch 2006, Gallup et al. 2006).

Available evidence supports this hypothesis: increases in perceived risk of cuckoldry is associated with escalating mate retention tactics and in-pair sexual violence. This includes low-risk factors, such as partner attractiveness (Goetz et al. 2005), time since last copulation (Camilleri and Quinsey 2009, Barbaro et al. 2019), and relative time spent apart (Shackelford et al. 2002, Shackelford et al. 2007); moderate risk factors, such perceived risk of infidelity (Camilleri 2004, Goetz and Shackelford 2006, Barbaro et al. 2015, Arnocky et al. 2015); and strong risk factors, such as actual cues/evidence of infidelity (Camilleri and Quinsey 2009, Burch and Gallup 2020) (for combinations of these factors – Pham and Shackelford 2013, Barbaro et al. 2019). As cuckoldry risk increases, so does the severity of male partner responses, and in a near exponential way (Burch and Gallup 2020). At lower levels, men increase their mate retention (Goetz et al. 2005, Goetz and Shackelford 2006, Barbaro et al. 2019) and guarding behaviors (Burch and Gallup 2020). At milder levels, men increase their copulatory urgency and eagerness (Shackelford et al. 2002, Shackelford et al. 2007, Pham and Shackelford 2013) as well as their anger and distress at sexual rejection (Shackelford et al. 2007, Pham and Shackelford 2013). At moderate levels, men increase their sperm competition behaviors ,which include decreasing their copulation duration (Barbaro et al. 2015), adjusting ejaculate composition to include more sperm (Baker and Bellis 1993), and using sexual techniques that increase the likelihood of semen-displacement (Gallup et al. 2003, Goetz et al. 2005). At high levels, men will increase their sexual persistence behaviors (Shackelford et al. 2007) which include sexual coaxing (Camilleri and Quinsey 2009) and sexual coercion, measured both by their reported likelihood of coercion (Camilleri 2004, Camilleri and Quinsey 2009) and their actual likelihood of coercion (Goetz and Shackelford 2006, Camilleri and Quinsey 2009, Arnocky et al. 2015, Burch and Gallup 2020), including forcible rape (Camilleri and Quinsey 2009, Burch and Gallup 2020).

Research into domestic violence provides additional evidence for a link between SIPV and cuckoldry risk. One piece of evidence is that the relationship between cuckoldry risk and IPV seems restricted to sexual violence – not extending into physical violence (Camilleri and Quinsey 2009, Burch and Gallup 2020) – with one exception. In homes of men with documented histories of domestic violence, men report switching from sexual violence to physical violence when his partner becomes pregnant, specifically using methods seemingly targeted at pregnancy termination (Burch and Gallup 2020). Additionally, this trend seems to extend into a post-partum effect: in these homes, children who were unrelated to or who did not resemble the man suffered significantly more violence than other children. They also suffered more violence with reports of increased feelings of sexual jealousy (Burch and Gallup 2020). Finally, male sexual proprietariness, in which an intimate partner feels ownership over his partner's sexual behavior, is strongly associated spousal homicide (Daly and Wilson 1988, Serran and Firestone 2004).

The likelihood of engaging in mate retention tactics and in-pair sexual violence is mediated several factors. One factor is the role of role of neurotransmitters. For passive-avoidant styles of sexual offending, which may be more common in SIPV scenarios, low turnover of both serotonin and dopamine has been associated with sexual coercion (Giotakos et al. 2004). Another factor is the interplay of an individual's feelings of sexual jealousy and their attachment style. Sexual jealousy is one of the strongest predictive factors for SIPV (Snead and Babcock 2019, Burch and Gallup 2020) and post-breakup stalking (Duntley and Buss 2012), and it is associated with increased perceived cuckoldry risk (Camilleri 2004). However, this predictive relationship is mediated by the individual's attachment style which can be characterized by the intersection of relationship avoidance and relationship anxiety (Brennan et al. 1998). High attachment anxiety is associated with chronic jealousy (Sharpsteen and Kirkpatrick 1997) and a hypervigilance to relational rejection and abandonment (Mikulincer and Shaver 2007). It is also associated with increased sexual motivation (Davis et al. 2004), perceived risk of cuckoldry (Kruger et al. 2013), and their engagement in MRT and SIPV, specifically sexual coercion (Barbaro et al. 2018). Further, the likelihood of coercion increases with increased scores on the attachment avoidance scale (Barbaro et al. 2018). Attachment styles may also mediate the emergence of sexual coercion for men with Dark personalities who are in relationships. Indeed, the use of MRT and IPV in response to cuckoldry risk has been identified for these men (Kardum et al. 2019), and each of the Dark personalities have been associated with varying degrees of high attachment anxiety and/or avoidance (Mack et al. 2011, Conradi et al. 2016, Christian et al. 2017, Nickisch et al. 2020).

Another way that sexual coercion may emerge is as a reproductive strategy for males who otherwise lack access to females. This pattern is common in other species, and it is characterized by low-status males resorting to sexual coercion when other attempts to mate have failed (Thornhill and Thornhill 1983 [review], Figueredo and McCloskey 1993, Figueredo et al. 2000). Commonly known as the mate-deprivation hypothesis, support for this hypothesis has primarily come from evidence that indicates that low socioeconomic status is associated with increased sexual coercion (e.g., Thornhill and Thornhill 1983 [review], Figueredo and McCloskey 1993, Kalichman et al. 1998, Figueredo et al. 2000). However, low socioeconomic status is also associated with increased crime and violence in general, trends that correlate with increased sexual violence, suggesting no evidence of an independent relationship. In fact, the association between low socioeconomic status, criminality, and sexual violence provides further evidence that sexual coercion may be a fast mating strategy for males who develop under the influence of specific socioenvironmental cues. However, support for this hypothesis has also come from research that indicates a correlated relationship between divorce rates and rape rates in the United States (Starks and Blackie 2000). Reasoning behind this research comes from three lines of evidence – (1) men tend to have more variable reproductive success than women, (2) men tend to remarry more than women, and (3) men tend to prefer younger, more reproductively capable, women. Thus, the reasoning is that higher divorce rates would indicate an increased monopolization of reproductively capable women, and men who are unable to compete for these women would be more likely to resort to rape. However, there are several problems with this reasoning. One problem is the assumption that the divorce rate is an appropriate proxy for the monopolization of younger women; instead, it should be the remarriage rate, unless the assumption is that divorce and remarriage happen nearly simultaneously. A second problem is that marriage is an appropriate proxy for sexual access; not only are sex-less marriages common, but sex outside of marriage is as well. Undoubtedly, many of these unmarried men have satisfying sex lives, particularly given the general propensity of men to avoid long-term relationships in the first place. A third problem is that it assumes that these reported rapes must come from unmarried men – that married men do not rape. As illustrated, in-partner, and in-marriage, rape is common. A fourth problem is that it assumes that unmarried men would rather rape women than engage in consensual sexual relationships with older unmarried women. While it may be that some men feel that way, I doubt they would comprise the majority of these men. Thus, I suspect that the correlation between divorce rates and rape rates is due to a third underlying factor: increased social instability. Indeed, thus far, direct tests of the mate-deprivation hypothesis indicate no relationship between sexually coercive tendencies and a lack of sexual access (Kanin 1985, Malamuth et al. 1991, Lalumière et al. 1996, Camilleri 2012 [review], Camilleri and Stiver 2014 [review]).

Finally, sexual coercion may emerge as a context-dependent strategy that is employed when the benefits outweigh the costs (Shields and Shields 1983 [review], Thornhill and Palmer 2001 [review], Goetz et al. 2010 [review], Jones 1999 [review], Gladden et al. 2008 [review], McKibbin et al. 2008 [review], Camilleri and Stiver 2014 [review], Ward and Beech 2016 [review]). The contextual factors taken into consideration in this cost-benefit analysis should include any immediate, tangible consequences (e.g., when a woman is inebriated – Devries et al. 2014 [review]) as well as consequences imposed by larger social influences. The acceptability of sexual coercion at the broader social level would, by definition, influence the degree to which that behavior would be considered antisocial. Thus, we may find that, in a society in which marital rape is condoned, committed men might be inclined to use rape as a mate retention tactic at relatively lower risk levels for paternal uncertainty. The social contexts would be largely influenced by the general social structure, and patriarchal social structures, having likely evolved under conditions of male consolidation of resources and decreased female-female alliances (Smuts 1995), may create an environment in which sexual coercive behaviors become socially acceptable and thus more prevalent. A broad approach to understanding context-dependent coercive strategies may help explain the prevalence of war-time rape. An environment with a high mortality rate would predict a shift in behavior toward a fast mating strategy, and an environment with a chaotic social structure would be unlikely to enforce social norms (Gottschall 2004 [review]).

This hypothesis is supported by the available evidence that sexual coercion is influenced by social factors that extend beyond early developmental experiences. In addition to the immediate familial/social interactions that influence developmental life histories strategies, broad, socially-influenced beliefs and attitudes are mediating factors (Tharp et al. 2013 [review]). For both those who are convicted of rape and who self-report a high likelihood of engaging in rape, sexual coercion can be predicted by the presence of attitudes associated with hostile sexism and masculinity (Malamuth et al. 1991, Malamuth et al. 1995), of their acceptance of rape myths (Malamuth 1981, Malamuth et al. 1991, Begany and Milburn 2002), and of their acceptance of violence, specifically when this acceptance is explicit (Blake and Gannon 2010) and when directed toward women (Malamuth et al. 1986, Malamuth et al. 1991, Begany and Milburn 2002), an effect that holds true even when the men are partnered (Camilleri 2004). The presence of beliefs associated with hostile sexism is also a predictor of Dark Triad traits in men and seems to account, to some degree, for the population-wide gender bias of the Dark personalities (Gluck et al. 2020).

In sum, it is likely that there are two general paths for male reproductive behavior. Evolutionary pressures toward optimal fitness have allowed potential influencing factors to act at various life stages. The overall tendence toward a relatively short-term relationship in males is heavily influenced by prenatal factors that also guide reproductive effort into either short-term or long-term relationships. Other biological factors, like plasticity in imprinting and conditioning potential, has allowed these two paths to be mediated by developmental factors that cue an individual to the kind of environment in which they are entering and then influence the adoption of behaviors likely to be most adaptive. The specific early social and environmental then overlays patterns, influencing their attitudes toward social attachment and sociosexuality; harshness and unpredictability seem to influence the development of social traits most strongly, particularly spectrums of pro/antisociality, honesty/deception, and empathy/callousness. Social norms further moderate trends, defining specific behaviors as pro/antisocial that individuals internalize and act upon. Finally, their behavior toward their mate and her offspring is likely to be affected by the degree to which they have invested in those offspring and his perceived cuckoldry risk. Thus, we see male reproductive behavior appear in two different forms: a short-term strategy that varies from a general fear of commitment at one end to a serial rapist at the other, and a long-term strategy that ranges from a committed and loving father and husband to a controlling and abusive partner.

Thus, sexual coercive behavior in humans represents a multifaceted problem. It develops from a variety of contributing factors at different developmental stages, and it manifests as an array of methods, motivations, individuals, and contexts. Thus, a multilayered and comprehensive approach is necessary to understand and mitigate it.

2.3 HUMAN FERTILITY

Thus far, we have addressed several factors that influence several types of mating dynamics, specifically those associated with life history dynamics, mate choice preferences, and reproductive strategies. However, engaging in mating behavior is only one aspect of reproduction. Another is the timing of that mating behavior and how it coincides with the chances of fertilization. In many species, fertility, or the time in which fertilization is possible, is influenced by several factors, including those both internal and external, and it is not always clear when a female might be fertile. Thus, the factors that control ovulation, signal fertility, and promote sexual behavior are critical to understanding mammalian reproductive behavior and result in the potential for unique dynamics.

2.3.1 The Evolution of Concealed Ovulation

In most mammalian species, reproduction is controlled through the female estrous cycle. These cycles are associated with alternating periods of sexual receptivity – “estrus” or “heat” – and non-receptivity. Estrus is often cued by external means and frequently manifests as a seasonal behavior, and it is only during estrus that copulation can occur. When copulation occurs, it can induce ovulation and thus conception. If conception does not occur, at the end of an infertile estrous cycle, the lining of the uterine wall (upper functionalis layer of the endometrium), having developed in preparation for pregnancy, is reabsorbed by their body.

In other mammalian species, females experience menstrual cycles. Occurring primarily in primates and bats (but also in a shrew and a spiny mouse species), menstrual cycles differ from estrous cycles in two primary ways. The first is that ovulation is not induced; it occurs spontaneously in response to cyclical hormonal changes. The second way is that the lining of the uterine wall is shed instead of reabsorbed in a process known as known as menses, or menstruation. Menses seems to be an adaptive response to demands of early fetal cognitive growth, allowing for the selection (or rejection, in the case of menses) of viable embryos (Brosens et al. 2014, Macklon and Brosens 2014). It also seems to be a response to particularly demanding immunoregulatory needs. While all pregnancies require careful maternal immunoregulations, some species have particularly aggressive degrees of fetal-uterine implantation which menses seems to help resolve (*Emera et al. 2012, Alvergne and Tabor 2018 [review], Thomas 2019*).

Though estrous and menstrual cycles differ physiologically, many menstrual females also undergo estrus. They show distinct behavioral and physiological changes associated with sexual receptivity and peak fertility. For many menstrual female species with estrus periods, copulation only occurs during estrus.

However, peak fertility is masked in some primate species. This phenomenon, known as concealed ovulation or concealed fertility, is made possible by the decoupling of estrus signals from hormonal control. Found in several species of haplorrhine primates, including those from monogamous, polyandrous, and polygynous mating systems (Sillén-Tullberg and Møller 1993, Garcia et al. 2021 [review]), concealed ovulation allows females to engage in sexual behavior throughout their cycles. This ability is a crucial component to complex primate social systems as it allows females to use sexual behavior to forge relationships and alliances (Wallen and Zehr 2004). Still, even with masked fertility, ovulation-associated peaks in sexual behavior have been documented in several of these species (Michael and Zumpe 1970, Wallen et al. 1984, Garcia et al. 2021 [review]).

Several hypotheses have been proposed to explain concealed ovulation, both its emergence in primate species and any adaptive functions its maintenance may serve. There are varying degrees of support for these hypotheses, and all may contribute in some degree to the emergence or maintenance of concealed fertility in one or more species. Most of these hypotheses propose an origin in sexual conflict and the coevolutionary arms race between the sexes.

The first hypothesis is the infanticide reduction hypothesis, and it proposes that concealed ovulation evolved to decrease the likelihood of infanticide, which is nearly ubiquitous in polygynous mating systems. In polygynous primate groups, alpha males will attempt to control the mating opportunities of fertile females. When a new alpha male gains control, he will kill the offspring of females who he has not mated, thereby ensuring all of the offspring are his and bringing the females back into estrus. Concealed ovulation has been proposed as a counteradaptation to infanticide as it would make it exceedingly difficult for an alpha male to control all of the fertile females. This would allow a female to mate with multiple males who would thereby be less likely to kill her offspring if he were to gain control (Hrdy 1979, Andelman 1987, Heistermann et al. 2001, Munoz 2014 [dissertation]).

This hypothesis is supported by several lines of evidence. One is phylogenetic evidence that indicates concealed ovulation has evolved most often in polygynous mating systems, not monogamous ones, and that monogamy emerges *after* concealed ovulation (Sillén-Tullberg and Møller 1993). Another line of evidence comes from primate behavioral studies. Species with concealed ovulation have less intense male-male competition, and males are less able to monopolize receptive females. Also, in species where infanticide is common, it is both most likely to come from immigrating high-ranking males and most likely defended against by males that the female has mated (Andelman 1987, Heistermann et al. 2001, Fürtbauer et al. 2011). This hypothesis may explain the tendency of pregnant primate females to mate with multiple males, particularly immigrants, until her pregnancy is visible (Andelman 1987). Finally, there are similar trends in humans: for example, one of the greatest risks to a child is the presence of an unrelated male in their home (Smithey 1998, Harris et al. 2007, Archer 2012).

The second hypothesis, the male-investment hypothesis, proposes that concealed ovulation facilitates monogamy (Symons 1979). The reasoning for this hypothesis is that increased sexual receptivity may induce males to provide continual resources and potentially care, particularly if in doing so he is more likely to monopolize the female and increase his certainty her offspring are also his (Symons 1979, Turke 1984, Miller 1998 [review], Slurink 1999 [review], Ramos et al. 2014).

There is mixed evidence for this hypothesis. Most food sharing in primates occurs within kin groups; approximately half of all primate species engage in adult-to infant food sharing, though direct paternal care is relatively rare. It is unlikely to occur unless kin-provisioned resources are inadequate and the father has reasonable certainty that the child is his. Because evidence suggests that adult food sharing evolved secondarily to offspring food sharing, it is possible that a male, already provisioning his potential offspring, may also provision resources to their mother (Jaeggi and Gurven 2013 [review]). This would have most likely evolved in species with particularly high reproductive demands. Indeed, the few primates with alloparental care that includes paternal provisioning – Callitrichids and humans – have offspring that require extensive resources (Fernandez-Duque et al. 2009 [review], Jaeggi and Gurven 2013 [review]), and all are monogamous (Sillén-Tullberg and Møller 1993). It is also possible that male provisioning acts as a signal of mate value in which females selectively mate with males who demonstrate paternal care, enhancing the pair bond; however, adult male-female provisioning is still relatively rare in these species as adult females generally provide their own food (Jaeggi and Gurven 2013 [review]). There is also some human-specific evidence supporting this hypothesis: research conducted on university students in the United States indicated the existence of a relationship between a woman's perception that her partner is less invested in their relationship and her likelihood of initiating sex in non-fertile stages of her cycle (Grebe et al. 2013). However, the strength of any selective pressures associated with this hypothesis is likely mediated by the degree to which a woman is dependent upon her partner for resources, and given the history of cooperative breeding in human evolution, this is unlikely to have played a significant role. Further, not all monogamous primates have concealed ovulation, which suggests at least one other selective pressure at work.

The third proposed hypothesis, the cuckoldry hypothesis, proposes that concealed ovulation evolved as a counter-adaptation to mate-guarding behavior in monogamous pairs. Females able to conceal their fertility could increase their fitness by seeking "good gene" sperm donations at points of highest fertility (Benshoof and Thornhill 1979, Thornhill and Gangestad 2015 [review]).

This hypothesize is predicated upon three things. The first is that male genetic quality varies significantly and that a signal of that quality is both clearly identifiable and preferred by females. The second is that the female's primary mate would consistently have "inferior" genes compared to other males. The third is that these indirect benefits would outweigh the costs of extra-pair mating. Masculinity has been hypothesized to be the signal of good genes in many species as there is some evidence that testosterone may be an honest signal of fitness through its association with immunodepression (Folstad and Karter 1992, Wedekind and Folstad 1994, Hillgarth et al. 1997).

However, there is relatively little support for this hypothesis. First, there have been only a few studies that indicate the existence of general "good genes," and most of them can be explained by other benefits (Jennions and Petrie 2000 [review], Forstmeier et al. 2014 [review]). Second, mating patterns in primates do not support a female extrapair preference for males with high testosterone/masculinity. On the contrary, the primary mate in many polygynous primates, the alpha male, has higher levels of circulating testosterone (Chapais 2010 [review]), suggesting that he would be the male with the most superior genes (as circulating testosterone is influenced by both social and genetic factors – Roosenboom et al. 2018). Thus, any extrapair copulations would be with males that are genetically *inferior*. Third, evidence in humans is similarly weak; testosterone does not show immunosuppressing effects in humans (Nowak et al. 2018), nor do women show a strong preference for highly masculine men (as illustrated above). Finally, while it is difficult to quantifiably determine the costs of extrapair mating for all species, males commonly punish females for extrapair copulations (Clutton-Brock and Parker 1995(a), Goetz et al. 2008(b)), and, as illustrated, high testosterone is associated with aggression, violence, infanticide, and death in humans. In sum, unless there is some signal that simultaneously has yet to be identified and is also a clearly identifiable signal of good genes, this hypothesis is a poor candidate for the emergence of concealed ovulation in primates.

Still, these pressures may play a role in the maintenance of concealed ovulation in some monogamous species. This may particularly be the case if it is not "good" genes that a female is seeking but "compatible" genes, as there is mounting evidence that variation in genetic contributions can be a substantial influencing factor in female mate choice (Brown 1997, Petrie et al. 1998, Jennions and Petrie 2000 [review], Tregenza and Wedell 2000 [review], Foerster et al. 2003). Research in humans suggest the presence of a fertility-mediated female preferences for men with high "short-term attractiveness" (Gildersleeve et al. 2014 [review]), which may indicate a preference for genetic variation. Also, this may vary with the degree a woman is dependent upon a partner for resources, as that would affect the potential cost.

The final hypothesis is the preeclampsia hypothesis. This hypothesis proposes that the extended sexual receptivity accompanying concealed ovulation is an adaptive response to preeclampsia (Robillard et al. 2008). Preeclampsia is a pregnancy-related hypertension disorder that only occurs naturally in humans, and it is one of the leading causes of maternal deaths globally (Abalos et al. 2013). Depending on the region, it is responsible for between 9-25% of deaths, and in some countries, represents more than 30% (Khan et al. 2006). Evidence indicates that preeclampsia develops in consequence to the high degree of uterine implantation found in human pregnancies. While high fetal implantation is associated with the evolution of menstruation in general (Emera et al. 2012, Brosens et al. 2014, Macklon and Brosens 2014, Alvergne and Tabor 2018 [review], Thomas 2019), the implantation found in humans is greater than that which is found in any other species and may be due to our exceptionally energetically-expensive fetal brain development (Cunnane and Crawford 2014). Thus, this increased degree of placental invasion in humans may require an exceptionally careful degree mediation. Because semen contains molecules that can aid in developing a maternal tolerance to paternal antigens, and thus to paternally derived components of the fetus's genotype (Robertson and Sharkey 2001, Robertson et al. 2003, Dekker and Robillard 2005, Robertson et al. 2013, Martinez-Varea et al. 2014), it is hypothesized that continual exposure to paternal semen, made possible through concealed ovulation and extended receptivity, may help prevent preeclampsia (Robillard et al. 2008).

There is considerable evidence linking preeclampsia to extended in-pair copulation. There is a strong negative relationship between a mother's exposure to paternal semen and her likelihood of developing preeclampsia, particularly in the months leading up to conception (Smith et al. 1997, Kho et al. 2009, Saftlas et al. 2013, Triche et al. 2014). Whole-genome analyses of non-human mammals indicate the presence of adaptations that counter this invasive placental penetration, suggesting that this degree of implantation carries a substantial cost (Elliot and Crespi 2015).

This hypothesis is also consistent with the universal aspects of human social serial monogamy, namely the relative stability of relationships and the prevalence of the residential pair-bond (Schacht and Kramer 2019 [review, cross-cultural]). Further, when non-monogamous mating systems are present, there is still a near ubiquitous pattern of a woman mating with one male at a time. The only system in which a female regularly mates with more the one male is in polyandry. Not only polyandry this rare, but it also often takes the form of fraternal or familial polyandry in which one woman will marry brothers or close relatives. It may be that the similarity between them allows her immune system to adjust to the fetuses without much difficulty. Other forms of polyandry often arise when one husband is sexually limited (Benedict 2017 [review]).

Because preeclampsia is only documented in humans, it is unlikely to be a factor in the emergence of concealed ovulation in other primates. However, it is reflective of the maternal-fetal conflict that seems to have driven the evolution of menstruation in primates. Human evolution has been shaped a great deal by the reproductive demands of offspring with high cognition, and this is consistent with that pattern. Within approximately 2 million years, pressures of human cognition resulted in cooperative breeding, increased female body size, sexually dimorphic patterns of fat deposition, permanent breasts, secondary altriciality, and rotational birth. It is entirely consistent that extensive placental invasion, having already driven the emergence of menstruation, would contribute to another adaptation – concealed ovulation – that acts as a selective pressure for the maintenance of serial, social monogamy.

These hypotheses have often been proposed as competing hypotheses for the evolution of concealed ovulation in primates. However, they might need not to compete. Because each primate species evolved under unique socioecological conditions, it is possible that all have played a role, contributing to varying degrees over time and responding to the unique conditions of the species.

- Infanticide hypothesis: when multi-male mating reduces infanticide risk.
- Male-investment hypothesis: when primary mate provisioned resources are especially valuable and when paternal certainty is relatively high.
- Cuckoldry hypothesis: when male quality is variable and clearly identifiable, and when the benefits of extrapair copulation outweighs the costs.
- Preeclampsia hypothesis: when pregnancy is threatened by difficulty in immunoregulation.

Given this information, and the likely socioecological conditions of the ancestral primates under which concealed ovulation first evolved, the most plausible explanation for its initial emergence is as an infanticide reduction adaptation in polygynous systems, allowing females to mate with a variety of males and reduce infanticide risk. Though the conditions necessary for the other hypotheses would likely have been uncommon in ancestral primates, it is possible that in some lineages, the other hypotheses played a more substantial role.

Regardless, once multi-male mating was feasible in a primate population, this may have allowed for the necessary conditions associated with the other hypotheses. If the males differed significantly enough in their genetic quality in such a way that the females could discern, she may be inclined to pursue extrapair copulations, particularly if the environment has indications of high variability. When kin-provisioned resources are insufficient, particularly if resources are scarce or the mother is unable to provision her own food, concealed ovulation could facilitate paternal investment if the father has reasonable confidence in his paternity. As paternity certainty increases, this would further promote long-term pairing, especially in species with altricial young. And in species that may have difficulty adequately regulating immune responses during pregnancy, regular, frequent copulation throughout pregnancy could help mediate this risk.

2.3.2 Human Behavioral Fertility

Even though humans have concealed ovulation, it has long been hypothesized that women do undergo shifts in their behavior as an adaptive response to maximum fertility. Exploring this possibility requires both an understanding of the human ovulatory cycle and the unique complications of human subject research. The primary focus of this research has been to identify evidence for concealed estrus behavior, namely shifts in a woman's physiology or behavior, such as shifts in mood or attractiveness, and the degree to which others, namely men, might respond in characteristic ways to her fertility.

2.3.2.1 The Human Ovulatory Cycle

The human menstrual cycle is comprised of three non-overlapping periods: the follicular phase, ovulation (essentially instantaneous), and the luteal phase (Barbieri 2014 [review], see Figure 2.2). The first phase of the cycle is the follicular phase which begins with the onset of menses. During this phase, the anterior pituitary releases follicle-stimulated hormone (FSH) and luteinizing hormone (LH) in response to gonadotropin-releasing hormone (GnRH). FSH and LH act on the primordial follicle in the ovary; LH acts in the outer layer of the follicle (thecal cells) to convert cholesterol into androgens; FSH acts in the inner layer (granulosa cells), producing inhibin and converting the androgens into estradiol. FSH also triggers the selection and development of the primary follicle in the ovary; the layers proliferate and estradiol production increases, ultimately growing expansively into a preovulatory (Graafian) follicle.

Estradiol has three main effects in this phase: it begins the proliferation of the functionalis layer of the endometrium, including endometrial vascular remodeling, cellular differentiation, decreased smooth muscle contractility; it encourages the development of cervical crypts and changes in cervical mucus; and at lower levels, it has negative feedback on further production of FSH and LH. Estradiol levels continue to rise in the bloodstream as a consequence of the growing follicle until it reaches a threshold. At this point it triggers a surge in GnRH and a subsequent surge in the production and release of LH and FSH. This surge causes three things to happen: the follicular wall weakens; the oocyte resumes meiosis and progresses to metaphase II; and the ovary increases progesterone production. About 24-36 hours after the LH surge, ovulation occurs, and this ends the follicular phase.

At ovulation, the follicle ruptures and releases the now oocyte and the follicle is converted the corpus luteum. Fertilization by sperm can only occur within the day after ovulation, but because sperm can survive in the reproductive tract for five days, the human fertile window comprises the last six days of the follicular phase (Wilcox et al. 1995). Conception probability without respect to survivability increases steadily throughout the 6-day fertile window (0.1, 0.16, 0.14, 0.27, 0.31, and 0.33 [ovulation] – Wilcox et al. 1995), but risk of embryo loss increases with oocyte ageing, resulting in survivable conception probabilities that peak on the fourth and fifth days of the 6-day window (0.04, 0.13, 0.08, 0.29, 0.27, and 0.08 [ovulation] – Wilcox et al. 1998).

After ovulation, the luteal phase begins. About 12 hours after the LH surge, the follicle has converted into the corpus luteum, and it begins producing inhibin, estradiol, and progesterone. Progesterone is the dominant hormone in the luteal phase, and it has two main effects: it maintains the uterine endometrium in preparation for implantation; and it, along with estradiol, has negative feedback on GnRH thereby preventing the production of both LH and FSH. Unlike in the follicular phase, LH does not bind to the corpus luteum; instead, it is maintained by the presence of human chorionic gonadotropin (hCG) which is not produced unless an embryo is implanted into the endometrium. Thus, during this time, the corpus luteum begins to degrade.

The released egg enters the fallopian tube after ovulation where it can be fertilized, becoming a zygote. By time it has reached the uterus, it has developed into a blastocyst which implants into the uterus and develops into a trophoblast. The trophoblast releases hCG which acts to maintain the corpus luteum, thereby maintaining levels of estradiol and progesterone, the latter of which is crucial in sustaining pregnancy. If fertilization does not occur and no embryo is implanted, the corpus luteum continues to degrade, causing progesterone and estradiol levels drop, and signals the start of menses and the beginning of the next cycle.

The phases of the menstrual cycle vary in length. The most variable phase is the follicular phase, which lasts an average of 16.5 days. However, this is highly variable – 95% of women have follicular phase lengths between 10 to 22 days. In contrast, the luteal phase is the least variable phase, controlled as it is by the semi-consistent degradation rate of the corpus luteum (Fehring et al. 2006). However, it is still variable, fluctuating between 9-16 days, most often lasting 12-14 days, and having a mathematical average of approximately 12.4 days (12.4 days – Fehring et al. 2006; 13 days – Wilcox et al. 2001, Trussell et al. 1998; 13.4 days – Baird et al. 1991; 14 days – Dixon 1980, Bull et al. 2019).

On average, the menstrual cycle will last approximately 28 days; however, this merely represents the mathematical average of cycles with incredibly large deviations within and across participants (Chiazze 1978, Wilcox et al. 2000, Fehring et al. 2006, Jukic et al. 2007, Taylor et al. 2010). Fertile cycles as short as 19 days and as long as 60 days have been reported (Wilcox et al. 2000, Fehring et al. 2006, Jukic et al. 2007). Only 13-15% of women have a 28-day cycle (Johnson et al. 2018, Bull et al. 2019), and younger women tend to have shorter cycles, with an average of 24-day cycles.

Predicting the point of ovulation, and thus fertility, is exceptionally difficult. The 28-day cycle is neither representative nor medically normal, so it cannot be relied upon to determine the phase of cycle for any given individual. Further, around one-third of women experience more than 7 days of follicular-phase variation in consecutive cycles (Fehring et al. 2006), making methods that rely on a degree of consistency in the follicular phase unreliable. Evidence to date indicates that no method of estimating ovulation has been found to have an accuracy of greater than 30% (see Table 2.4, reproduced with permission from Blake et al. 2016).

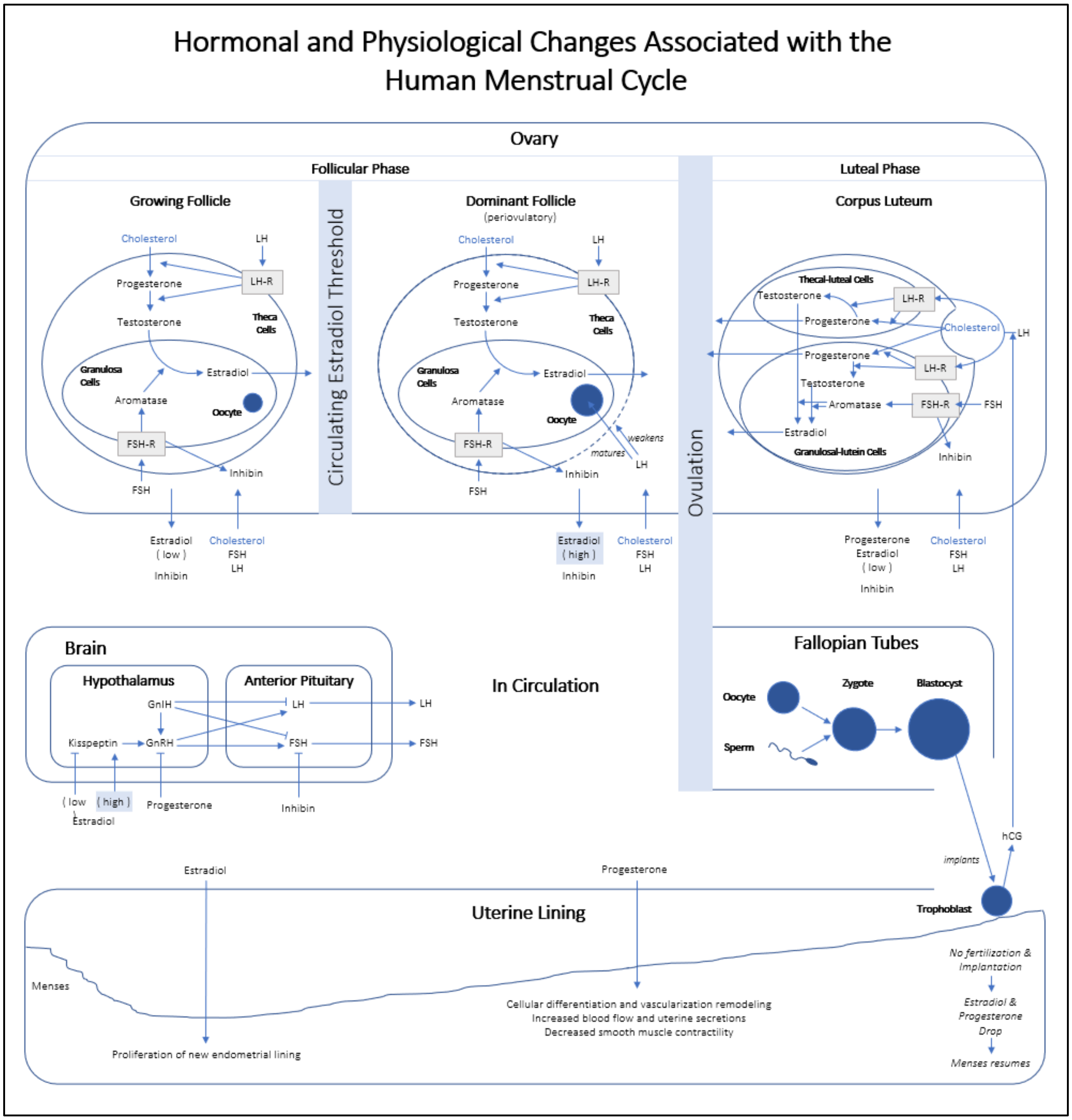


Figure 2.2. Hormonal and physiological changes associated with menstruation.

Table 2.4. Accuracy of ovulation estimation methods.

Ovulation prediction accuracy and conception probability of alternate cycle length estimators, by cycle length restriction (ovulatory cycles only) (reproduced with permission from Blake et. al 2016).

Cycle length estimate	**Restriction 1**[a]				**Restriction 2**[b]			
	Prediction accuracy [c]	N	Correlation with actual conception probability		Prediction accuracy [c]	N	Correlation with actual conception probability	
			R	N			R	N
Forward-counting method	11.10%	90	0.11***	1260	10.50%	76	0.12***	1064
Backward-counting methods								
Reported length	31.10%	90	0.35***	1021	25.00%	76	0.26***	842
Length of prior cycle	12.70%	79	0.24***	875	14.50%	76	0.26***	862
Prior cycle + reported average	20.30%	79	0.28***	893	19.70%	76	0.24***	857
Average of all measured and reported lengths	21.50%	79	0.30***	893	21.10%	76	0.26***	857

[a] Reported cycle length 25-33 days

[b] Prior cycle length 26-35 days

[c] Percentage of LH surges 1-2 days prior to ovulation as estimated by each counting method

*** $p < 0.001$

More accurate methods of fertility determination rely on directly observing or measuring physiological and/or hormonal changes. These can allow for individualized predictions of fertility that incorporate variation in phase and cycle length. Physiological indicators of fertility include a rise in basal body temperature (Ferin 1947); increased viscosity of cervical mucus (Billings et al. 1972); salivary ferning (Barbato et al. 1993); and, in some cases, the presence of mittelschmerz, a lower abdominal pain associated with ovulation (O'Herlihy et al. 1980, Marinho et al. 1982). However, using these to predict fertility can be difficult, as women do not always experience them and because they are subjective. Still, they are more reliable than estimated methods, and using more than one biomarker increase reliability even more (Ecochard et al. 2001, Manhart et al. 2013). The most accurate methods to determine fertility require hormonal and/or medical tests (Guida et al. 1999, Guermandi et al. 2001), specifically sonographic tests or those that measure hormonal fluctuations using assays on blood (World Health Organization 1980), saliva (Li et al. 1989), or urine (Collins et al. 1979).

Given the difficulty of identifying ovulation and the fertility window for research or medical purposes, it is therefore unsurprising that it is commonly accepted that women are also unable to intuitively identify their own fertility (Burley 1979, Marlowe 2004). Most of the studies that have examined individual perceptions of fertility have relied on participants who track their fertility, often to conceive, and who report high confidence in their knowledge of fertility. Even among these women, predictions of ovulation and fertility are most often inaccurate, missing ovulation between 73 and 87% of the time (Blake et al. 1997, Sievert and Dubois 2005, Zinaman et al. 2012, Hampton et al. 2012). Even menstrual-tracking mobile applications, which many women rely on to estimate their fertility, often inaccurately predict fertility (Duane et al. 2016).

Of course, these studies cannot address intuitive perceptions of fertility, as they specifically study women who track their fertility. However, studies on general populations of women are complicated by modern medicine and sex education which introduces the possibility of bias: women may have been told they are fertile mid-cycle and thus they "feel" as though they are fertile, attributing shifts in behavior and/or mood to hormonal fluctuations that may or may not be present. Studies of fertility perception among Indigenous people may therefore be the most reliable way to identify self-perception of fertility, and so far, the evidence indicates that, while they know sex causes pregnancy, they are generally unable to accurately identify the period of the cycle in which sex is most likely to result in pregnancy (Marlowe 2004).

2.3.2.2 Unique Research Complications and Consideration

It is notoriously difficult to collect and analyze human subject research. Several factors must be taken into consideration that are often less important in other types of research. The safety and well-being of research subjects is paramount, and in order to ensure this, there are unique procedural and ethical limits on how research on humans can be and should be conducted. Additionally, while all research is subject to a variety of biases and preconceptions, human subject research contains the potential for unique biases. For example, participants and researchers may not have the same understanding of the relevant concepts; participants' responses may be influenced by their beliefs or perceptions regarding the research intention; participants may fail to report events or feelings accurately, either due to errors in memory or hesitancy in responding honestly; and participants drawn to a particular research study are often likely to be interested in that subject already, giving them awareness that the general population might not (Popovic and Huecker 2021).

Studies on human fertility face some additional unique challenges. The first challenge is in choosing the method used to determine fertility. There are three general types of methods for predicting or identifying ovulation, and consequently, fertility: (1) estimation methods, which assume certain consistencies in cycle phases and length; (2) "fertility awareness-based methods," which rely on tracking common physiological shifts; and (3) medical diagnostic methods, which uses hormonal assays or ultrasounds to pinpoint ovulation. I will review each of the types as well as some of the most common specific methods below.

Estimation methods are some of the most common methods in fertility research. They are the least invasive and expensive, but they are also the least accurate, relying as they do upon consistent menstrual cycle patterns both across-women and within each woman. While it is true that the general pattern of the menstrual cycle is consistent across most women, the actual timing and length of each phase varies considerably, even among women with regular and predictable cycles (Münster et al. 1992, Wilcox et al. 2000, Wilcox et al. 2001, Alliende 2002, Creinin et al. 2004, Fehring et al. 2006). While estimation methods are generally unreliable for research, their accuracy can be improved. For example, researchers can ask for a more complete menstrual cycle history, such as the degree of variation they normally experience and how confident they are in their reported information. They could also include various physiological indicators, including cervical mucus, basal body temperature, and cervical position. Unfortunately, these symptoms can present within a short window of time, and this can make scheduling data collection difficult. Further, relying on research participants to accurately assess and report this information requires a degree of burden on research participants that makes their use impractical.

Perhaps the most common method is the forward-counting methods (FCM), which estimates ovulation as a set point in time from the start of the menses of the same cycle. Because it relies on assumptions regarding the regularity and predictability of the follicular phase, this method is highly unreliable (around 10% accuracy, Blake et al. 2016). This method is most often used to predict when fertility *will* occur, but it can also be used retrospectively to estimate when fertility *did* occur. The most common FCM is the +14 method – estimating fertility as 14 days from the first day of the menstrual cycle.

Another counting method is the backwards-counting method (BCM). It estimates ovulation based on the first day of the next cycle, and thus relies on the more consistent rate of degradation of the corpus luteum. Because of the nature of the method, it is most often used retrospectively to pinpoint when ovulation did occur, but it can also be used (less reliably) to estimate when it will occur by first estimating when menses will occur and then counting backwards from there. Thus, using the more reliable methods of estimation makes the conducting the research more difficult, as it requires regular data collection over at least one menstrual cycle to increase the likelihood of capturing the fertile window and knowing precisely when the next menses occurs. Using the BCM while relying on a projected date of menses decreases the accuracy, but it does make diverse methods of data collection more feasible.

Fertility can also be estimated using actuarial data. Actuarial tables give a daily conception risk that has been calculated from a large population. However, the use of these tables is limited in estimating individual conception risk. For example, one woman out of a thousand may be fertile on the first day of her cycle, and as a result, the actuarial table would indicate a conception risk of 0.001 on day 1. However, this does not mean that any given woman has an actual conception risk of 0.001 on the first day of her cycle. Outside of her fertile window, a woman has a zero percent chance of conceiving, and chances of conceiving within the fertile window vary from 0.08 to 0.36 (Wilcox et al. 1995). Any other estimates of conception probability for an individual are false.

A final method is the use of cycle standardization, which compresses or extends a woman's actual cycle to either a 28- or 29-day cycle. Relying on the proportionate lengths of the phases of the cycle to remain consistent even as the length of the cycle itself changes, it then assumes ovulation will be a set number of days from menses. Standardization methods are less systematic, and few, if any, have been tested for validity. Some researchers will first standardize participants' menstrual cycles and then overlay their expected hormone profiles, but this is also unvalidated.

There is a special kind of fertility determination that needs to be highlighted. Fertility awareness-based methods of family planning, also known as FABMs, are a common contraceptive method for women who want to avoid hormonal contraceptives (Dunson et al. 2001, Manhart et al. 2013, Duane et al. 2016). To be classified as a FABM, the method must rely on one of seven evidence-based methods. The goal of these methods is not to identify the day of ovulation, but to minimize the chances of conceiving while maximizing the number of intercourse days. Most of these methods rely heavily on tracking various physiological changes, though one method does rely only on a calendar (Standard Days Method, SDM) (Manhart et al. 2013). As the goal of these methods are vastly different from that of researchers tracking behavioral changes with fertility, it is inadvisable to use them without careful consideration. For example, the Standard Days Method estimates fertility will occur within a 12-day window, though the fertile window is only 6 days. However, researchers should be aware that participants may be familiar with and even using these methods themselves.

The most reliable way to determine fertility is to get a medical diagnosis. These can be done through relatively simple blood, urine, or saliva hormonal assays, or through a more invasive ultrasound. While more reliable, they do add expense and complication to research protocols (see Blake et al. 2016 for maximizing efficiency and minimizing cost), and they also increase the likelihood of participants knowing not only that the study involves their menstrual cycles, but knowing when they ovulate specifically.

Another major challenge of studying fertility is the effect of confirmation bias due to fertility awareness. Women are generally aware of their menstrual cycles and of the behavioral and physiological shifts that may accompany them. A 2014 survey of the general US population indicated that over 75% of women report knowing that having sex at certain times during the menstrual cycle increases their chance of getting pregnant. They also generally know this occurs in the middle of their cycles, and they track it primarily using methods of estimation (Lundsberg et al. 2014). Most seem to estimate fertility using the forward-counting method (Swift and Liu 2014), though many are aware of the relatively consistent length of time between ovulation and the start of the next cycle (Ozsoy et al. 2012, Lundsberg et al. 2014).

The potential for confirmation bias has been increased by the introduction of menstrual tracking applications for mobile devices. Widely popular and with an international user base, nearly half of women in some populations use them (Gambler-Ross et al. 2018, Ali et al. 2020, Ford et al. 2020). Most often used to track menstruation, many of these apps do much more; they track menstrual-based changes in fertility, mood, intercourse, and other symptoms (Ali et al. 2020), and they educate women on their menstrual cycles and what they might expect at different phases (Gambler-Ross et al. 2018, Ali et al. 2020). However, most of these apps use highly unreliable methods to track fertility – even in apps specifically advertising pregnancy prevention (Duane et al. 2016, Ali et al. 2020).

The potential for confirmation bias can be amplified by the population under investigation. Some populations of women are more aware of their fertility than others. Fertility awareness is highest in populations that are white and educated (Swift and Liu 2014), a trend helped along, no doubt, by recent movements to normalize menstruation (Hunter 2016, Weiss-Wolf 2017, Hodge 2019, Bobel and Fahs 2020). However, while many women believe they are educated on fertility, few of them have gotten their information from reliable sources, and as a result, many of their beliefs are inaccurate (Peterson et al. 2012).

Because women are both aware of their fertility and have beliefs about it, their beliefs may affect the results of the research. This risk may be particularly high when the researchers use methods of estimation, as women often use these methods themselves. Unfortunately, researchers studying behavioral fertility rarely, if ever, take into consideration the preexisting beliefs women have about their own fertility. This effect is likely compounded by the overreliance on university students for this research, who tend to be white, educated, and more likely to use menstrual-tracking apps. They also often recruit women who are not on hormonal contraceptives, meaning they are likely to be fertility-awareness based methods, especially if they are in a relationship. Indeed, that naturally-cycling women in relationships show stronger ovulatory effects is one of the reasons some authors prefer to recruit only from these women (Haselton et al. 2007). Further, many research subjects are pooled from students studying psychology or biology who might be familiar with the science behind fertility-mediated behaviors or even the research focus of their instructors. Finally, many researchers provide clues that the nature of the research is related to the menstrual cycle. Participants have frequently been asked to report their menstrual cycle information before providing responses, to track their menstrual cycles along with daily attitudes and behaviors, to schedule data collection around their menstrual cycles, or to take hormonal assays that coincide with the middle of their cycles. This type of research methodology effectively primes participants to think about their menstrual cycle and any potential cycle-mediated behaviors as they complete the research.

In sum, research into behavioral fertility requires careful consideration. Participants have beliefs and expectations that exist outside of the research paradigm that influences their behavior on an everyday basis. Research designs that may prime participants to think about their menstrual cycles before providing data or that rely on methods of estimation may increase the likelihood of the results having been influenced by fertility belief. Two other methodological factors can compound this effect. The first is by studying behavioral or attitude shifts that women already associate with fertility, such as sexual behavior or attractiveness. The second is particularly unfortunate: increasing the reliability of the method of fertility determination increases accuracy but also increases the likelihood that the participants will be aware of and thinking about fertility-mediated changes.

2.3.2.1 Proposed Trends in Behavioral Fertility

Investigations into menstrual-cycle shifts in human behavior have been ongoing since at least 1891 (Campbell 1891 – see Hart 1960). Several aspects of human behavior have been proposed as being associated with fertility, and they can generally be categorized, if imperfectly, into one of several groups: changes in female attractiveness, in male responses to females, in female moods, in female preferences for sexual partners, for changes in female sexuality, and changes in female social behavior. However, identifying consistent patterns in these behaviors has been difficult (Schreiner-Engel 1981 [dissertation], Hill 1988 [review], Steklis and Whiteman 1989 [review], Regan 1996 [review], Wood et al. 2014 [review]).

What follows is a review of the literature organized by each of the aforementioned categories. This review includes not only the identified trends but as well as trends that have been examined but for which no support has been found. Thus, the same study may appear in multiple categories, having examined different types of fertility-mediated shifts. It also discusses the research designs of the studies, particularly the degree to which priming and confirmation bias may have contributed to the results. However, even though the method of fertility determination contributes a great deal to the whether fertility is actually captured in the study, the wide variety of estimated methods employed without having been externally validated makes it difficult to compare the likelihood of any one study having actually captured a valid effect. Thus, excepting unique cases, or when the method is likely to contribute to a priming effect, I generally do not discuss the method of fertility determination and otherwise assume that results that indicate an effect of fertility are accurate. Finally, the intention of this review is to identify reliable and consistent patterns that may be associated with the menstrual cycle. This is not a comprehensive survey of all the research that has been done, though it is intended to be a thorough analysis of the literature I had found to date.

2.3.2.1.1 ATTRACTIVENESS

Fertility has been proposed to cause various shifts in a woman's attractiveness. Because humans are a female choice species, I would not expect to see a trend toward behavior that would attract a mate. However, women are highly intrasexually competitive and compete for status primarily through social means, and because other female primates demonstrate fertility-mediated peaks in their intrasexual competition, I might expect similar trends in humans. There have been three general areas of research with regards to attractiveness: changes in self-ornamentation, in physical attractiveness, and in behavioral attractiveness.

2.3.2.1.1.1 Self-Ornamentation

Self-ornamentation behavior is often presumed to be a mate attraction behavior. However, female-female competition for social status is intense, and status is associated with access to costly ornamentation. Thus, any trends associated with self-ornamentation may be indicative of fertility-mediated increases in intrasexual competition.

One of the more popular areas of investigation into changes in self-ornamentation has centered on whether women are more likely to wear the color red or pink while fertile. The reasoning behind this line of investigation is that red/pink is associated with the swollen genitals of other estrus primates and that this might be a behavioral form of that in humans. The results are highly inconsistent. Of the five studies found that explored this question, two found an increased likelihood (Beall and Tracy 2013, Eisenbruch et al. 2015), whereas three found no effect (Prokop and Hromada 2013, Tracy and Beall 2014, Blake et al. 2017).

Three studies examined self-ornamentation through self-reported clothing or product choices. All of these studies found an effect of fertility, though they also all had high degrees of priming. The results suggested that fertile women reported increased attractiveness (Röder et al. 2009), interest in styling (Röder et al. 2009), appearance-related product usage (Saad and Stenstrom 2012), and provocative, figure-hugging, and sexy clothing (Schwarz and Hassebrauck 2008). Saad and Stenstrom (2012) also found a decreased interest in food which they also attribute to self-ornamentation interest.

Three other studies examined other-rated self-ornamentation with inconclusive results. Haselton et al. (2007) found an increase. However, they stated they recruited partnered women specifically for their stronger ovulatory effects, so it is difficult to determine how universal this finding may be. Durante et al. conducted two studies (2008, 2011), and both had high degrees of priming: women took hormonal urine tests to confirm ovulation before they were allowed to provide data for the fertile portions of the study. The 2011 study found an increased interest in sexy products, particularly when primed with attractive female rivals. The 2008 study examined self-ornamentation over 125 different contexts: they included different determinations of attractiveness (e.g., "sexiness", "general revealingness," "skin revealingness"), sexual experience and sociosexuality, relationship status and satisfaction, self-rated levels of attractiveness, and whether the ornamentation was actually worn or whether it was included as an illustration drawn by the participant. This study also included a wide variety of menstrual cycle comparisons, including comparing all non-fertile days to peak fertility, to non-peak fertility, and to the entire fertile window. Of all of their comparisons, twelve of their findings were statistically significant. Only four of these emerged as effects that might represent a general shift in attractiveness (i.e., not occurring under specific circumstances), and all were specific to the illustrations the women draw. They found that, in comparison to when they were not fertile, women drew illustrations with increased skin revealed (peak fertility), revealingness (both peak fertility and fertile window), and sexiness (fertile window). The other eight findings emerged under extremely specific comparisons. For example, one of them was an increased composite rating (made by others) of the degree of sexiness and revealingness of the clothing worn by sexually experienced women (only) when all non-fertile days are compared with the fertile window. Another finding was an increase in revealed skin in an illustration drawn by women who were not in a committed relationship when comparing peak fertility with all non-fertile days.

Overall, these results suggest that women may show a fertility-mediated increase in self-ornamentation (though probably not red/pink preferences). However, given the high degree of priming in these studies, they should be replicated. Further, if there are effects, they may be indications of increased intrasexual competition and not necessarily mate attraction.

2.3.2.1.1.2 Physical Attractiveness

Several studies have examined changes in physical attractiveness using both subjective and objective measurements. Subjective ratings of attractiveness have included both self-reported and other-reported perceptions.

Four studies examined changes in self-reported attractiveness, and the results are inconsistent. Two results suggest no change in sexual desirability (Brinsmead-Stockham et al. 2008) or self-attractiveness (Cobey et al. 2013), though another indicates an increase in both (Haselton and Gangestad 2006), and Slob et al. (1996) found a decrease in rated self-image. Most of these studies had relatively high potential for priming (Cobey et al., Haselton and Gangestad, and Slob et al.), often having used invasive measures of fertility determination, so it is difficult to draw any conclusions from these studies.

Five studies have compared attractiveness ratings given to women by others. Three of them examined facial attractiveness, and two reported a general increase in facial attractiveness as rated by both men and women (Roberts et al. 2004, Oberzaucher et al. 2012). However, Roberts et al. (2004) found a fertility shift when compared to random chance, not in comparison to any other phase of the cycle, and Oberzaucher et al. (2012) found it in comparison to menstruation (14 days after ovulation). Thus, neither of these suggest a strong effect of fertility itself. The third study compared both facial and vocal changes across the entire menstrual cycle, and they found no effect of fertility; instead, they found a decrease in attractiveness with progesterone in the luteal phase (Puts et al. 2013). One study examined the effects of fertility on body movement, specifically that of walking and dancing, and their results showed an increase in attractiveness ratings given by men (Fink et al. 2012). However, the women in these studies knew that the study involved changes in their menstrual cycles, so the results here could be influenced by a priming effect. A few studies have examined physical attractiveness using more objective measures of attractiveness, and their results generally showed fertility-mediated increases, specifically in soft-tissue symmetry (Manning et al. 1996, Scutt and Manning 1996, Oberzaucher et al. 2012) and in skin quality (Oberzaucher et al. 2012). It should be noted that Oberzaucher et al. (2012) made these comparisons against menstruation which, again, could be an influencing factor.

A few studies have examined changes in vocal attractiveness, and the results suggest that there might be some fertility-mediated shifts. Studies on subjective ratings of voices have had conflicting results, showing both decreases (Fischer et al. 2011) and increases (Pipitone and Gallup 2008) of attractiveness ratings. Two studies examined changes in specific vocal parameters, finding increases in vocal pitch (Bryant and Haselton 2009) and decreases in the degree of unvoiceness and noise-to-harmonic ratios in sustained vowels (Fischer et al. 2011). How these translate exactly to perceptions of attractiveness is unclear.

Overall, these results suggest that if menstrual cycle changes in attractiveness are present, they are most likely subtle, and possibly be a by-product of hormonal shifts throughout the cycle and not only fertility. Studies regarding self-perceptions of attractiveness are too inconsistent to draw conclusions.

2.3.2.1.1.3 Behavioral

We found one study that examined fertility shifts in what the authors deemed to be behaviors associated with mate attraction. Markey and Markey (2011) examined across-the-cycle self-reported shifts in feelings of warmth and dominance, having already identified warmth as a trait that men prefer in their potential mates. They found a significant relationship between fertility and self-reported feelings of warmth, but not dominance, for naturally-cycling women. While this study had high potential for priming, the participants may not have had strong beliefs about their fertility and these feelings, so it may be moderately robust to priming effects.

2.3.2.1.1.4 Summary

In sum, evidence for fertility-mediated shifts in female attraction is relatively weak. The most consistent findings are those indicating the presence of subtle shifts in physiology throughout the entire menstrual cycle, an effect unlikely to have strong adaptive significance. There may be an increase in self-ornamentation as well, though if it does exist, it may be attributable to intrasexual competition. There may also be an increase in warmth with fertility, though replication is needed. Future research should be designed to help elucidate and control for the effects of priming, confirmation bias, and intrasexual competition by examining pre- and post-study changes in beliefs, conscious and subconscious participant motivations, and their perceptions regarding their social status.

2.3.2.1.2 Male Responses

Another area of investigation has been whether men can discern a woman's fertility, and if he can, how he responds to it. This research is distinguished from the male-rated attractiveness above because its research subjects are the men, not the women, and the interest is in their response to the women, not in identifying the aspect of the woman's fertility to which the men may be responding. It generally assumes the men are responding to shifts in female attractiveness in response to either olfactory or visual cues.

This research can be categorized as whether it examines in-pair or extra-pair behavior: in-pair behavior looks at how a partnered man responds to his own partner's fertility, whereas extra-pair behavior looks at how a man (partnered or not) responds to the fertility of women (partnered or not) to whom he is not attached. Notably, we would expect this research area to be more robust to priming effects, as men are less likely to expect fertility-mediated shifts or to know where a woman is in her cycle, particularly if it investigates extra-pair behavior. However, the reliability of this assumption may be dependent upon the research design and the degree to which men have their own expectations about fertility and behavior, which might be more prevalent in partnered men.

The direction of male responses to female fertility is uncertain. As discussed, concealed ovulation and extended sexual receptivity likely serves an adaptive purpose in human. Thus, I would not expect to see behaviors that would indicate men showing marked preference for women while fertile – adaptations to maintain concealed ovulation should prevent this. However, the male bias for short-term relationships may result in male counteradaptations for fertility detection in short-term contexts. Additionally, if the fitness benefit of concealed ovulation purpose would be strongest for in-pair relationships, as we would expect under the influence of preeclampsia prevention, then this effect might be strongest in in-pair relationships. Thus, if we do see an effect of fertility that would suggest increased sexual attraction or behavior, then we might see it primarily for extra-pair behavior.

2.3.2.1.2.1 Extra-Pair Behavior

Extra-pair research investigates how a man responds to fertile women with whom he is not partnered. For extra-pair behavior, we might expect to find that men show increased sexual attraction to fertile women as a result of the general male-bias toward short-term mating and optimizing their fitness by preferring to mate with fertile women. This research can generally be divided into three groups: responses to body odor, responses to visual cues, and facial categorization rates.

Body odor research has been heavily explored, with at least ten studies having examined it in some capacity. Seven of these studies used subjective measures of attractiveness, asking men to rate female odor on some aspect of attractiveness (e.g., sexiness, attractiveness, pleasantness, intensity, etc.). Three of these seven studies found strong support for increased attractiveness with fertility (Thornhill and Gangestad 1999, Singh and Bronstad 2001, Thornhill et al. 2003). However, each of these three studies had high potential for priming effects, even for their male subjects, including recruiting participants from classes that the authors taught, labeling bags of shirts with “F” and “L,” and telling the participants ahead of time that the research relates to women, fertility, and attractiveness. The other four studies had lower degrees of priming and also found support for this hypothesis (Kuukasjarvi et al. 2004, Havlíček et al. 2005, Miller and Maner 2011, Roney and Simmons 2012). However, two of these studies found fertility effects only in contrast to control shirts that were not worn by women: one found that men with high chemical sensitivity had increased sexual impulses after smelling the shirts of fertile women (Miller and Maner 2011), and the other showed that men gave fertile shirts higher ratings for familiarity and intensity, but not for attractiveness, and there was no accompanying change in the man’s mood in response (Roney and Simmons 2012). Overall, these results suggest the possibility of an effect of fertility on female body odor in some way that men might be able to discern; however, they are far from conclusive and indicate no clear pattern.

Two studies have examined how female body odor might affect a man’s testosterone level. Neither study has found an effect of fertility (Roney and Simmons 2012, Miller and Maner 2010(b)). Instead, Miller and Maner (2010(b)) found a decrease in testosterone in the luteal phase. This again suggests an influence of progesterone, not estradiol. It should be noted, however, that this study included a re-analysis of their results using a different method of fertility determination and found an increase in ratings of pleasantness when compared to non-fertile shirts (though they did not include the control in this analysis). In general, these results suggest that if men are responding to fertility changes in scent, it is either not reflected in testosterone or it shifts in response to progesterone-mediated changes.

The results of research exploring a man's response to visual cues of fertility are similarly unclear. Of the four studies that have explored this, the clearest results suggest that men are more likely to engage in behavioral mimicry and risky decision-making in response to fertile women (Miller and Maner 2011). The other three studies had men rate images of women, and their results were more complex. Schwarz and Hassebrauck (2008) found an increase in attractiveness ratings with fertility compared to luteal; however, this might be an effect of changes in the luteal phase, given that Puts et al. (2013) found a decrease in both vocal and facial attractiveness in the luteal phase compared to the rest of the cycle, but no effect of fertility. The last study, Miller and Maner (2010(a)), found a difference in the ratings given depending on whether they were partnered or single – fertility-mediated decrease in partnered men and a "marginal" increase in single men ($p = 0.9$). These results suggest that men might respond subconsciously to visual changes in the menstrual cycle in a relationship-maintenance behavior, and potentially through a combination of both fertile and luteal effects.

One of the most famous studies to examine male responses to fertility did not pre-determine the specific cue that men might respond to. Miller et al. (2007) compared the effects of naturally-cycling and non-naturally-cycling (pill usage) exotic dancers on the variation in tips earned during the fertile window and the rest of the cycle. Their results suggested that naturally-cycling women make significantly more money when fertile. However, there are a few caveats to note. The authors reported significant main effects that included both pill usage ($p < 0.001$) and effect of cycle ($p < 0.05$), but the authors did not report the results of those comparisons. A visual inspection of the graph of the data suggests naturally-cycling women make more money across their entire cycles, with peaks in both the fertile and the luteal phase. Thus, it is possible that there is an effect of oral contraceptives on body odor independent of fertility and that it might be driving the reported effect of fertility. Additionally, the authors did not compare the phases of the cycle using a typical method, making it difficult to compare the results of this study with other studies. Given the study design, they have been expected to compare the differences between the two groups of women for each of the three phases of the cycle (e.g., pill vs. non-pill for fertile window) and/or the differences within the groups of women between the phases (e.g., fertile vs non-fertile for non-pill). Instead, they reported the results of only two statistical comparisons associated with the interaction of fertility and pill usage. Upon finding no effect of pill usage to explain the differences between the menstrual and luteal phases, they combined the two phases and compared them to the fertile phase, and found an effect ($p < 0.01$). A visual inspection of the graph suggests the presence of other, less clean, patterns, including non-pill women earning higher tips than pill women during the luteal phase, and no difference in the fertile to luteal earnings for non-pill women. Thus, it is difficult to conclude that these results are evidence for a strong fertility effect on men and not evidence of effects of hormonal contraceptives in general.

One study looked at the rate that men were able to categorize women's faces, and the results are similarly unclear. Johnston et al. (2005) examined how fast men could categorize a woman's face taken at different points in her cycle, and they reported an increase with fertility. However, this effect occurred for both naturally-cycling and non-naturally-cycling women, and it was found in direct comparison against menstruation, which is likely to affect a woman's facial appearance in both sets of women. Finally, they did not report their actual p-values, making it difficult to draw reliable conclusions. Thus, there is inadequate support for changes in categorization rates.

Overall, research into a man's ability to detect the fertility of women to whom he is not partnered is inconclusive. Both luteal and fertile effects were found, and many of the fertile effects under conditions of high priming. The most reliable results suggest the possibility of a general increase in odor attractiveness and, for partnered men, a decrease in visual attractiveness, suggesting the potential for a relationship-maintenance effect.

2.3.2.1.2.2 In-Pair Behavior

Research investigating in-pair behavior is also common, having been examined in at least nine studies. It has explored fertility-mediated changes in male sexuality, in perceptions of his partner's attractiveness, in mate retention behaviors, and in male-male competition. For in-pair behavior, we might expect three trends: a man being more likely to find his partner attractive and/or initiate sex when she is fertile, though this is dependent upon the selective pressures for concealed ovulation; a man being more likely to engage in mate retention behaviors to avoid the chances of cuckoldry; and a man being more competitive with other men, both to advertise his dominance to his partner and to discourage other men from cuckoldry attempts.

Three studies have shifts in attractiveness/sexual behavior, and the results generally show no effect of fertility. Two of them examined changes in male sexuality and revealed no trend in male-initiated sexual behavior (Caruso et al. 2014) or in sexual interests and attitudes (Gangestad et al. 2010(a)). The other study examined perceptions of partner attractiveness, and while their results showed increases in ratings given in the fertility-window, this emerged for both naturally-cycling and non-naturally-cycling women (Cobey et al. 2013).

Mate retention behaviors have been examined in at least four studies, and all show increases with partner fertility. However, all four of these studies have serious methodological concerns. Only one study included male-reported behavioral changes, and their responses were averaged along with the woman's responses (Gangestad et al. 2014); all of the other studies relied exclusively on female reports (Gangestad et al. 2002, Haselton and Gangestad 2006, Pillsworth and Haselton 2006). Further, all four had the potential for high priming effects. For three of them, including the study that included male responses, the participants came into the lab to test their LH levels and were only allowed to give their fertility-window data after they received a positive test (Gangestad et al. 2002, 2014, Pillsworth and Haselton 2006). The fourth study had women complete daily reports that included both their menstrual cycle information and their perception of their partner's behavior (Haselton and Gangestad 2006). Thus, there is a high likelihood that the women's perceptions of their partners' mate retention behavior were influenced by their own beliefs regarding what is supposed to happen during fertility.

We have found two studies in which direct male-male competition has been explored, and both had lower levels of priming. Burriss and Little (2006) studied the effect of partner fertility on how men perceived the images of other men. They found that men whose partners were fertile were more likely to perceive other men as dominant. While the men reported their partner's place in their menstrual cycle, it would be unlikely that they would have many preconceived ideas regarding how his partner's fertility should affect his feelings of dominance with respect to other men. Fales et al. (2014) tested male-male competition using measures of testosterone instead of subjective ratings. Their results indicated that testosterone increased for all men after viewing images of men (high dominant or low dominant) and that there was no effect of fertility on mediating the intensity of the increase, even for dominant male rivals. However, the authors suggested there was an effect of fertility status ($p = 0.08$), one that was amplified for men exposed to images of dominant rivals, even though the interaction between fertility and dominance was not significant ($p = 0.29$). These studies suggest that fertility might have an effect on increasing male-male competition, but that this effect might be subjective and/or not entirely correlated to an increase in testosterone.

Overall, there seems to be little evidence that a man's behavior toward his partner shifts in response to her fertility. Men might show increased intrasexual competition with fertility, but more evidence is needed.

2.3.2.1.2.3 Summary

In sum, these results present inconclusive to weak support for the hypothesis that men respond to fertile women in ways that indicate an increased sexual response. There were few effects of fertility, and in contrast, some of the more rigorous findings indicated an effect of progesterone. Furthermore, the findings that did indicate an effect of fertility often had methodological problems, including having high degrees of priming, using unprecedented methods of window determination and comparison, or failing to report all findings, or the results indicated no clear adaptive pattern (e.g., what does an increased rating of "familiarity" mean with respect to extra-pair men and fertility?).

However, there do seem to be some patterns. Two of the strongest fertility-related results supports the hypothesis that fertility might increase mate retention behaviors: partnered men show a decrease in attractiveness to extra-partner fertile women, and they show an increase in dominance behaviors toward other men when their own partner is fertile. It is possible that the fitness benefits of social, serial monogamy may have resulted in fertility-mediated behavioral adaptations that act to increase the likelihood of maintaining relationships once pair-bonded. If there is such an adaptation, exploring the boundaries of it, including how it is formed, maintained, and dissolved, would be a fruitful avenue of research.

Another pattern is that there does seem to be evidence that men respond to the luteal phase, showing an increase in ratings of attractiveness and a decrease in levels of testosterone, both of which emerged in extra-pair research. It is possible that this might be an adaptive response to this phase of the cycle, though it is difficult to explain why that might occur. However, it might also be a byproduct of the effect of progesterone, the hormone dominant during both the luteal phase and pregnancy. Expectant fathers experience a drop in testosterone throughout the pregnancies of their partners (Berg and Wynne-Edwards 2001, Saxbe et al. 2017), and these results suggest that the physiological cue to which men might be attuned to respond is progesterone. Indeed, given the considerable risk of miscarriage early in pregnancy, when pregnancy is not even visible, having a cue that is both subtle and effective at decreasing the degree of dominating behavior in nearby males would undoubtedly be adaptive. Determining the intensity, reliability, and boundaries of any progesterone-testosterone effect should be explored; for example, it is possible that men might be responding not only to partners, but to close female relatives or any previous sexual partner, following a heuristic pattern that has adaptively incorporated the degree of (potential) relatedness of the (future) children in his immediate environment.

2.3.2.1.3 MOOD

Fertility-mediated changes in general mood have also been explored, though much less extensively than other areas. Because mood is a somewhat amorphous concept, these results may overlap with some of the other categories and should be considered broadly; for example, increased feelings of assertiveness and power might influence a woman's interest in an extra-pair partner or interest in social events. Predicting ad hoc fertility-mediated patterns might be is difficult, and thus care should be taken to avoid post-hoc story-telling, particularly without incorporating the patterns found elsewhere.

I have found four studies that have examined fertility and mood. Two studies have found no effect of fertility on mood – specifically on "general mood" (Slob et al. 1996) and on "loneliness" (Bullivant et al. 2004). Two others have found an effect, though the results together do not suggest a specific directional effect of fertility. Gangestad et al. (2002) found a fertility-mediated increase with "worries of offending someone", and it is uncertain what this might indicate. Haselton and Gangestad (2006) found an increase in feelings of "relative power and desirability" compared to their partners, which the authors suggest is an indication of extra-pair interest. Importantly, each of these four studies had high potential for priming, with participants being fully aware of the research's purpose, having had blood and urine work done either while self-reporting the information or in order to schedule the data collection session, making these results inconclusive.

In sum, there does not appear to be a significant impact of fertility on mood, though more research is needed before any conclusive decision is made. An adequately designed study would need to be long-term, include a wide range of demographic and socioeconomic variables, use diagnostically accurate methods of fertility determination, and include daily mood assessments with socially-relevant journaling. Still, it would be unclear how any fertility-mediated shifts in mood would impact the women in ways that was not washed out by the effects of other factors that influence mood, and thus this area of exploration may not reveal much about any adaptative significance between fertility and mood.

2.3.2.1.4 SEXUAL PARTNER PREFERENCES

Changes in sexual partner preferences is one of the most extensively researched areas with regards to fertility-mediated behavior. There have been no fewer than 32 papers examining the degree to which women prefer different kinds of partners at different stages in their cycles. Our understanding of female preferences for male partners indicates the existence of a universal preference for men with high social status and financial stability. Other preferences emerge from various trade-off decisions, but in general, dominance is preferred only in the presence of indications of prosociality, and men with indications of potential antisociality, including those associated with masculinity, are avoided. If these preferences were to shift with fertility, we might predict a preference toward those who would be able to gain resources as that might have an indirect effect on her future offspring's social status; thus, indications of investing in parenting effort might be less important. Finally, we might predict an increase in preferences for male genetic variety, both in comparison to her own genes and to a long-term partner.

2.3.2.1.4.1 Apparent Health

Two studies have examined fertility-mediated fluctuations in female preferences for apparent health. Apparent health in men may be an indication of good genes, if it is a valid measure of immune system responses, or it may be an indication of a history of success in resource acquisition, if it is a measure of the ability of a man to get access to relatively better health care resources.

Both of these studies were conducted by Jones et al. (2005(a)(b)). Four separate comparisons were made, and three of them indicate a luteal effect: an increased preference for apparent health with progesterone across the cycle (2005(a)) as well as in direct comparisons to the fertile phase (2005(a)(b)). Only one comparison indicated a fertility-related effect: both fertile and luteal women showed a preference for apparent health in short-term partners when compared to random chance (Jones et al. 2005(b)).

While apparent health has been one of the least studied areas of fertility-mediated sexual partner preferences, the results seem remarkably consistent, and they seem to indicate an effect of progesterone. This may again be an indication of pregnancy-related selective pressures, perhaps as a disease-avoidance bias. However, much more research should be done on across-the-cycle preferences for apparent health and should include the use of different proxies for health. Further, these results should be compared to research on pregnancy-related preferences for apparent health and/or aversion to signs of disease or illness.

2.3.2.1.4.2 In-Pair/Extra-Pair Interest

Fertility-mediated fluctuations in attraction to primary partners and extra-pair mates is another area that has been well-studied. This research has relied exclusively on either questionnaire responses completed after taking, and receiving positive results on, urine ovulation tests (Gangestad et al. 2002, 2005, 2010(b), Pillsworth and Haselton 2006) or on daily journaling in which women also recorded their menstrual cycle information (Pillsworth et al. 2004, Haselton and Gangestad 2006). Therefore, there is a good chance that these results could have been influenced by any beliefs they might have about their behavior and fertility.

The results of these studies are inconclusive. Two studies found a general increase in attraction to or fantasies about extra-pair men (Gangestad et al. 2002, 2005), but one of them also found an overall increase for all men as well (Gangestad et al. 2005), and the other found an increase in time spent with their current romantic partner (Gangestad et al. 2002). Three other studies found no overall effect (Pillsworth et al. 2004, Haselton and Gangestad 2006, Gangestad et al. 2010(b)), though they did find effects under specific conditions: when their primary partners had low facial symmetry (Gangestad et al. 2005), low facial masculinity (Gangestad et al. 2010(b)), or low sexual attractiveness (Pillsworth and Haselton 2006); when they had been in the relationship for a long time (Pillsworth et al. 2004); or for sexually attractive extra-pair men (Haselton and Gangestad 2006).

However, one study found that these trends may be strongly mediated by relationship satisfaction (Gangestad et al. 2005). One study examined in-pair/extra-pair interest through the lens of reported shifts in female behavior. Gangestad et al. (2014) used both male and female reports to examine shifts in a woman's behavior that they attributed to be related to mate guarding. They found an overall increase in self-assertiveness and unobservable resistance to mate guarding behaviors. However, behaviors attributed to self-assertiveness may also be related to intrasexual competitiveness, so it may be useful to explore any reported motivations for these behaviors to help ensure that researcher bias is not influencing the results.

Importantly, several of these studies did not report all their results, making cross-study comparisons and thus forming general conclusions difficult. This is particularly difficult when the results go unreported for the control group that was used for comparison purposes, such as shifts related to in-pair relationships (Gangestad et al. 2010(b)) and for those who were not in serious relationships (Gangestad et al. 2002). Additionally, several studies used language that erroneously implied statistically significant relationships, either by drawing attention to directional effects that were not significant (Haselton and Gangestad 2006) or by misrepresenting results as significant when they were not (reported a "marginally significant" relationship between decreased relationship satisfaction and extra-pair sexual desire; $p = 0.1$, Pillsworth et al. 2004).

Overall, there does not seem to be an effect of the menstrual cycle on interest in extra-pair relationships. Several of the studies that found an effect also found effects in the opposite direction or in a control group as well (or did not report all of their results), while others found effects only under specific conditions even though the overall tests of significance indicated the lack of an interaction. The more reliable of these results suggest the possibility of two patterns. One is that a woman's interest in extrapair men might be as related, if not more related, to her general relationship satisfaction and interest in a new relationship. The other is that a woman's independence-related behaviors may increase with fertility, though attributing this to a desire for extrapair relationships is questionable, particularly given the possibility for an increase in intrasexual competition with fertility. More rigorous studies that control for priming effects, relationship satisfaction, and female-directed motivation are needed to adequately assess the existence of a fertility-mediated shift in in-pair/extra-pair men.

2.3.2.1.4.3 Long-term/Short-term Mates

At least 10 papers have examined fertility-mediated preferences for long and short-term mates, and the results are mixed. The studies examined "long-term" and "short-term" mates using a wide range of definitions and scenarios, making it difficult to draw general conclusions. Further, several of the studies had high degrees of priming, with participants providing menstrual cycle information before providing responses to obviously sexual partner-related scenarios and/or questions (e.g., Little et al. 2007, Durante et al. 2012).

Five studies did not find a fertility-mediated shift in preferences for short-term relationships. Two of these found no effect of the menstrual cycle at all (Penton-Voak et al. 1999 [but no menstrual cycle determination methods given], Garver-Apgar et al. 2007); one found fertility increased preference for faithfulness in long-term relationships (Gangestad et al. 2007); and two others found luteal-related effects (Jones et al. 2005(a), Puts 2006). Specifically, Jones et al. (2005(a)) found an increased preference for relationship commitment, and Puts (2006) found a decreased preference for masculine voices as either a long-term or short-term mate (along with a prolactin-increased preference for masculinity for both short and long-term relationships). The results of Jones and Puts are noteworthy and together indicate the possibility of a progesterone-related effect.

Six studies indicated the presence of a fertility-mediated effect. Specifically, the results of these studies suggest that fertility influences the qualities women deem desirable in short-term mates: fertile women perceived "sexy men" as having qualities typically associated with long-term mates (Durante et al. 2012), showed interest in men with qualities associated with masculinity and dominance for short-term relationships (Gangestad et al. 2004, 2007, Little et al. 2007 [but no p-values given]), and preferred lower-voiced men for short-term relationships (Puts 2005).

The results of Haselton and Miller (2006) warrant particular attention. They reported a fertility-mediated increase in preferences for creativity over wealth for short-term relationships. The authors suggest that this might indicate a preference for "good genes" as opposed to a "good dad," but this conclusion assumes that creativity is a better indicator of good genes than wealth. However, wealth is also associated with dominance, social status, and masculinity, and thus may be an indication both of good genes and of resource provision. An alternative explanation may be that creative men have other attributes, such as sensitivity and emotional intelligence, that women may find particularly valuable, though those attributes are difficult to explain using a "good genes" model of selection.

Overall, the presence of a fertility-mediated preference for short-term mates is inconclusive. While several studies reported results fertility effects, the relatively high degree of priming in many of them is concerning. Further, the presence of a progesterone-documented effect, for increased relationship commitment and decreased masculinity, must be taken into consideration when the method of fertility determination is set. If there is a progesterone-documented decrease, then its use in the comparison window might result in findings that suggest an "increase with fertility" that is actually a "decrease with progesterone." Indeed, the luteal phase was included in the comparison window for all of the studies that reported an effect except for Puts (2005). Future research should prioritize study designs that control for the effects of participant beliefs and that include across-the-cycle comparisons to determine the degree to which progesterone, and not fertility, might be responsible for any actual patterns. Progesterone-related effects might be a byproduct of the effect that progesterone, being dominant during pregnancy, might have on a woman's mating preferences throughout pregnancy. Given the importance of regularly mating with the father of the fetus to pregnancy maintenance, a progesterone-mediated preference for long-term mates might exist.

2.3.2.1.4.4 Masculinity/Femininity

Another major area of investigation has centered on the degree to which women's preferences for masculinity shifts across the cycle. Either for masculine bodies or masculine faces, most of these studies assume that testosterone acts as a signal of good genes and thus hypothesize that masculinity preferences increase with fertility. However, as discussed, masculinity is an unlikely candidate for a good genes signal as there is little evidence of testosterone-related immunosuppressing effects in humans. Still, masculinization may be a signal of good genes in some other way, though through a mechanism that has yet to be proposed. In fact, the association between masculinity and antisocial behavior, and the aversion that women show toward masculinity in general, might suggest the existence of a fertility-mediated shift away from masculinity, if women are associating masculinity with a potential threat.

The bulk of this research has focused on facial masculinity, most of which has been done by using images that have been digitally altered to display different degrees of masculinity and femininity. Of the seven studies identified, three found an effect of fertility. Little et al. (2008) reported an increased preference for masculinity, but only for partnered women. However, this study had high degrees of priming potential: the participants answered in-depth menstrual cycle and sexual information before they did the study, and the study itself consisted of forced-choice paired image trials in which they selected either a masculinized or a feminized version of the same image. Participants would be able to easily guess the intention of the study and select the option that confirmed their beliefs. Penton-Voak and Perrett (2000(b)) found that fertile women were statistically unlikely to be choosing images at random. However, they did not conduct a statistical test as to the direction of that effect, instead indicating that they "inspected" the figure that showed a preference for the slightly masculinized face. Johnston et al. (2001) also found an increased preference. However, in a footnote, they reveal that they had originally found no effect and thus changed their method of fertility determination, choosing one that defined the day of "highest conception risk" as 9 days pre-ovulation. This is obviously inaccurate as it is outside of the fertile window entirely. In contrast, four other studies found no support for an increased preference for masculinity with fertility. Two found no menstrual cycle-related effects at all (Harris 2013, Jones et al. 2018), and two found luteal effects of masculinity: a decrease in masculinity preferences (Jones et al. 2005(a)), and a decrease in masculinity preferences when judging White faces but no shift in Japanese faces (Harris 2011).

Only one study examined preferences for masculine bodies (Little et al. 2007). They reported the existence of an overall fertility preference for masculine bodies along with an interaction effect for body type, relationship type, and fertility. However, this interaction effect was only significant using one-tailed tests, and the authors did not report the results of the pairwise comparisons associated with the interaction, thus making it difficult to assess the actual direction and strength of the effect or to discern any other patterns. Additionally, this study design was identical to Little et al. 2008 (above) and thus had high priming potential, making it difficult to ascertain whether this effect is associated with fertility and not belief.

Overall, there is no convincing evidence that women prefer masculine faces while fertile. All of the studies that reported an effect had serious methodological problems, making their results inconclusive. And while these results do not support the idea that women might show a decreased interest in masculinity with fertility, that some studies found evidence of a luteal effect is interesting. These results again seem to suggest an effect of progesterone and the presence of a hormonally-mediated pregnancy-maintenance behavior. Progesterone is primarily associated with the physiological changes necessary to maintain pregnancy, and it is high during both pregnancy and the luteal phase. In addition to physiological changes, it may act to stimulate behavioral changes, and these behaviors could appear in the luteal phase as well as during pregnancy. If masculinity is a reliable cue of the potential harm a man is capable of, then decreased preference in masculine men, and specifically men with whom the woman has not been sexually intimate, might be an adaptive behavior for pregnancy maintenance.

A great deal of rigorous work still needs to be done to examine the degree the menstrual cycle influences preferences for masculinity. Several factors needed to be included in these study designs, including controlling for the effects of fertility belief, avoiding design paradigms that may compound the effect of participant bias, and using across-the-cycle comparisons to examine the potential influence of other hormones. Further, statistical rigor needs to be enforced, including reporting all results and avoiding the use of one-tailed tests that fail to take into consideration the possibility of an effect in the opposite direction. This is particularly important given the evidence that progesterone, often used as in direct comparison to fertility, may be having an influence on masculinity preferences instead of fertility.

2.3.2.1.4.5 Mate Attractiveness

Other research has focused on how the menstrual cycle influences the attraction a woman feels for a man. In these studies, male attractiveness has usually been independently determined by external raters or by the use of symmetry as a proxy. This is then compared to the responses of the research subjects, which includes how they rate them, how much attention they pay them, and how well they remember them. This research can generally be divided into those that focused on visual cues, olfactory cues, or self-reported preferences.

Visual cue research has primarily focused on the effects of fertility on attention/memory and attractiveness ratings. There are mixed results for an effect of fertility on attention paid to attractive men. Fisher et al. (2004) found no effect, but Anderson et al. (2010) did, though they also found a smaller effect for the control group of attractive women that the research participants also rated, which might indicate the presence of increase intrasexual competition. However, they did not report the results for control group of non-fertile women, which makes an overall pattern difficult to identify and a conclusion difficult to draw. They have also been the only identified study to examine memory effects, for which they found no effects. Studies examining changes in how women judge a man's visual attractiveness have also had mixed results. There seems to be no relationship with symmetrical faces (Koehler et al. 2002), but there might be one with regards to overall attractiveness – but not physical attractiveness, social presence, or intrasexual competitiveness (Gangestad et al. 2004).

Four studies have focused on preferences for male odors, with odor assumed to be an indication of some quality about the man (e.g., how symmetrical or attractive he is). Each of these studies report a relationship between a man's scent attractiveness and a woman's fertility risk (Gangestad and Thornhill 1998, Thornhill and Gangestad 1999, Thornhill et al. 2003, Garver-Apgar et al. 2008). However, other results from these same studies suggest that this trend may not be as strong or clear as indicated: there are strong and statistically significant correlations between the ratings given by *both* fertile and non-fertile women (Gangestad and Thornhill 1998); a significant relationship with symmetry but not facial attractiveness; a significant *decrease* in ratings with very high conception risk (Thornhill et al. 2003); an increase in ratings given to *control* shirts when fertile but not non-fertile; and a possible *increase* in ratings given by women on a specific type of oral contraceptive (Thornhill and Gangestad 1999). Further, the reported significant difference found in Thornhill and Gangestad (1999) seem to be the result of an error: the authors state that they inverted the sign for symmetry in the methodology of all sections that examined naturally-cycling women, but in their analyses for non-naturally-cycling women, they did not. As a result, when they tested for a significant difference between the correlations (as reported: NC = 0.43, N-NC = -0.35, for full sample of men), they found a significant difference that may not have been present had the sign been inverted for both.

Only one study looked at self-reported importance of attractiveness in a mate (Gangestad et al. 2010(a)), and they found an increased preference for physical attractiveness with fertility. However, this result should be weighed carefully, as it had a particularly high degree of possible priming. The women took urine tests each day leading up to their fertile session, and the questionnaires asked for their preferences for features in a potential mate along Likert scales. It would have been clear to subjects that the study was examining fertility effects and sexual preferences.

Overall, there is inconclusive evidence for a menstrual cycle effect on a woman's preferences for a man's attractiveness. One of the primary impediments in drawing a conclusion is the lack of consistency in the results, such that non-fertile women or non-naturally-cycling women often show the same pattern as those being reported for the fertile women, or they show similar patterns toward controls as they do toward the men. There are several possible explanations for this, including an effect of participant beliefs on their responses and the influence of other menstrual-cycle trends, such as for competitiveness with other women. Future studies should control for participant beliefs about the menstrual cycle and fertility as well as their feelings and/or motivations about specific subject under investigation. This may help elucidate the existence of any fertility-mediated shifts in mate attractiveness.

2.3.2.1.4.6 Mate Discrimination

At least seven studies have explored shifts in mate discrimination. These studies propose that the increased cost associated with mating when fertile, compared to mating during other times, might result in a fertility-mediated increase in discrimination of potential mates. In contrast to other studies on mate preferences, this area of investigation does not predict the direction of ultimate preference, only that she becomes more discriminatory of potential mates.

The results of five studies generally support this. Rule et al. (2011) found that women's ability to identify a man's sexual orientation is increased when fertile. Fessler and Navarrete (2003) found that fertile women show an increased disgust response, but only toward aberrant sexual behavior (e.g., bestiality, age-disparate unions, incestual relationships). Three studies examined differences in how quickly women can accurately categorize faces and items associated with potential mates, and all suggest increased speed: Brinsmead-Stockham et al. (2008, faces) found support using lesbians; Macrae et al. (2002, faces and items) and Johnston et al. (2003, faces) found support using heterosexual women. However, the results of Johnston et al. (2003) deserve particular attention. They ran multiple comparisons on their data and found that women who were naturally-cycling took less time to categorize male faces when fertile than when they were menstrual, a pattern that was reversed for non-naturally-cycling women. However, the authors of this study indicated in a footnote that they had originally used a method of fertility determination that found no effect of fertility, and thus they chose to define the date of "highest conception risk" as 9 days pre-ovulation. This method of categorization is untenable as it places peak fertility outside of the fertile window entirely. Regardless, there does seem to be relatively moderate support for increased potential-mate based identification and discrimination with fertility.

The results of two other studies seem to suggest that this may be particularly strong when women are identifying potential mating threats. Garver-Apgar et al. (2007) found that women are more likely to think that a man might be sexually coercive when they are fertile; however, when using a snake as a proxy for potential threat, Masataka and Shibasaki (2012) found no fertility-based shift (though they did find an increase when not fertile). These results suggest that these fertility-effects may have a threat-detection component.

Overall, these results suggest that women might show tendency toward increased discrimination with regards to potential mates, and particularly toward indications of a sex-related threat. The presence of a fertility-mediated threat identification response is not surprising, particularly for sexual stimuli. Exploring the degree to which a larger fertility-mediated threat identification heuristic might exists in women, as well as the bounds of that heuristic, could reveal the interaction of different selective pressures at work.

2.3.2.1.4.7 Variety

A few studies have examined the effects of fertility on a woman's preferences for variety, and specifically male partner variety. These studies generally hypothesize that fertile women would show a preference for men who might not share similar genes. Researchers have measured different preferences which they have proposed to be proxies for genetic similarities: they have used preferences for self-resemblance, a desire for a variety in dating partners, and the ratings given to the scent of men who differ in major histocompatibility complex (MHC), a set of genes related to immune functioning. We might expect that these studies would be generally robust to priming effects; not only are women are less likely to have many beliefs regarding the relationship between fertility and their preferences for variety, but the women were blind to the intention of the studies, to varying degrees.

At least three studies have examined this, and each had different results. The results of DeBruine et al. (2005) indicate that preference for self-resemblance varies across the menstrual cycle in response to progesterone, and that this effect is particularly strong for female faces. In contrast, Faraji-Rad et al. (2013) reported a fertility-mediated increase in desire for ice cream, for hedonic food, and for variety in their dating partner. Finally, Thornhill et al. (2003) found that women do not seem to show a fertility-mediated preference for men with different MHC (though the authors implied significance in the second of these two comparisons, $p = 0.055$).

The results of DeBruine et al. (2005) deserve particular note. While this study expected to find evidence for a relationship between fertility and a desire for partner variety, they may have found evidence for one between progesterone and a desire for female family. Given the importance of intergenerational female relationships in the human cooperative breeding dynamic – for offspring care, for access for resources, and for birthing assistance – it is not surprising to see an increased desire for those relationships with progesterone, the hormone dominant during pregnancy. This is further support for menstrual cycle studies to include across-the-cycle comparisons that include the possibility of non-fertile effects on behavior.

Overall, there is little evidence for a preference for variation, though this weakness may be driven by a general lack of research interest. Future research on fertility-mediated preferences for variation should include across-the-cycle analyses, hormonally-confirmed methods of fertility determination, and different proxies for variety to determine the degree to which any preferences may exist as a general heuristic and what the bounds of that heuristic may be.

2.3.2.1.4.8 Summary

Shifts in sexual partner preferences is one of the most studied areas of behavioral fertility. It is also one of the areas for which fertility-mediated shifts are commonly accepted, specifically the belief that fertile women show an increased preference for attractive and masculine mates, particularly for short-term and extra-pair relationships. However, this review indicates that this belief is largely unfounded. Many of the studies that reported fertility effects had concerning practices including methodology with high priming potential, attributing trends to fertility that also emerged in control groups, and failing to report the results of all statistical tests, which makings drawing overall conclusions difficult.

However, there does appear to be three reliable menstrual-related effects. One is associated with fertility and suggests increased mate discrimination, particularly toward indications of a potential threat. Women are already more sexually discriminatory than men because of their higher per-mating event cost. We should expect to see this effect amplified when that cost is even higher – when she is fertile. The specific outcome of this discrimination should vary based on her unique circumstances, namely those that would moderate the cost/benefit trade-off. Of particular concern would be the general socioenvironmental condition, her socioeconomic status, and her access to both adequate healthcare and alloparental care.

The other two effects are related to progesterone and show an increased preference for female relatives and indications of health. While this may not have adaptive significance with regards to the luteal phase, it may very well have adaptive significance with regards to pregnancy, with its emergence as a luteal effect a byproduct of the effects of progesterone and the demands associated with pregnancy.

Future research into menstrual cycle-mediated effects on sexual partner preferences needs to improve upon previous research. Methodology should rigorously control for the effects of participant beliefs, particularly with regards to research areas whose findings might be integrated into common knowledge, and across-the-cycle comparisons using hormonally determined fertility should be prioritized. Further, effort should be taken to explore the effects of other hormones and their potential adaptive significance on behavioral shifts that might be found across the menstrual cycle.

2.3.2.1.5 SEXUALITY

Changes in female sexuality across the menstrual cycle have been studied to some degree since 1937, though interest in the subject began to increase considerably in the

1970's. This research can be generally divided by which specific aspect of sexuality was studied: sexual behavior or sexual desire. Many of the researchers expected to find an increase in sexuality associated with fertility, though they often disagree as to the cause: women may be seeking good genes during that time which may manifest as a shift in sexuality, partnered men may be initiated sexual activity more often, or sexual activity may be more intense or pleasurable when fertile because that might serve a fitness function by encouraging sexual activity. Because of the pressures involved in the evolution of concealed ovulation, I would not expect to see an increase in sexuality with fertility. Sexual behaviors outside of fertility serves an adaptive purpose in primates, and this may be especially important in humans if it helps maintain pregnancies.

This area of research differs from the others in some notable ways. The first is that the authors often used unique methods of phase of cycle comparison. Instead of direct fertile/luteal or across-the-cycle comparisons common in other types of studies, most of these divided the menstrual cycle into smaller subphases, unique to that study, which were then compared to other phases. They also often used physiological methods of determining fertility, which would have increased reliability at the expense of increased potential priming effects. Thus, for clarity in analyzing the results and in comparisons to other studies, I have expanded on the methodology used in these studies. Finally, because the research reviewed here goes back to 1960, and because methodology and beliefs about fertility and sexuality have changed considerably during that time, I have divided each area of investigation based on whether they were conducted before or after 2000, and I generally review the early studies chronologically.

2.3.2.1.5.1 Sexual Behavior

2.3.2.1.5.1.1 Pre-2000

Early research on sexual behavior and fertility was usually conducted on committed couples, and they were often long-term studies that lasted across several cycles (and in some cases, several years). Hormonal tests were less common, and researchers often relied on other physiological indications of shifts in fertility, including changes in basal body temperatures, cervical mucus, and the presence of mittelschmerz (ovulation associated pain in lower abdomen). As a result, participants were undoubtedly aware that this research concerned menstrual cycle changes in sexuality. However, researchers often specifically excluded women who used the rhythm method of contraception, a practice that has not continued in more recent research.

The earliest research focused on across-cycle patterns of intercourse. Of the five studies I found, three found no effect of the menstrual cycle (James 1971, Morris et al. 1977, and Udry and Morris 1977). Two of these studies explicitly excluded women who used the rhythm method and looked at patterns across at least three menstrual cycles (James 1971, Morris et al. 1977). James also re-analyzed the data from three previous studies that included data from over five years, and Morris et al. included both male and female reports of behavior. In contrast to James and Morris et al., the methods used in Udry and Morris (1977) were specifically designed to test the accuracy of different methods of fertility determination (forward and backward counting methods, cycle standardization, basal body temperature, and blood LH) and to see if any showed a relationship with intercourse. They found that each method used gave different results, and concluded that there was no across-the-cycle pattern.

Two other early studies documented menstrual cycle-related effects – but not necessarily of fertility. Spitz et al. (1975) conducted general descriptive comparison of various kinds of sexual interactions using estimated data. They found that the greatest number of days with intercourse occurred immediately after menses and concluded that there is “little sign of hormonal influence, and seem, instead, to be influenced by cultural and cognitive factors," specifically that of avoiding intercourse during menstruation. Adams et al. (1978) was the only study pre-1980 that documented any effect of fertility. They hypothesized that sexual activity should increase with ovulation, and that the findings to date – those indicating peaks pre- and post-menstruation – were due to inadequate methodology and statistics. Using both estimated methods and the presence of mittelschmerz, he reported a peak in autosexual, male-initiated, and female-initiated sexual behavior with ovulation, though he attributed the latter two findings to statistical artifacts.

Thus, in general, the research into menstrual cycle effects on sexual behavior prior to 1980 indicated no overall pattern. The only two studies that did find an effect did not agree: one found an increase associated with the days around menstruation, the other found a peak with ovulation.

Research in the 1980’s on sexual activity began to concentrate their efforts on identifying distinct types of sexual behavior during the menstrual cycle, and they began using unique methods of fertility to do so. Matteo and Rissman (1984) looked at sexual behavior within lesbian couples using estimated cycles, and they reported several mid-cycle peaks in sexual behavior, namely increases in orgasms, self-initiated sexual encounters, and total sexual encounters. However, the methods used to determine phase of cycle were highly inconsistent and poorly defined: these effects were found in either the “midcycle” or “the entire midcycle segment,” broken down into either 3-, 6-, and 9-day segments, and were found in comparison to menstruation, the end of the follicular phase, the phase immediately following ovulation, and during the luteal phase. Hedricks et al. (1987) examined coital rates in Zimbabwe and found an effect for the day of LH surge, but no effect of the fertile phase as a whole (or peak fertility, or the days immediately before or after the surge). Finally, Harvey (1987) assessed the pattern of initiating sexual behavior across the cycle. This data, which included female-initiated (autosexual and heterosexual), male-initiated, and mutually-initiated behavior was grouped into different combinations and were then compared against linear, quadratic, and cubic patterns. Quadratic relationships were found with autosexual, total female-initiated (both autosexual and heterosexual), and male- or mutually-initiated sexual behavior (but not male-initiated only or female- or mutually-initiated behavior) as well as a linear relationship in sexual arousal and pleasure (but not orgasm). Importantly, the authors admit that, when they only used cycles for which they had basal body temperature, they found no relationship with sexual behavior; when they included all of the cycles, including those for which they had to estimate fertility, they did, and thus chose to use all of the cycles for their analyses. Also, the authors repeatedly implied significant findings without statistical significance (such as there being a linear relationship with the proportion of orgasms to all sexual behavior). Overall, research during this period tended to show increases in sexual activity with fertility, though without consistency in either the methods used or the patterns identified, making the reliability of those results questionable.

Bellis and Baker (1990) was the first study that did not look at across-the-cycle comparisons. Instead, they relied on "snapshots" of the sexual behavior of women at a moment in time, and then estimated their fertility at that time. Their study focused on the potential for sperm competition in humans and examined recent in-pair and extra-pair copulations of over 2700 women reported from a magazine survey. Their results indicated a non-uniform pattern in extra-pair copulations as a proportion of total copulations (6.6%:7.3%:5%). Given the remarkably high sample size, getting a significant result from this analysis is unsurprising. Important for menstrual-cycle effects, this study did not control for hormonal contraceptive use; the authors only looked at protected and unprotected sex. Thus, there is no way to discern the degree to which any identifiable pattern would be the result of naturally-cycling women.

Overall, these early studies of sexual activity reveal no consistent effect of the menstrual cycle. This is true even though these studies had generally high potential for priming. This is possibly due to both the removal of participants who used fertility-awareness based methods to avoid pregnancy and to fewer beliefs about fertility-mediated shifts in behavior. However, as the research progressed, more studies began to report mid-cycle related effects, though without a clear pattern. The only consistency in results was congruence between Matteo and Rissman (1984) and Harvey (1987) suggesting an increase in female-initiated sexual behavior. Importantly, as this behavior is female-initiated, it could also be explained by an increased awareness of fertility and the fulfillment of expectations regarding it – an effect that the early research indicated would occur.

2.3.2.1.5.1.1 Post-2000

Recent research into menstrual cycle related changes in sexual activity has included a wide range of behaviors. Most of this research has been conducted under high degrees of potential priming, often using hormonally-confirmed fertility and some using ultrasounds and blood tests. A complicating aspect of this research is that many of the authors divided the menstrual cycle into sub-phases unseen in other areas of research. These subphases are rarely consistent in either the reasoning behind phase delineations or in the language used to describe them, making cross study comparisons difficult.

Research into changes in general or overall sexual activity suggest an influence of fertility. Two studies compared behavior in the fertile phases against either one phase or an amalgamation of non-fertile days (luteal phase – Gangestad et al. 2002; non-bleeding non-fertile days – Wilcox et al. 2004). Both studies used hormonally-confirmed methods (urine samples, LH) to identify the fertile window from the comparison window, though they used different methods to collect the urine. Gangestad et al. (2002) required participants to come to the lab to test their urine daily until they received a positive result, at which point they provided survey responses. Wilcox et al. (2004) had participants store their urine each day for eventual collection and analysis. Both studies identified the fertile window as the five days preceding ovulation, though Gangestad et al. also included the two days following ovulation. Finally, both studies found an increase in intercourse and/or sexual activity with fertility. Notably, Gangestad et al. reported a stronger effect in the women who had partners, though they did not report the results of un-partnered women, and they suggested the existence of a within-fertile window trend that was, in fact, non-significant (changes in sexual activity as a function of days until LH surge, $p = 0.112$).

Two other studies compared sexual activity across multiple sub-phases of the menstrual cycle. Bullivant et al. (2004) developed an algorithm based on changes in basal body temperature, vaginal secretions (descriptions of consistency, color, and amount), and urine samples for LH confirmation (collected six times each day for several days). They then divided the menstrual cycle into six phases based on that algorithm (early menses, late menses, follicular phase, ovulatory phase, early luteal phase, late luteal phase – ranges unspecified). Caruso et al. (2014) used blood samples to identify changes in various hormones and proteins (estradiol, progesterone, testosterone, sex hormone binding globulin, and free androgen index) along with ultrasounds to confirm changes in the dominant follicle and pinpoint ovulation. They then divided the menstrual cycle into four phases (menses – blood flow; follicular – day 5-7; periovulatory; luteal – day 21-25). The results of both of these studies indicated increased sexual behavior with fertility (fertility defined as: follicular + ovulation – Bullivant et al.; periovulatory – Caruso et al.). They differed on the effect of having a partner: Bullivant et al. found no effect, whereas Caruso et al. found a stronger effect in single women than partnered, though there was no difference between them in direct comparisons of the periovulatory phase.

Only one study looked at across the cycle changes in response to hormonal fluctuations. Roney and Simmons (2013) had participants take (and store) saliva samples and complete a daily online survey. They looked at across the cycle comparisons and factored in possible time delays in the effects of ovulatory hormones on behavior. Therefore, their study not only looked at current hormonal profiles, but also at the possibility of a 1- and 2-day lag effect. In contrast to the other findings, they found no effects of the menstrual cycle.

Overall, most of the studies found an effect of fertility on overall sexual behavior. The only study that did not also used a different, though generally more standard, method of menstrual cycle comparison, comparing changes across the cycle instead of small, unique sub-phases.

Other research has focused on patterns in sexual initiation: male-initiated, female-initiated, or mutually-initiated. No pattern has been found in either male- or mutually-initiated behavior (Bullivant et al. 2004), though there may be patterns in female-initiated behavior. This has been examined in three studies, and results are mixed. Bullivant et al. reported increases with fertility (follicular + ovulation), but they did not provide p-values, so this cannot be confirmed. Gangestad et al. (2002) also found increases with fertility. Their study incorporated the effects of a wide range of variables including the relationship status of the women, whether the partnered women were feeling strongly attracted to or fantasied about their partners and/or to other men, whether their partners were engaging in a variety of mate-retention behaviors ("high tactics" and "low tactics" using two different metrics for each), and whether those tactics could be classified as "proprietariness" or "attentiveness" behaviors. They also used two different comparison methods with regards to fertility: they compared the fertile phase to the luteal phase, and they looked at the trend within the fertile window with regards to days until the LH surge. In all of these comparisons, they found two significant results, both of which indicated increased self-initiated sexual activity: one in fertile/non-fertile comparisons and the other as a function of days to LH surge. (It should be noted that the authors reported other trends in their findings that were not statistically significant: increased sexual attraction and fantasies toward men who were not their partners within the fertile window [$p = 0.068$], and increased male monopolization behaviors in fertile window in comparing the fertile phase to the luteal phase [$p = 0.063$]). The last study that examined changes in initiation behavior is again the only one to compare across the cycle changes in response to hormonal fluctuations; as before, they found no effect (Roney and Simmons 2013). Overall, these trends match those of overall sexual behavior in that they generally found an effect of fertility in female-initiated sexual behavior with the only study not finding a pattern looking at across the cycle changes.

One study explored sexual initiation behavior under context of perceived mate investment. Grebe et al. (2013) had couples complete partner investment inventories to determine how each member felt their partner was invested in the relationship. These inventories were completed twice: once after the woman tested positive for in-lab ovulation tests, and once during the luteal phase (between 5 days post-LH surge and 3 days pre-menses). Their only significant finding was an interaction between perceived investment and phase of cycle: women initiated sex more often in the *luteal* phase when they perceive their partner as being less invested than the woman was. Notably, while the use of hormonal ovulation tests would be expected to increase the priming potential of this study, the unique perspective of this research might have helped offset any effect of confirmation bias: participants would not likely have had many preconceived ideas about a relationship between luteal phase and partner investment. Thus, this study seems moderately robust to the effects of confirmation bias.

The last major area of sexual behavior research has focused on whether sex occurred with or without a partner (allosexual vs. autosexual). Only one study examined allosexual behaviors outside of the context of sexual initiation. Brown et al. (2011) tested their results using both estimated and hormonally-confirmed methods (participants took daily urine tests and recorded the results, stopping with a positive test). They then divided the menstrual cycle into five phases (menses – days 1-3; follicular – days 5-7; ovulatory – either LH surge +2 day or -16, -2 [estimated]; luteal – either surge +7, -9 or menses -7, -2 [estimated]; premenstrual – ≥ 3 days pre-menses). The only trend they found was unsurprising: a decrease in allosexual behavior with menses (though this emerged only in estimated cycles). Three studies examined autosexual behavior, two of them using phase of cycle comparisons: Brown et al. (2011, described above) and Burleson et al. (2002). Burleson et al. had participants record daily basal body temperature and changes in cervical mucus, and they divided the menstrual cycle into five phases (menses – blood flow; follicular – until BBT nadir; ovulatory – BBT nadir +4 and spinnbarkeit cervical mucus present; early luteal – 6 days pre-menses; premenstrual – remaining days pre-menses). Both Brown et al. and Burleson et al. found increased sexual activity with fertility (defined as: ovulatory – Brown et al. 2011; follicular + ovulation – Burleson et al. 2002). The final study, like before, found no effect at all in using across-cycle comparisons with hormonal profiles (Roney and Simmons 2013). Overall, these trends match the other findings: fertility effects were generally detected for all studies except two: one that used across-the-cycle comparisons – which found no effect – and one that conducted direct fertile-luteal comparisons and included partner-investment considerations – which found an effect of the luteal phase.

In sum, these results would suggest a strong influence of the menstrual cycle, and specifically fertility, on sexual activity: allosexual activity consistently decreases with menstruation, and there seems to be an increase in both general and female-initiated sexual behavior with fertility (but not male- or mutually-initiated). However, all of these studies except two used highly invasive methods of fertility determination such that the participants themselves knew precisely when they were fertile. Additionally, none of these studies took any effort to address this bias by either hiding the purpose of the study or by incorporating participants' beliefs into their analysis. There were only two studies that used methods of determination that did not also give participants information about their fertility results – Wilcox et al. (2004, daily urine samples) and Roney and Simmons (2013, daily saliva samples). Wilcox et al. found effects in overall sexual activity, and Roney and Simmons consistently found no impact of fertility on sexual behavior of any kind.

Thus, it is possible that the results indicating an effect of fertility are an artifact of fertility belief and not fertility. Future studies should implement controls for this possibility, incorporating participant beliefs into their analyses. Further, they should avoid using unique, unvalidated methods of phase of cycle comparison. Their usage not only makes it difficult to examine across-the-cycle patterns in behavior, but it also makes it difficult to compare results across studies.

The results of Grebe et al. (2013) deserve particular note. The authors attributed their finding to the selective pressures associated with concealed ovulation: extended sexual receptivity allows women to initiate sex throughout their cycle to as a mate-retention behavior, and thus should do so more often when *not* fertile, particularly when they fear their partner lacks investment. The authors state that this should happen throughout the cycle, but they only tested for a luteal effect, which they found. However, this effect may also be the result of any pregnancy-maintenance effects of progesterone; when progesterone is high, so are the chances of pregnancy and the need for frequent intercourse to avoid preeclampsia. This effect would be expected to be amplified when the woman fears abandonment as that may increase that risk. However, this is the only study I have found to specifically examine luteal effects on sexuality, and a great deal more work is needed to explore the bounds of any potential effect.

2.3.2.1.5.2 Sexual Desire, Arousal, and Fantasies

2.3.2.1.5.2.1 Pre-2000

Only five studies have been found that examined changes in sexual desire prior to 2000. The earliest identified is Hart (1960). He asked his patients who were seeking contraceptive advice both how their libido through their cycle changed and what they knew about the "safe period" in which they could have sex without conceiving. He reported that most women had peak sexual desire with menstruation; only 6% had maximum libido in the middle of the cycle. This pattern corresponded strongly with participants' beliefs regarding the "safe period" in which they could have sex without conceiving, and Hart indicated that this suggested a strong influence of belief on their cycle-related behavior. Notably, even though most of the participants knew that fertility increased mid-cycle, this did not coincide with their sexual desire. This suggests that either they had no expectation that fertility and sexual desire was linked, or that they responded in direct contradiction of that belief. Importantly, this study occurred before oral contraceptives were widely available (not legal nationwide in the U.S. until 1965). It is therefore likely that these participants, already coming to the researcher for contraceptive advice, were trying to avoid pregnancy by the use of a calendar or rhythm-based method, which often teach that pregnancy is unlikely during menstruation. Thus, it is very possible that these participants' sexual desire was a result of either a self-fulfilling prophesy (which might help avoid sex during fertility) or a conditioned response (they have become accustomed to having sex during that time).

A few decades later, other researchers began to explore a relationship between fertility and sexual desire. Stanislaw and Rice (1988) found increased sexual desire with fertility; however, they recruited participants exclusively from groups that promote the use natural planning for conception purposes through the use of methods that specifically taught that increased sexual desire was a sign of increased fertility. Furthermore, they determined fertility by the use of fertility-awareness methods that the participants were tracking, including changes in basal body temperature. Thus, these results seem to be a clear result of confirmation bias. Schreiner-Engel et al. (1989) examined menstrual cycle-related hormonal fluctuations to determine if it might provide insight into hypoactive sexual desire disorder among women. They used both blood and basal body temperature to determine fertility, and they found no effect. Slob et al. (1996) examined changes in sexual arousal both across the menstrual cycle and as a result of potential sexual conditioning. They brought the participants to the lab twice during which they collected blood samples and participated in the experiment. Through the use of erotic videos, clitoral vibrotactile stimulation, and a thermistor clip attached to participants' labials, they found that fertile women showed increased subjective responses of arousal but no objective changes in physiological responses. Upon repetition in the opposite portion of their cycles, this effect continued (but without significance) for women who had previously been fertile. The authors concluded that these differences were likely due to learned and conditioned effects more than they were fertility.

The final paper deserves particular attention. Englander-Golden et al. (1980) examined the effects of "aware" and "unaware" conditions on reported sexual arousal. Their purpose was to determine the degree to which a woman's reported sexual arousal was influenced by whether she perceived the study having to do with her menstrual cycle. The went to great lengths to blind the participants to the purpose: they included male participants, they told participants the study was on biorhythms, and the participants filled out extensive daily questionnaires (80-item) with only a small amount dealing with the menstrual cycle, which they told the participants they would "factor out." At the end of the study, the participants filled out a questionnaire that asked them to complete the questionnaire again, this time retrospectively on the average feelings they felt during the three phases of their last menstrual cycle: premenstrual, menstrual, and luteal (defined as the days 13 through 7 preceding menses). Because the authors were not examining fertility effects, they did not include the fertile window. The results showed that when the participants were unaware of the purpose of the study, they reported the lowest sexual desire during the luteal phase; when they were aware, they showed the highest ($p = 0.003$). This study is thus strong evidence that a woman's beliefs regarding her cycle can have a strong influence on what she reports, particularly if she is aware of the study's intention.

Overall, these early research findings suggest that there is no hormonal influence on sexual desire. Instead, they point to a strong relationship between sexual desire and other factors, namely confirmation bias, conditioned effects, and self-fulfilling prophesies.

2.3.2.1.5.2.2 Post-2000

Recent research into menstrual cycle-related changes in sexual desire and interest have looked not only at the overall fluctuations in sexual desire, but also the effect of relationship status and whether the women had been "mated" – presumably, those who have had any prior sexual experience regardless of current status, though this is not defined (Pillsworth et al. 2004).

There have been four studies that have looked at menstrual cycle fluctuations in sexual desire and/or interest across all women. Gangestad et al. (2002) found no effect of fertility, either in fertile to luteal comparisons or in days to LH surge within the fertile window (methods described above). Röder et al. (2009) used daily journaling and estimated methods (fertile – 15 days pre-menses, -5; non-fertile – all other days) and found increases with fertility. Brown et al. (2011) found a decrease with menses using the hormonally confirmed cycles but not with the averaged cycles (methods described above). The last study is Roney and Simmons (2013). Unlike their analyses on sexual behavior, they used both phase of cycle comparisons and the across-the-cycle changes in response to hormonal profiles (follicular – all days until fertile window; fertile – estradiol drop/progesterone increase, -5; luteal – all days pre-menses). They found an increase in sexual desire in the fertile window as well as with a 2-day lag in estradiol, and a decrease with progesterone (real-time changes as well as 1-, and 2- day lags). Overall, these results suggest an increase in desire with fertility and a possible decrease with menses.

Four other studies have examined the impact of either relationship status or previous sexual experience on sexual desire. Three studies looked at the effects of relationship status. Gangestad et al. (2002) found no effect for partnered or single women using either of their methods of comparison (methods described above). Haselton and Gangestad (2006) used daily journaling and estimated fertility (fertile – 15 days pre-menses, -4; luteal – 3 days pre-menses, -8) and reported an increase in sexual desire in partnered women but did not report the results of the single women. Pillsworth and Haselton (2006) examined several potential influencing factors on sexual desire including attractiveness ratings for their partner's "investment" quality and "sexual" quality as well as their and general relationship satisfaction. They used in-lab urine tests (fertile – surge -2, +4; luteal – 3 days pre-menses, -7 days) and questionnaires completed after they received a positive urine test and found only one effect: sexual desire increased in the fertile window for women with high relationship sexual satisfaction. Only one study has looked at sexual desire in "mated" women. Pillsworth et al. (2004) used actuarial data to estimate the conception risk of participants based on their answers to a one-time survey (ovulation – -15, Wilcox et al. 2001 actuarial) and found an increase in sexual desire with conception probability. In general, these results suggest that being in a relationship, particularly one with high sexual satisfaction, might increase sexual desire around fertility.

Two studies examined the impacts of the menstrual cycle on sexual fantasies, and both had relatively high priming potential. Bullivant et al. (2004) looked at sexual fantasies as part of a larger, multi-part study on sexual behavior and desire. In their second part of the study, they examined fantasies in-depth, and they found no effect; in their third, they found an increase in fantasies with the ovulatory phase compared to all other phases. Dawson et al. (2012) had participants complete daily journal entries and provide in-lab urine samples once a week (follicular – menses until LH surge; ovulation – LH surge +2; luteal – all other days). They examined a variety of fantasy components: frequency of fantasies; degree of arousal; gender and familiarity of individuals; the presence of emotional, visual, and sexual components, and what specific sexual components were included; how they were generated or triggered; whether it was recurring; and how it may have impacted their ultimate sexual behavior. They found menstrual cycle changes in two sets of phase comparisons. The first finding was that the frequency of fantasies and the number of males in the fantasies were lower in the luteal phase than the other two phases. The second set of changes showed higher degrees of arousal and emotional content (versus visual or sexual) in the ovulatory phase than the follicular phase. Overall, these results suggest that there might be a positive association between fertility, emotional fantasies, and sexual arousal, and possibly a negative association between the luteal phase and interest in multiple male partners, but there is no other identifiable trend.

In sum, recent research on changes in sexual desire suggest a menstrual effect (decreased desire), a possible luteal effect (decreased interest in multiple males), and a fertile effect. The fertile effect seems two-fold: a marked increase in for partnered women in sexually satisfying relationships, and an increase in the emotional content and sexual arousal of fantasies. It should be noted, however, the methodology of most of this research included invasive methods of fertility tracking, and not only did the participants know that the study involved sex and their cycles, but they also knew exactly when they were fertile. Thus, if they had beliefs about their sexual desire and fertility, they may have emerged in these results. This makes it difficult to ascertain the degree to which any of these patterns are the result of fertility and not fertility belief. Future research should take steps to control for the effect of confirmation bias on sexual desire. Further, the only luteal finding agrees with other research that shows a decreased interest in extrapair relationships with progesterone, again suggesting the possible influence of pregnancy-related selective pressures. The possibility of this should be explored.

2.3.2.1.5.3 Summary

Research on female sexuality in response to the menstrual cycle has an extensive history. Early research indicated no hormonal effect on either sexual behavior or desire. Instead, the only patterns that emerged were those related to sexual desire, and they indicated that desire was strongly influenced by attitudes and beliefs regarding sex and conception (and whether they wanted to avoid it). By the mid-80s, a trend of increased female-initiated sexual behavior began to appear, and it was accompanied research that indicated that women's menstrual-cycle related sexual desire was not being influenced by hormonal changes but instead by fertility beliefs. Thus, while it is possible that the reported shifts in sexual behavior were due to hormonal effects, but it is at least as equally possible they were in response to increased exposure to concepts regarding fertility and sexuality, including through fertility-awareness based methods of contraception. That increases in sexual behavior at this time were entirely female-initiated is supports this hypothesis – there was no evidence that men were aware of and responding to their partners' fertility.

The relationship between sexuality and fertility beliefs is further supported by recent research. The results that suggested fertility-associated peaks in sexual activity indicated that the activity was being largely driven by the women, a trend that corresponded with the research that suggested fertility-mediated peaks in sexual desire. Importantly, this trend is strongest in sexually satisfied women in committed relationships, and as these women are naturally-cycling, there is a fair chance that they may be familiar with fertility-awareness based methods of contraception and with the commonly held association between fertility and sexuality. All of this suggests that these findings may not be due to hormonal fluctuations but instead to the beliefs and expectations that these women have about their sexuality and fertility. Thus, future research should account for the possibility of confirmation bias and control for participant beliefs, which would allow them to ascertain whether these shifts are due to fertility and not fertility belief. It is also important that validated and standardized methods of phase of cycle determination be used, preferably those that look at across-the-cycle shifts thereby allowing for the detection of an effect of progesterone. Indeed, two studies found notable luteal-effects: increased female-initiated sexual behavior with perceptions of decreased partner investment and a decrease in the number of males present in sexual fantasies. Both of these findings support an influence of progesterone and pregnancy-related selective pressures. However, much more research is needed before any conclusions can be drawn.

2.3.2.1.6 SOCIAL BEHAVIOR

Several areas of research have explored the degree to which fertility might influence a woman's social behavior. Classification in this category is particularly imperfect, as behavioral shifts associated with sociality may also be associated with many of the other trends. In this section, I have included shifts associated with the likelihood of responding positively to courtship solicitations, engaging in behaviors associated with increased danger, and dominance-related behaviors.

2.3.2.1.6.1 Courtship Solicitations

One study examined how fertility might influence a woman's response to courtship solicitations. I have placed this study under the social category as it could not be easily categorized under any of the other sections, as it is related to neither sexuality nor sexual partner preferences, and it has a stronger social element than the studies included in those sections. The authors proposed that women would show an increased inclination to respond positively to courtship solicitations when fertile. However, I might have expected to see increased hesitancy due to potential risks of meeting with a stranger, though I expect this would depend upon how masculine the stranger is.

In this study, Guéguen (2009) staged male confederates in public places to solicit women. The man would stop a woman, tell her that he found her pretty, and ask her for her phone number and to go out for a drink. After the interaction, a female confederate would approach the woman, explain the research study, ask for her consent, and collect her menstrual cycle information. The authors found that women who were naturally-cycling were more likely to respond favorably than those who were non-naturally-cycling, and that naturally-cycling fertile women were more likely to respond favorably than those in the other phases of their cycle. However, the authors did not ask whether the women were in a relationship already, and since many women who are on hormonal contraceptives have an active sex partner, their lack of interest may be an artifact of relationship maintenance behaviors.

Overall, this is some evidence for an increased inclination toward romantic relationships. However, more work is needed. The novel approach of this study proves real-world data with no potential for priming, but it should be replicated to include additional, more complete surveys that include collect relationship and sociosexual information, that introduce variation in male solicitors, and that allow for follow-ups to determine fertility more accurately.

2.3.2.1.6.2 Risk of Harm

A woman's responses to potentially harmful situations or individuals have been examined through various lenses. Above, I reviewed this in context of sexual partner preferences, with results indicating that women do show fertility-mediated enhancement of mate discrimination tendencies, specifically toward potential threats. It is possible that this pattern is the result of a heuristic that applies to a variety of social circumstances. If so, I would expect women to demonstrate a fertility-mediated bias against a variety of potentially untrustworthy, harmful, or dangerous scenarios or individuals.

Three studies have examined this in the context of pursuing activities with various levels of risk. Two studies asked women to indicate behaviors they have engaged in recently. These behaviors ranged from being low risk (e.g., watching TV at home, going to work, church or to the movies) to high risk (e.g., drinking in public, going to a bar, walking in dimly lit areas). They found that naturally-cycling women in the fertile phases of their cycle showed less tendency to engage in the high-risk behaviors (Chavanne and Gallup 1999, Bröder and Hohmann 2003). The third study, Guéguen (2012), tested how women responded to a potentially threatening man in their presence. The authors state that the appearance of this man was constructed make him appear "doubtful;" he had large tattoos, a shaved head, and a scarred face, and he glared angrily at the participant. The authors found that fertile women sat farther away and were less likely to either smile or verbally greet the man than women with either low or medium fertility risk. Overall, these studies seem to suggest that fertility might increase a woman's aversion toward risky or dangerous situations overall, not just in a mating context.

Three other studies have examined this in a larger context of group identity. It is possible that any identifiable trend might be an artifact of a threat identity bias, as out-groups are generally perceived as less trustworthy than in-groups. Two of these studies looked at fertility's effects on in-group/out-group bias, particularly with respect to racial groups. McDonald et al. (2011) found that fertility increased bias against out-groups, using both actual racial groups and groups assigned based on t-shirt color. This effect has been replicated using election-related data (Navarrete et al. 2010): women who perceived Barack Obama as being more light-skinned than he is were more likely to say that they would vote for him as their conception risk increased. The converse was also true: those who viewed him as more dark-skinned were less likely express support as their conception risk increased. One study examined this in the context of implicit association with sexual orientation; Brinsmead-Stockham et al. (2008) found that, when fertile, lesbians had increased self-identification with homosexuality. These studies indicate that women do show a tendency to be more discriminating against others who might be outside of their group.

Overall, these studies suggest that women do show fertility-mediated shifts related to potential harm or danger: fertility consistently seems to increase paranoia tendencies. However, compared to the other avenues of fertility-mediated research, relatively little has been done to explore this. Given the pattern in both social and sexual scenarios, this might suggest a larger heuristic at work, and more research is needed to explore this. Of particular interest is how it develops, dissolves, shifts in response to other variables, and responds to various priming stimuli, which may reveal the interaction of different selective pressures at work.

2.3.2.1.6.3 Dominance and Intrasexual Competition

The intersection of fertility and dominance behaviors have been examined in several contexts. They include fertility-mediated shifts in *response* to dominance (in men) as well as shifts *in* dominance, including both dominance in general and toward women specifically. Shifts in intrasexual competition has been the most studied area, which is unsurprising given the degree of female-female competition seen in humans. Indeed, other female primates show fertility-mediated shifts in intrasexual competition, and I would expect to find the same trend in women. I might not necessarily expect to see the same trend in general social conditions or toward men, though this might depend upon the degree to which the individuals are direct rivals for high status resources. The same might be the case for shifts in response to dominance – I would expect women to behave differently based on the situational context and the degree to which she is a direct competitor of the dominant individual.

I found one study that explored fertility-mediated shifts in response to dominance. The study used a mock job negotiation scenario to determine how fertility influenced the salaries that women offered to high-dominant and low-dominant men. The authors reported that fertile women allocate significantly more resources to dominant men than non-dominant men. However, there were several problems with the study: there was a high potential for priming, the authors failed to report many of their results, and they suggested a significant difference between the male and fertile female allocators that did not exist ($p = 0.06$, Senior et al. 2007). Thus, it is difficult to determine how universally applicable these results actually are.

A few studies have examined fertility shifts in dominance. One study examined this using self-reported feelings of dominance, and they found no across-the-cycle effect for naturally-cycling women (Markey and Markey 2011). Two other studies examined this using more concrete measures of dominance – the use of status and ornamentation items. Both found a fertility-mediated increase in attention paid toward and memory of these items (Lens et al. 2012, Zhuang and Wang 2014). Zhuang and Wang's (2014) research showed particularly interesting effects: women showed different effects when they primed with male and female faces – an amplified fertility effect when primed with women, and a luteal effect when primed with men.

Intrasexual competition has been studied in a variety of ways. Three studies have explored this using direct forms of competition. Durante et al. (2014) conducted a dictator game in which participants gave money to potential "mates" (males) or "rivals (females). They found that fertile women gave more money to mates – and less money to rivals – than luteal women did. However, they did not report whether the difference in the money given to mates and rivals were significantly different. Piccoli et al. (2013) studied shifts in the kinds of words that women used to describe each other. They found that naturally-cycling fertile women were significantly more likely to use animal-related words, and less likely to use human-related words, to describe female targets than other women were likely to use. They also found a relationship between the use of animal-related words and intrasexual competition scores in naturally-cycling women that was not found in non-naturally-cycling women. Maner and McNulty (2013) examined competition through the lens of changes in testosterone. This study involved two groups of women. One group was naturally-cycling and wore t-shirts at different points in their menstrual cycles (“volunteers”). The other group was composed of both naturally-cycling and non-naturally-cycling women (“participants”), and they smelled the shirts of the volunteers - notably, no attention was paid to the phase of cycle of the participants. The authors found that women who smelled fertile shirts had higher levels of testosterone than those who smelled the non-fertile shirts. However, this was driven by a *decrease* in testosterone in those that smelled the non-fertile shirts, particularly for women who were in a committed relationship. The implication of this is that the level of intrasexual competition, as measured by testosterone, drops in conditions of low threat: when they are in a committed relationship and when potential rivals are not fertile. The authors found that this effect was more consistent for participants who were not naturally-cycling; women who were naturally-cycling showed a less consistent decrease in testosterone. I propose that this effect might have been due to the fertile status of some of the naturally-cycling participants. It is possible that fertile women remain in a state of proverbial “high alert” to potential rivals – those who might also be fertile, potentially due to increased competition for resources – and that these women would not demonstrate a substantial drop in testosterone. This should be explored further.

Three other studies have examined more indirect types of female intrasexual competition. Fisher et al. (2004) found a fertility-mediated *increase* in the attractiveness ratings given to other women. Koehler et al. (2002) found a similar pattern for *non-naturally-cycling* women: they showed an increased preference in for female symmetrical faces during their would-be fertile window. Finally, Miller and Maner (2010(b)) conducted an ancillary analysis in which the confederates who were assisting in the research rated the female participants who varied in their cycles. The confederates did not rate the women differently on attractiveness, flirtatiousness, or extroversion. However, as this was not a planned comparison, and we do not know where the confederates were in their cycle, this result is not particularly meaningful. However, these studies suggest that, at least for the metrics used here, there is little evidence to suggest an increase in indirect competition.

Overall, these results suggest that fertile women do show fertility-mediated shifts in dominance-related behavior. This effect seems particularly consistent for competition for resources and direct female-female competition, potentially in response to the degree of perceived threat. It is possible that women show shifts in dominance behavior when competing with men, but I do not know of a study that has examined this; the only male-related study suggests that fertile women might be more rewarding of dominance from men. However, male-female competition for resources might be a fruitful area of research. The socioeconomic dynamics in the United States – with the predominance of the nuclear family and more women competing with men in the workplace – might suggest the presence of fertility-mediated increases in competitive behavior toward all potential competitors as the byproduct of a general heuristic toward fertility-mediated resource-acquisition. Testosterone-related shifts in female-related competition might be another avenue to explore. Testosterone may act to increase a fertile woman’s awareness of resource acquisition opportunities, potentially allowing her to recognize and respond to potential threats to those resources, including other fertile women. Further, the contextual differences between the direct and indirect tests of female intrasexual competition suggest that the precise conditions matter a great deal to female-female competition. This may be due to complex relationship between women that has emerged as a result of cooperative breeding. Exploring the contexts under which female-female competition ebb and flow should be explored.

2.3.2.1.6.4 Summary

In sum, evidence does suggest that women show fertility-mediated shifts in social behavior. I expect that these research findings are generally robust to priming effects due to an increased reliance on real-world scenarios, the authors being fairly circumspect about the expected outcomes, and the general lack of preexisting beliefs about fertility and these social scenarios.

The research has focused primarily on behaviors that minimize risk and increase social status, with particular focus on competition for resources and between women. Growing evidence from multiple lines of investigation suggests the presence of a fertility-mediated risk-avoidance heuristic that deserves dedicated attention. It is possible that this heuristic – including degree of attunement and assessment criteria – emerges from the confluence of developmental biosocial factors in ways that mirror life history strategies, and this should be explored. Dominance behavior should also be explored in a broader context, branching into an exploration of the hormones involved as well as various status-related avenues including various methods of competition and male-female competition for resources. A particularly intriguing area of investigation is the intersection of these domains – fertility-mediated competition for status while avoiding risk. For example, exploring how fertility might influence stock-investing behavior, particularly given different socioeconomic circumstances, might be quite interesting.

2.3.2.1.7 OVERALL TRENDS

Even though research exploring menstrual-cycle shifts in human behavior has been ongoing for more than a century, little progress has been made in the identification of consistent and reliable trends. This review argues that many of the commonly-accepted beliefs – for example, that women show increased sexual desire and preference for masculine men when fertile – may have little substantial evidence supporting them. Instead, these findings seem to be the result of the beliefs of the participants causing a confirmation bias effect, an effect amplified by the research methodology often employed. There does seem be evidence for some of these commonly accepted findings, however. Women may undergo subtle physiological shifts across the menstrual cycle, though this does not necessarily appear to be associated with a strong mate attraction affect. Also, women may engage in increased self-ornamentation behavior, but this may also be related to increased intrasexual competition. And finally, men may increase mate retention behaviors when their partners are fertile, which may represent a relationship maintenance behavior that emerges with pair-bonding due to the selective pressures associated with the benefits of serial, social monogamy.

Three other less-widely known trends demonstrate reliable and consistent patterns. One pattern suggests the presence of a fertility-mediated risk-avoidance heuristic. Thus far, it indicates an increased avoidance of risky behavior, bias against out-group members, and discrimination of potential mates, particularly those who might represent a sexual threat. This pattern might indicate that the general bias women have toward a more cautious sexual and behavioral strategy might be reflected in menstrual cycle shifts. Another pattern is that of a fertility-mediated interest in social status, supported by evidence of increased competition with women and for resources. This pattern suggests that fertility might prime women toward resources in preparation for possible pregnancy. The last pattern is a luteal-mediated effect, and it suggests an increased preference for relationship commitment, for female relatives, and for indications of apparent health, and an increased bias against masculine men. This pattern suggests an effect of progesterone that might act to optimize behavior in response to pregnancy-related demands.

Research into menstrual cycle-related shifts in behavior has focused on the adaptive significance of fertility and its relationship to sexuality. However, the evolution of human reproduction has been primarily shaped by the demands of caregiving and the resources necessary to optimize the cognitive growth of a woman's offspring. Future research into menstrual cycle-related shifts must take into consideration the broader pressures that have shaped human evolution in order to identify what forces might actually be at work.

2.4 SUMMARY

Understanding human reproductive behavior requires an interdisciplinary and comprehensive approach. The evolutionary pressures that have shaped all live on earth have also shaped human evolution, and thus understanding human behavior must begin with an understanding of these dynamics, including those related to sexual conflict. Most species have a female choice system due to the higher cost that females often pay for each mating event. In mammals, the evolution of lactation widened this asymmetry while simultaneously contributing to mammalian success. This adaptation added unique pressures to the mother while allowing for increased dissemination, socialization, and cognition.

Primate reproductive behavior is tied tightly to lactation, sociality, and cognition. In primates, and a few other mammalian species, the costs of increased cognition and sociality seems to have driven the emergence of menstruation due to the demands that cognitive growth places on the mother during pregnancy. It also seems to have driven the development of intensely competitive hierarchies in female primates as a means to compete for reproductive resources. Additionally, several primate species evolved the ability to conceal their fertility, and while this adaptation likely originated to protect their infants from unmated males, it may also have allowed for a variety of other adaptive behaviors to emerge. The coevolutionary dynamic between social and cognitive complexity seems to have had a substantial influence on the hominin lineage in particular. It seems responsible for several unique characteristics indicative of modern humans including female sexual dimorphisms; the prevalence of social, serial monogamy; and a multigenerational social system built on allomaternal care.

Universal patterns in modern human mating behavior reflects these forces. Women show a universal preference for resource- and/or care-provisioning partners and an avoidance of potentially dangerous men. The high per-mating event cost of women seems to be reflected in menstrual-cycle related shifts. When the cost of mating is highest, women show increased interest in resources and social status and decreased interest in potentially risky situations. They also seem to show luteal effects that mirror those associated with pregnancy and that seem to indicate the presence of behavioral shifts associated with pregnancy maintenance. In response to these preferences in a female choice system, men engage in a more varied set of strategies. These strategies emerge in response to biosocial developmental factors and result in a continuum of behaviors associated with investment in parenting or mating effort, as well as in sexual coercion.

The review resolves that there are several lines of current investigation that should be reconsidered, and it also identifies several new avenues of exploration. Mate preference research has often relied on the assumption that women are dependent on male resource-provisioning, a trend that is neither universal nor historic. Further, behavioral fertility research has often assumed that fluctuations in a woman's sexual behavior during her menstrual cycle must be reflective of a fertility-associated shift instead of being the result of cognitive bias or other hormones necessary for pregnancy-maintenance. Future research should prioritize exploring these factors, including various paths for resource acquisition (e.g., intrasexual competition, career paths and financial independence, access to healthcare, and familial support) as well as pregnancy-maintenance behaviors that might emerge in menstrual cycle trends. Finally, all future research on menstrual cycle-effects should control for the effects of participant beliefs and confirmation bias.

CHAPTER 3. FEMALE MATE CHOICE AND THE EMERGENCE OF MALE COERCION

3.1 ABSTRACT

When females choose mates, males may respond in several ways: by allowing an evaluation by the female and investing substantially in subsequent reproduction (here, type 1); by allowing evaluation but withholding investment following mating (type 2); or by preventing evaluation and attempting to coerce the female to mate (type 3). In this modeling analysis, we examine the conditions under which these strategies, individually or in combination, are expected to persist in the population primarily using the criterion of evolutionary stability. We also consider the roles of female resistance, social policing, and extra-pair paternity in influencing these outcomes. Using six focal systems taken from primates, fish, birds, and insects, we derived parameters for a game-theoretical model to determine the expected evolutionary stable frequencies or unstable combinations of the male strategies based on system-specific parameter magnitudes. In chimpanzees, guppies, Japanese water striders, and scorpionflies, males making the highest investment in each reproductive event were the sole persisting type; in mallard ducks, an evolutionarily stable mixture of types 1 and 3 prevailed; and in humans, a stable mixture of types 1 and 2 persisted. In accord with the infrequency of consistent coercion across taxa, our results suggest that coercion may often be evolutionarily unstable and available only opportunistically as the strategy of last resort.

Author's Note: This chapter is presented as it was published in 2017 in Behavioral Ecology and Sociobiology. I have updated the formating and style (primarily of the figures and tables) to match this dissertation, but I have otherwise made no edits. I have therefore added a brief comment at the end that reflects on the findings given a more complete understanding of coercion in humans.

3.2 INTRODUCTION

Many mating systems across animal species in nature feature female mate choice, including choice exerted before mating (e.g., leks [Hoglund and Alatalo 1995] and female physical or social dominance [Clutton-Brock et al. 1988, 2006]) and after mating (e.g., selective sperm sequestering [Eberhard 1996] and some forms of last male precedence [Boorman and Parker 1976, Eady and Tubman 1996]). But coercive male mating is also found in many of these systems. Male coercion is common though not ubiquitous in systems with pre-mating female choice (Palmer 1989, Clutton-Brock and Parker 1995(b)), often with effects detrimental to the female (Rowe et al. 1994, Crudgington and Siva-Jothy 2000, Stutt and Siva-Jothy 2001, Blanckenhorn 2002) and sometimes to the chance of successful reproduction from the mating (Warner et al. 1995, Dunn et al. 1999). Coercion can take the form of forced copulation, harassment, and intimidation (Clutton-Brock and Parker 1995(a)(b)). In some systems, male coercion may be opportunistic, expressed in individual encounters (Mineau et al. 1983, Mitani 1985, Emlen and Wrege 1986, Smuts and Smuts 1993 [review]); in some haremic or despotic mating systems, coercion may be more integral to the mating system (Smuts and Smuts 1993 [review], Marlowe 2000).

Game theory provides an appropriate theoretical framework for understanding mating systems because of the inherent mix of cooperation and conflict both within and between sexes (Maynard Smith 1977, Crowley and Hart 2007, Hart et al. 2011). The key processes of female choice among available males and competition between males for access to females (Darwin 1871, Kokko and Jennions 2008) have been well documented for many systems (Andersson 1994 [review]). But studying these processes in isolation (see Kuijper et al. 2012) or without adequate attention to internal consistency (e.g., Maynard Smith 1977, see Kokko et al. 2003 and Houston et al. 2013) may oversimplify the analysis and fail to account for important patterns. Previous theoretical approaches to sexual coercion have simulated arms races between males and females with costs to morphological armaments (Parker 1979, 1983) or have taken a human-centric perspective to understand the causal relationships for sexual violence against women (Malamuth et al. 1995, Knight and Sims-Knight 2003).

Female choosiness incurs costs (e.g., time, risk) in the necessarily imperfect evaluation of potential benefits of a possible mate (Luttbeg 1996, Roff 2015). These benefits may be direct, such as extensive paternal care, or indirect, through good genes for offspring (Kokko et al. 2003, Kuijper et al. 2012, Roff 2015). In response to female choosiness, males may (1) devote substantial time and energy to maximize reproduction if chosen, at the possible expense of other pairing opportunities; (2) invest little in each pairing but more into increasing pairing frequency; or (3) pre-empt evaluation by the female via coercive mating, thus avoiding rejection and maximizing pairing frequency, though female resistance to coercion and other factors may reduce the likelihood of mating success. The imperfect male assessment expected when females pay a cost based on the extent of assessment and the vulnerability of females to coercion make it likely that male type (2) or (3) can persist or even dominate type (1) males in some circumstances. Here we address the interaction between optimizing the precision of female choice and determining the frequencies of competing male strategies. Our premise is that the evolutionarily stable (or unstable) outcomes of this game may account for some of the strategic patterns generated by animal species in nature.

The implications of variation in time available for mating were considered in an earlier series of studies (Clutton-Brock and Vincent 1991, Clutton-Brock and Parker 1992, Parker and Simmons 1996). These analyses showed that population mean values for relative times available for mating, along with adult sex ratio, can determine sexual selection and sexual competition (see also Fromhage and Jennions 2016). The relationship between the survival-determined adult sex ratio and the investment (e.g., time commitment)-determined operational sex ratio is also important (Kokko and Jennions 2008). Our model incorporates these features and uses them to evaluate three key male strategies when choosy females can at least sometimes discriminate among them.

Studies of female choice to date have emphasized male ornaments (Scribner et al. 1989, Pradhan and van Schaik 2009) and their mating signals or displays (Reid et al. 2004, Mowles and Ord 2012). Though weapons used in male-male competition are sometimes used to coerce females, particularly in mammals, females may avoid using weapons as indicators of male quality because of this coercion potential (Pradhan and Van Schaik 2009). Females avoid coercion by avoiding exposure to coercive males and by directly resisting mating (Arnqvist 1992, Kokko 2005); but some males have specialized structures to facilitate coercion (Pradhan and van Schaik 2009), and in some cases females could benefit indirectly from mating with forceful males if forcefulness is heritable (Thornhill 1980(b), Kokko 2005), though we do not expect these indirect benefits to recoup the direct costs of coercion (Cameron et al. 2003) and thus do not include them in this model. When evaluated by a female, males may display repeatedly to improve their chances of mating even when such signals are costly, according to a modeling study (Mowles and Ord 2012). Models have also shown that males may honestly advertise a commitment to parental care, depending on details of the ecological and social context (Kokko 1998, Alonzo 2012, Kokko et al. 2014), so females may gain valuable information by investing in assessment (Luttbeg 2004).

Our main goals in this study are to understand (1) the basic mating game between choosy females and males that differ in reproductive investment per offspring; (2) the circumstances in this context that allow for the persistence of a coercive male mating strategy; and (3) the resemblance between patterns generated by the model, when parameterized for certain natural systems, to those observed in nature. The systems in the comparative part of our study are six species that include primates, fish, birds, and insects, chosen for taxonomic diversity and reasonable fit to the model's assumptions. We address ways that our approach may be extended to incorporate other potentially important features and species in future work.

In the model, available males, which collectively constitute the male pool, wait until randomly selected for evaluation by unpaired, reproductively active females. Males join the pool when they are not otherwise occupied with a female. Females prefer the male type that commits more time or other resources to the liaison and maximizes reproductive success (i.e., type 1). (We generally refer to the committed resource as time but allow in some case studies that follow for physical resources to substitute for time.) With only male types 1 and 2 present, where type 2 commits less time to the liaison, with generally less reproductive success as a result, the female may spend discrimination time td to improve her ability to discern the type of male she has encountered and decide whether to pair with him. Male courtship costs are included as the time spent under female discrimination, though some competition costs are included as reduced reproductive lifetimes. The female's ability to discriminate between types 1 and 2 is assumed to increase with the time spent discriminating, but with diminishing returns (see Luttbeg 1996). We assume that she chooses discrimination time t_d to maximize her fitness F_f. Coercive males (type 3), when encountering a female, bypass discrimination and force immediate mating. When the female pairs with a type i male, there is some chance the pair will break up following reproduction, $0 < b_i \leq 1$. Expected reproduction from each liaison with type i depends on the type-specific chance of fertilization γ_i and on offspring production r_i, given fertilization.

The frequencies of male types in the population f_i and the fitnesses F_i associated with each male type i combine to determine average male fitness $F_m = f_1F_1 + f_2F_2 + f_3F_3$. The male type with maximal reproductive success is assumed to increase in frequency and may thereby eliminate the other types; more than one type can persist through frequency-dependence when fitnesses are equal or when outcomes are evolutionarily unstable. A persisting mixture of male types can result from competition among individuals of pure types or from an identical probabilistic mixture of strategies expressed by all males. Proofs are provided demonstrating that neither a stable mixture of all three male types nor a continuing (unstable) sequence of replacements of one male type by another is possible under our assumptions. Relative abundances of male types in the male pool p_i determine the frequency of encounter between females and each male type. When females are discriminating, the *pi* will in general differ from the frequencies of mating with each type M_i.

Fitnesses are the multiplicative product of the expected rate R_i at which females and each male type produce offspring and the expected reproductive lifetime λ_i over which reproduction occurs. Social policing, in which there is some probability x that a coercer will be apprehended and removed from the male pool following a coercive event, can effectively shorten the reproductive lifetime of type 3 males, reducing the number of forced matings and potentially eliminating these males from the population, as we demonstrate. Resistance by females themselves results in reduced magnitudes of the fertilization and reproduction parameters γ_3 and r_3, though for simplicity we assume the cost of resistance to females is negligible.

3.3 THE MODEL

3.3.1 Overview

The basic conceptual framework of the model, depicting a continuous-time mating and reproduction game between choosy females and three types of male strategies, is presented in Figure 3.1. Given differences in time commitment to reproduction by males and females, in reproductive success with each male type, and in the effectiveness of discrimination, we solve the game by determining the evolutionarily stable frequencies of the male types (as opposed to traits) to be expected in the population and the optimal discrimination time. The complete mathematical derivation of the model is available in Appendix A; the instructions to run the MATLAB® program and the MATLAB® program itself may be found in Appendix B and C, respectively; and the required parameters are listed in Table 3.1. Here we summarize the logic underpinning the derivation.

The model also accounts for extra-pair paternity (see Kokko 1999) as a proportion of the reproduction associated with a social pair including male type i that is instead attributed to a male of type j, k_{ij}. (Note that any extra-pair reproduction within type has no effect on the model's behavior.) We assume (i) that previously mated and unmated males are equally likely to achieve copulations with females and (ii) that time expenditure on extrapair copulations for both males and females is negligible compared to expenditure on reproductive success and mate assessment.

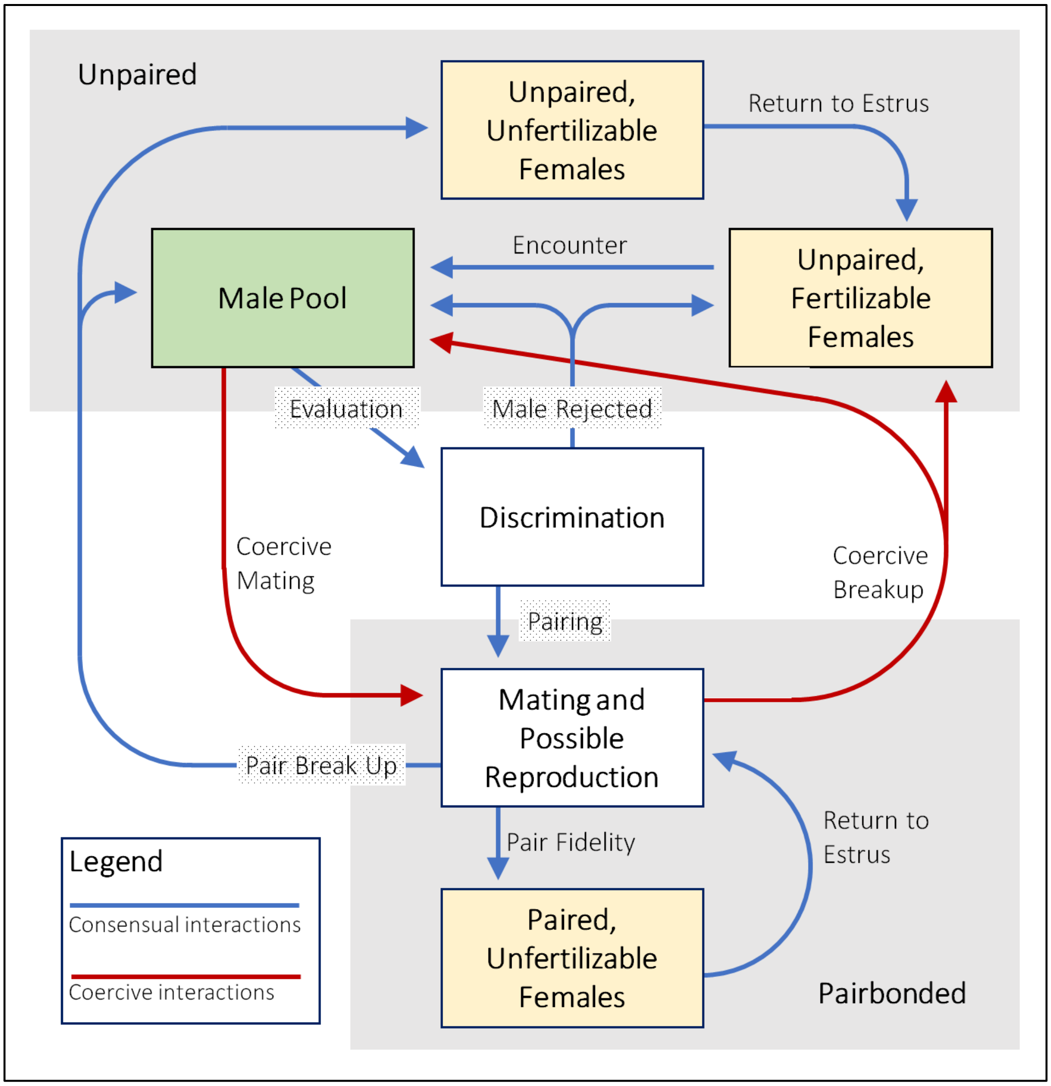


Figure 3.1. Graphical depiction of the model framework.

Males spend time τ in the male pool before being selected by a female or before initiating coercion. Females visit the male pool, pick a random male, and, when both male types 1 and 2 (but not 3) are present, evaluate him for an optimal time t_d. If recognized, type 2 males are generally rejected, and the female picks another male for evaluation. The chance that the female encounters and reproduces with the favorable (1) or unfavorable (2) male type also depends on the respective frequencies of the types in the male pool p_i and probabilities of successful fertilization given mating γ_i. Females invest time t_f in each round of reproduction and then wait time t_n before either becoming fertilizable (and returning to the pool to choose a male) or reproducing again with the same male if the pairing persists (with probability $1-b_i$). Males invest time t_i in the mating or, if the pairing persists, wait $t_f + t_n$ with the female before reproducing again. For coercive (type 3) males, $t_d = d(t_d) = 0$, $b_3 = 1$, and $t_3 \approx 0$. Females paired with a male of type i may conduct some fraction $f_j k_{ij}$ of their reproduction with type j via extra-pair mating, redistributing fitness between the two male types without influencing total fitness.

Table 3.1. Default model parameters.

Symbol	Definition	Default Magnitude and Units
r_1	Reproduction from fertilization by a type 1 male	1 unit of reproduction
r_2	Reproduction from fertilization by a type 2 male	0.6 units of reproduction
r_3	Reproduction from fertilization by a type 3 male	0.48 units of reproduction
t_f	Time female spends in a reproductive event	12 time units
t_n	Time female is not in estrus per reproductive cycle	1 time unit
t_1	Time type 1 male spends in a reproductive event	12 time units
t_2	Time type 2 male spends in a reproductive event	1 time unit
t_3	Time type 3 male spends in a reproductive event	0.001 time units
b_1	Break-up probability after mating with type 1 male	0.5
b_2	Break-up probability after mating with type 2 male	1
b_3	Break-up probability after mating with type 3 male	1
D	Exponential discrimination parameter	3 (time units)$^{-1}$
γ_1	Chance mating with type 1 results in fertilization	1
γ_2	Chance mating with type 2 results in fertilization	0.4
γ_3	Chance mating with type 3 results in fertilization	0.1
λ_f	Relative duration of female reproductive lifetime	1
λ_1	Relative duration of type 1 reproductive lifetime	1
λ_2	Relative duration of type 2 reproductive lifetime	1
λ_3	Relative duration of type 3 reproductive lifetime	1
ω	Choice function exponent for undiscriminated males	0
k_{12}	Fraction of type 1 paternity cuckolded by type 2	0
k_{13}	Fraction of type 1 paternity cuckolded by type 3	0
k_{23}	Fraction of type 2 paternity cuckolded by type 3	0

Using MATLAB® 2015b, we solved numerically for the optimal discrimination time and for the persistent male type or types, evaluating evolutionary stability based on whether a rare male of another type reached a fitness as great or greater than the otherwise optimal (fitness maximizing) male type or combination of types. In addition to results for our best-estimate default parameter magnitudes in each case (Table 3.2), we evaluated outcomes across plausible ranges of all key parameter values to establish the sensitivity of results to particular magnitudes. Except for unstable combinations, we determined the stable (ESS) frequencies of persisting male types i (f_i), proportions of the male types in the male pool (p_i), proportions of mates of each male type (M_i), proportion of encountered males successfully discriminated by females (d), the time females spent discriminating (t_d), average time of males in the male pool (τ), and the fitnesses of females (F_f) and of males (F_i).

The model produces a broad array of patterns, including both evolutionarily stable and unstable combinations of male types, depending on parameter magnitudes. These include the evolutionarily stable exclusive presence of any of the three male types, any two of the male types in either evolutionarily stable or unstable combination, and all three types in an unstable mix.

Single-type outcomes imply non-invasibility by either alternative type. Persistent pairs of male types result when each can invade the other member of the pair but the excluded type cannot invade the stable pair. The pair is stable if there is a mixed ESS (or evolutionarily stable state) with both frequencies strictly between 0 and 1. The pair is unstable if the two frequencies are 0 and 1, since the eliminated member of the pair can still invade the other type on its own. Though an unstable mix of all three male types is possible, we show (see Appendix A) that a stable mix of all three types of males is impossible, and that an unstable repetitive sequence of one male type replacing the other is also impossible for the parameter magnitudes of interest here.

3.3.2 Default Outcome and the Effects of Social Policing

Key parameters in our analysis, for which we typically have only rough estimates of magnitude, are the reproductive rates per fertilization by type 2 and type 3 males, r_2 and r_3. We therefore show most of our results along an r_2 axis (or an r_3 axis in the absence of type 2) between 0 and 1 ($= r_1$); r_3 is set to some proportion of r_2. Other parameters are held at default values (Table 3.1) unless otherwise indicated. At low values of r_2 and r_3 under default conditions, the outcome is pure type 1 (Figure 3.2). Intermediate values result in a stable mixture of types 1 and 2, with females using discrimination to bias mating toward type 1 in the middle part of this range. When r_2 and r_3 closely approach r_1 and r_2 approaches r_3, the outcome becomes pure type 2. Note that over this range, the mean time in the male pool increases, as females become less available for mating than the less-encumbered males via their time commitment to reproduction, with the decreasing frequency of type 1 males. The fitness of type 3 males never emerges in this example.

We equate the fertilization and reproduction parameters for types 2 and 3 (i.e., $\gamma_3 = \gamma_2 = 0.4$ and $r_3 = r_2$) and introduce substantial extra-pair paternity by type 3 on types 1 and 2 ($k_{13} = k_{23} = 0.5$), this yields pure type 3 at the default magnitude of r_2 (Figure 3.3a). But by introducing a modest level of policing, in which a coercer has some non-zero probability of being permanently removed from the male pool after coercing a female, the outcome can be altered. For this example, we suppose that each type 3 individual expects to have 20 coercive mating episodes over his lifetime ($n = 20$), and that $x = 0.18$, which means that each coercion results in an 18% chance that the coercer is apprehended and prevented from further mating. This reduces the expected number of coercive matings to about 5.6, 28% of the expected number before intervention (see the light blue line and its intersection with the red dashed line in Figure 3.3b). This amounts to a reduction of the reproductive lifetime of the coercer λ_3 to 28% of its default magnitude, which returns the pattern to the stable combination of types 1 and 2 exactly as in Figure 3.2. Even at only an 18% apprehension rate, policing has eliminated type 3 males from the population, indicating the potential effectiveness of this response to coercive behavior.

To compare patterns generated by the model with those found in nature, we parameterized the model for animal species with internal fertilization and that show sexually coercive behavior as a potential male strategy (see Tables 2.1, 2.2, Appendix D), excluding species in which male strategy shifts are strongly developmentally controlled. We identified six species for which parameters could be estimated: Japanese water striders (*Gerris elongates*), scorpionflies (*Panorpa latipennis*), guppies (*Poecilia reticulata*), mallard ducks (*Anas platyrhynchus*), chimpanzees (*Pan troglodytes schweinfurthii*), and humans (*Homo sapiens sapiens*).

We do not claim that these parameters are full and precise explanations of these species' behavior. We use these species to indicate the applications of the model and understand the emergence of sexual coercion in variety of scenarios. We explored the sensitivity of the model to each parameter and found the model generally insensitive to small parameter changes; exceptions are noted in the text. In the event of absent or ambiguous data, we varied the parameter estimates, focusing on values most consistent with current literature. For full derivation of the parameters for these species, see Appendix D.

3.3.3 Focal Systems

Male Japanese water striders engage in one of three strategies. Type 1 males are those that defend territories, call for mates, and guard their females while they lay eggs. Type 2 males are non-territorial males that only call for mates. Type 3 males are non-territorial males that engage in forced copulations. Flexibility in mating behavior is not correlated to male morphology, and strategies vary throughout the breeding season (late March to early June), with males engaging in type 1 strategies mid-season (Hayashi 1985). There is no information on the reproductive lifetimes and on fertilization rates for each mating strategies, and these parameters were explored.

There are three mating strategies for male scorpionflies. Type 1 males guard an arthropod as a nuptial gift that the female consumes while mating. If a male cannot find an arthropod, he produces and offers a salivary mass (type 2). In the absence of both an arthropod and the ability to produce a salivary mass, type 3 males engage in forced copulations (Thornhill 1980(a)(b), 1981, 1982). The amount of time a female devotes to each mating (Thornhill 1982), the number of eggs per mating (Thornhill 1982), the fertilization rates (Thornhill 1980(b), 1981, 1982), and reproductive lifetimes (Thornhill 1980(a), 1981) vary with male strategy.

Table 3.2. Parameters for six mating systems.

Species	**Mating System**	**Female Choice**	**Male Types**	**Altered Parameters**[1]	**Outcome**[2]
Humans (*Homo sapiens)*	Mutual-choice pairing with extra-pair mating	Inspection: physical and behavioral	1: Long-term investment, fidelity 2: Short-term investment 3: Negligible investment, coercion	$r_2=0.9$, $r_3=0.81$, $t_f=36$, $t_1=36$, $t_3=0.5$, $t_n=0.8$, $b_1=0.06$, $\gamma_1=0.95$, $\gamma_2=0.\ 44$, $\gamma_3=0.08$, $k_{12}=0.01$, $k_{13}=0.1$, $k_{23}=0.2$, $\lambda_f=\lambda_1=0.75$, $\lambda_2=0.95$, $\lambda_3=0.9$	1,2
Chimpanzees (*Pan troglodytes schweinfurthii*)	Mutual-choice pairing with extra-pair mating	Inspection: physical and behavioral	1: Consort males 2: Opportunistic males 3: Possessive males	$r_2=r_3=0.9$, $t_f=70$, $t_n=0.72$, $b_1=1$, $t_1=0.3$, $t_2=0.001$, $t_3=0.075$, $\gamma_1=0.\ 5$, $\gamma_2=0.042$, $\gamma_3=0.13$, $\lambda_f=0.95$	1
Guppies (*Poecilia reticulata)*	Promiscuous movement and posture signals	Inspection: posture and motion signals	1: N/A 2: Short-term mating 3: Sneak/forced mating	$r_2=1$, $r_3=1$, $t_f=0.033$, $t_n=0.87$, $t_1=t2=t3=0$, $\gamma_2=0.008$[L], $\gamma_3=0.001$, $b_1=1$, $D=4300$, $\lambda_1=\lambda_2=$ 0.28[L], $\lambda_1=\lambda_2=\lambda_2=0.53$*[H]*	2
Japanese Water Striders (*Gerris elongates*)	Haphazard encounter- based polyandry	Inspection: calls and territory	1: Territorial 2: Non-territorial opportunistic 3: Non-territorial forced copulation	$r_2=1$, $r_3=0.95$, $t_f=0$, $t_n=10$, $t_1=t_2=t3=0$, $\gamma_1=0.\ 9$ $\gamma_2=0.3$, $\gamma_3=0.6$, $b_1=1$, $D=4300$	1
Mallard Ducks (*Anas platyrhynchos)*	Mutual-choice pairing, long-term fidelity	Inspection: physical and behavioral	1: Long-term partner 2: N/A 3: Forced copulation	$r_3=0.74$, $t_f=9$, $t_1=7$, $t_3=0$, $t_n=1.5$, $\gamma_1=0.\ 59$, $\gamma_3=0.\ 37$, $b_1=0.019$, $k_{13}=0.14$	1,3

[1] Baseline parameter magnitudes for the model are in Table 2. Only the magnitudes modified from those in Table 2 to fit the particular mating systems are indicated under "Altered Parameters". The rationale for these parameter magnitudes is in Appendix B.

[2] The persistent male type or combination of types for each system, with the default parameter magnitudes for that system, are shown in the "Outcome" column. In these cases, an ESS result with type x males only is symbolized as x; and ESS combination of types x and y is indicated as xy; and an unstable combination of types x and y dominated by type x is symbolized as xy. (xy results when types x and y can both invade pure populations of the other, but the stable frequencies of x and y in the mixture are respectively 1 and 0.) In each case, we evaluated the sensitivity of these outcomes to key parameters while separately varying r_2, r_3, λ_f, γ_2, γ_3, t_f, and t_n, generally subject to the reasonable constraints $r_1 > r_2 > r_3$, $2 > \lambda_f > 0.5$, $\gamma_1 > \gamma_2$, $\gamma_1 > \gamma_3$, $t_f > t_1$, $t_f > t_2$, $t_f > t_3$, and $2 > t_n > 0$ (except Japanese water striders, which were $20 > t_n > 5$). In all cases, the outcomes were qualitatively unchanged.

[3] Two parameters differ as indicated for guppies between low-predation areas [L] and high-predation areas [H]

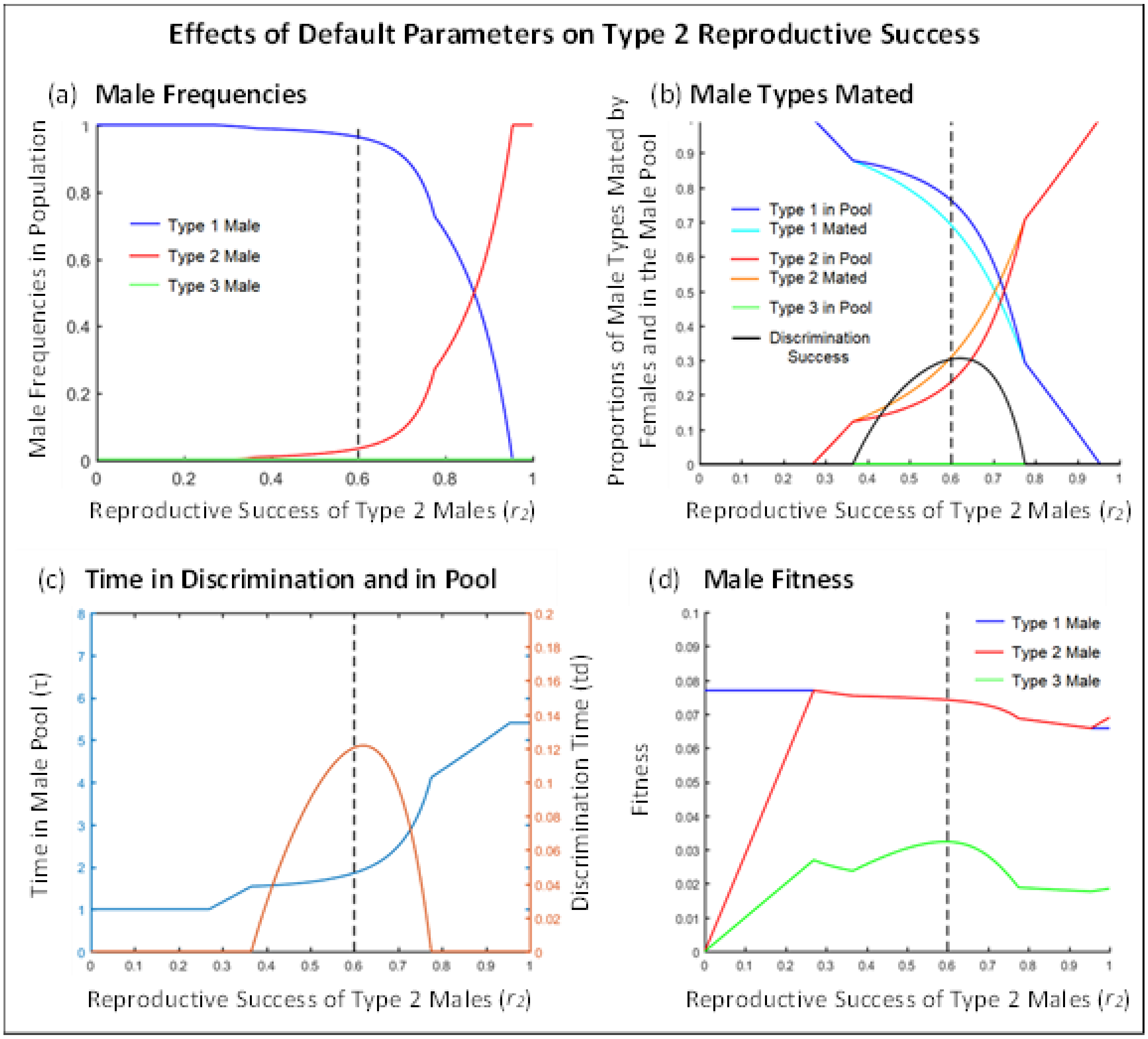


Figure 3.2. Results of default run of the model (parameters from Table 2.1).

(a) The population is pure type 1 for low r_2 and r_3 and pure type 2 for high r_2 and r_3. The type 3 reproduction parameter $r_3 = 0.8r_2$ along the abscissa (vertical dashed line). From approximately $r_2 = 0.27$ to 0.95, there is a stable mix of the two types, dominated by type 1 with the help of discrimination until r_2 exceeds about 0.77, above which there is no discrimination, and type 2 becomes more abundant. Above about $r_2 = 0.95$, the population abruptly becomes pure type 2.

(b) Here, M_1 and M_2 are the proportions of type 1 and 2 males mated by females; p1 and p2 are the proportions of these two types in the male pool, illustrating the discrimination bias when compared against M_1 and M_2. The proportion of encounters in which the two types were successfully distinguished is the black line d. Within the stable mixture interval, $t_d = d(t_d) = 0$ for approximately r_2 0.27 to 0.37. But between approximately 0.37 and 0.77, $d > 0$, and female discrimination biases mating frequencies toward type 1 males.

(continued)

(c) Time in the male pool is low for pure type 1 males, increases with the proportion of type 2 in a stable mixture, and is maximized for pure type 2. Discrimination times increase with r_2 and follow the pattern of d in panel B.

(d) Consistent with the other results, fitness of type 1 males is highest below about $r_2 = 0.27$; fitnesses of types 1 and 2 are equal from 0.27 to 0.95; and fitness of type 2 is highest above 0.95. Type 3 never achieves sufficient fitness to invade successfully. Female fitness and overall male fitness follow the magnitudes of the highest male types

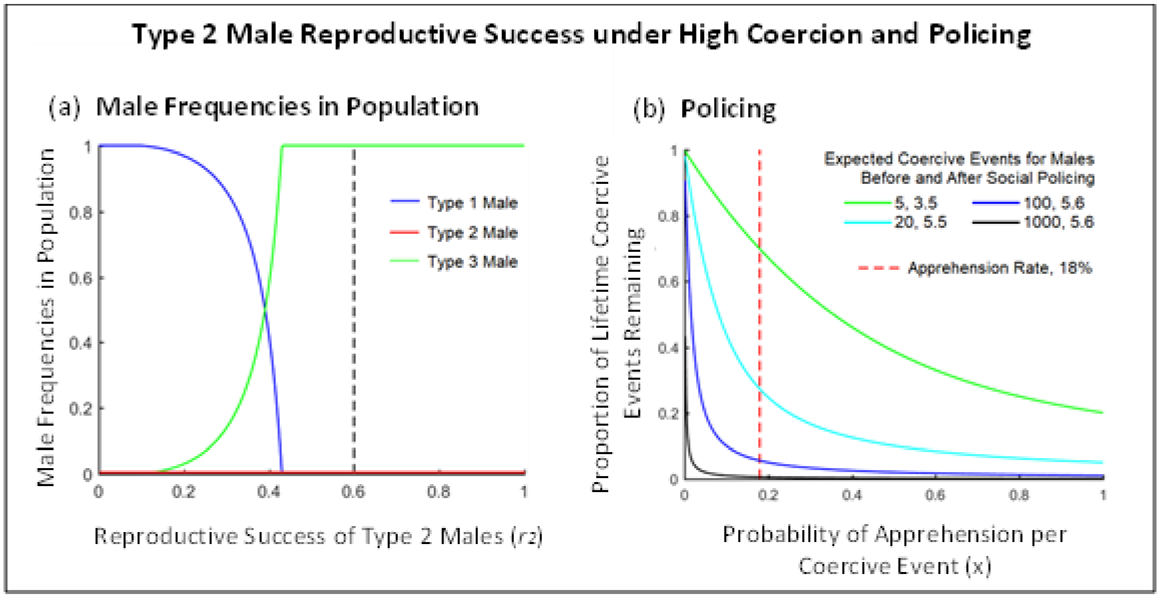


Figure 3.3. A modification of the default model and the impact of policing.

(a) Frequencies of male types vs the magnitude of reproductive success of type 2 males for the default case of Table 2.1, except with γ_3 increased from 0.1 to 0.4, $r_3 = r_2$, and $k_{13} = k_{23} = 0.5$. The result is pure type 1 for $r_2 \leq 0.0098$; a stable mixture of types 1 and 3 for $0.098 < r_2 \leq 0.43$; and pure type 3 for $0.43 < r_2 \leq 1$. Pure type 3 is the default outcome. This is used to consider the implications of policing for the presence and behavior of type 3 males.

(b) The proportion pC of the expected number of lifetime coercive events that occur for different levels of policing (x) and different expected numbers of coercive events (n). The four lines correspond to n = 5 (green), 20 (light blue), 100 (blue), and 1000 (black). The red dashed line marks an example magnitude of x = 0.18, an 18% chance that a coercer is apprehended after a coercive event. This level of policing results in reduced expected numbers of lifetime coercions per type 3 individual: 3.5 for n = 5, 5.5 for n = 20, 5.6 for n = 100, and 5.6 for n = 1000. (Note that as n -> ∞, the number of lifetime coercions C -> 1/n.) Policing not only reduces those expected numbers but can also eliminate type 3 from the population. Type 3 is eliminated, causing the pattern to revert to that of Figure 2.2, for cases with $x \geq 0.18$ or $n \geq 20$.

Guppies have two different male short-term mating strategies: those that display and are chosen by females to mate (type 2) and those that engage in sneak copulations when females are unreceptive (type 3) (Liley 1966), and there is no pair fidelity. Females are receptive for the first 3-5 days after giving birth, which occurs once per month, and are subsequently unreceptive until giving birth (Liley 1966, Magurran and Nowak 1991). There is no known difference in reproductive success for type 2 and type 3 males, and these parameters were explored.

Fertilization rates vary with each strategy and predator density in the habitat (Baerends et al. 1955, Liley 1966, Pilastro et al. 2002, Magurran and Seghers 1994, Endler 1987, Rodd and Reznick 1997), and sex ratios vary with predator density (Rodd and Reznick 1997), and we explored the effect of both low and high predatory density habitats.

Chimpanzee males have three different mating strategies. Type 1 males are chosen by females as consorts, exclusively mating for an extended period while she is in estrus and providing her with resources. Type 2 males are opportunistic males that copulate with estrus females within the group. Type 3 males are possessive opportunistic males that aggressively defend estrus females from other males to mate exclusively with them for several days (Tutin 1979). Fertilization rates vary with male strategy and are estimated from the time the males spend guarding and mating with each female (Tutin 1979).

Mallard reproduction consists of long-term pairs that mate annually during the breeding season. These pairs primarily mate consensually with each other; in addition to this type 1 strategy, however, males often switch strategies and sexually coerce females mated to other males. Offspring viability (Bluhm and Gowaty 2004) and the chances of fertilization (Cunningham 2003) vary with each male strategy. Reproductive lifetimes are influenced by hunting regulations and were varied to explore this effect (Giudice 2003).

In humans, type 1 males contribute time (and other resources) to child rearing; type 2 do not contribute appreciably in this way; and type 3 males coerce females when they encounter them. Reproductive success estimates considered nuclear families, single parents, and multi- generational support (DeLeire and Kalil 2002) as well as the effects of sexual coercion on conceived offspring (see van Ee and Kleber 2013 for review). Fertilization rates are estimated according to the time committed to each male strategy, with a variety of relationships explored. Type 1 matings included established break-up rates (Kawamura 2009) and estimated conception rates (Potter and Parker 1964). Type 2 relationships included single to multiple matings incorporating female fertility variability (Wilcox et al. 1995). Type 3 fertilization rates are established empirically (Gottschall and Gottschall 2003) as are extra-pair paternity rates (Larmuseau et al. 2016). Reproductive lifetimes for type 2 and type 3 males are estimated to be progressively shorter as short-term reproductive strategies in humans are often associated with decreased reproductive lifetimes (Lalumière and Quinsey 1996, Gladden et al. 2008, Jonason et al. 2009).

3.4 RESULTS

Japanese water striders were pure type 1 males with the default parameters for this species in the model. Unlike other water striders with coercive promiscuous mating systems (i.e., pure type 3 in the model), this species is territorial. We consider this territorial type to be type 1 via resource benefits gained (i.e., good access to suitable ovulation sites and food) by mated females. Pure type 3 can be obtained for this species when increasing the number of extrapair fertilizations that type 3 males gain from females mated with type 1 males ($k_{13} \geq 0.34$) or when type 1 and type 3 males have equal fertilization success, parameter magnitudes that may be more consistent with other water strider species that have coercive mating systems. Changes to other parameter magnitudes had no influence.

Scorpionflies yield pure type 1 males based on the resources they provide and are similarly insensitive to the magnitudes of the other parameters. Here it is primarily the low r_3 magnitude and the shorter reproductive lifetimes of male types 2 and 3 that ensure dominance of type 1.

For guppies, in both the low and high predation regimes considered, type 2 males alone constituted the ESS; there was no type 1 to consider in this species, since all choice-based pairing is very short-term and not linked to resources. This result was insensitive to the magnitudes of r_2, r_3, γ_3, and k_{23}. The male-biased adult sex ratios put other outcomes out of reach.

In mallards, in the absence of the type 2 male, there is a narrow interval of type 3 reproductive success (r_3) magnitudes with a stable mix of male types 1 and 3, including the default $r_3 = 0.74$ (Figure 3.4). This result is dependent on a female-biased sex ratio ≤ 1.0; if instead of high female reproductive lifetimes ($\lambda_f = 1$), as estimated from data for moderately or weakly regulated duck hunting (Giudice 2003), we set $\lambda_f = 0.85$, as indicated for strictly regulated hunting (Giudice 2003), then the sex ratio becomes 1.17, and the outcome is pure type 1 males for all magnitudes of r_3. The default magnitude $r_3 = 0.74$ results in the stable 1-3 mix for magnitudes of the extra-pair reproduction parameter for type 3 males with type-1-paired females within the range $0 \leq k_{13} \leq 0.18$, but $k_{13} > 0.18$ yields pure type 3. For $\gamma_3 < 0.27$, the ESS becomes pure type 1. The mallard results are generally insensitive to modifications of the other parameters.

For chimpanzees, type 1 males are the ESS. This outcome was robust against substantial parameter shifts, apparently because of the long pairing interval for females with type 1 males. Obtaining the pure type 2 ESS, more consistent with the pattern in nature, requires heavy intervention such as reducing λ_3 to 0.3 (strong social policing or decreased life expectancy from higher levels of aggression) and reducing γ_1 from 0.5 to $<$ 0.038 (presumably from intense pressure by aggressive male competitors).

For humans, default parameter magnitudes result in a stable mixture of male types 1 and 2 (Figure 3.5 A-D). The results are qualitatively unchanged across a plausible range of the extra-pair reproduction parameters. The stable 1-2 mixture is the outcome for $0.09 \leq \gamma_2$, so uncertainties about the magnitude of type 2 fertilization rates (Appendix D) are of minor significance. The default outcome remains the stable mix of male types 1 and 2 with $\lambda_f = 0.75$ for $0.68 < \lambda_1 \leq 0.77$ (the result is pure type 2 for $0.68 \geq \lambda_1$ and pure type 1 for $\lambda_1 > 0.77$) and even with a major increase in type 3 fertilization rates (γ_3) from 0.08 to 0.4 (Figure 3.5E). If type 2 pairing is very brief, comparable to type 3, then $\gamma_2 = 0.061$ (see Appendix D) and $t_2 = 0.5$ (as for type 3), yielding the unstable mix of types 1 and 3 at the default $r_2 = 0.9$ (Figure 3.5F). Similarly, coercive types can persist in unstable mixtures in the extreme case that $\gamma_3 \geq 0.4$. Setting $r_2 > 0.99$ (i.e., nearly the same as $r_1 = 1$) shifts the ESS to pure type 2. We address $r_2 > 0.99$ and $\lambda_1 > \lambda_f$ in the Discussion. None of the other parameters have substantial effects on the patterns for humans.

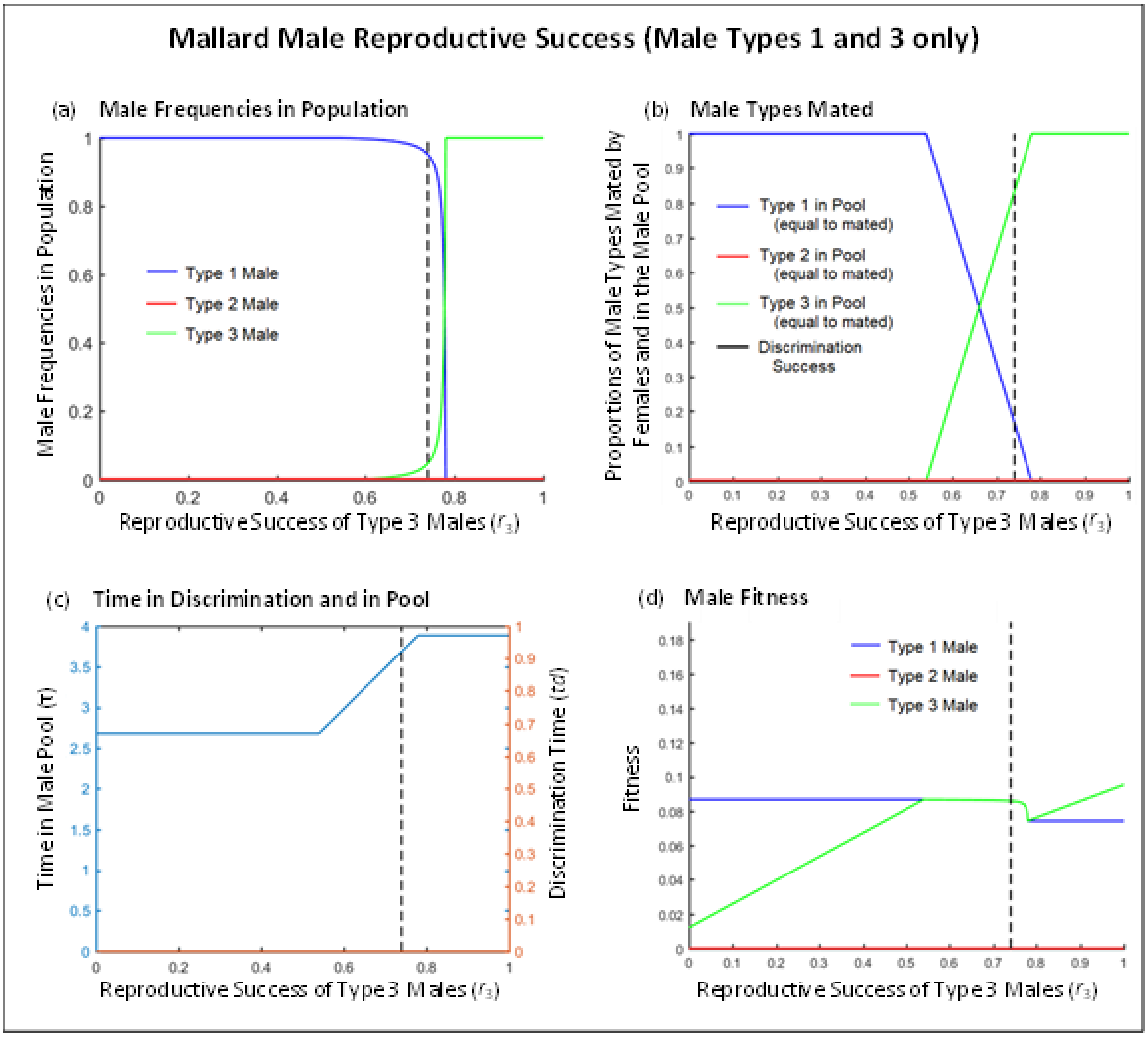


Figure 3.4. Mallard ducks, with parameters as in Table 2.2 except that λf= 1.

At the default magnitude of $r_3 = 0.74$, there is a stable mixture of male types 1 and 3, with about 96% type 1. The frequencies of the two types are sensitive to the magnitude of r_3. “Default magnitudes” here are those for mallards in Table 2.2.

(a) Type 1 alone is the ESS below $r_3 = 0.54$. The type 1 frequency gradually and then rapidly declines for higher r_3, reaching zero at about $r_3 = 0.78$, above which type 3 alone is the ESS.

(b) In contrast to the frequencies in panel A, the mating proportions with the two male types shift almost linearly with r_3 over the interval of the stable 1-3 mixture. Proportions of mated only diverge from proportions in pool when discrimination is successful.

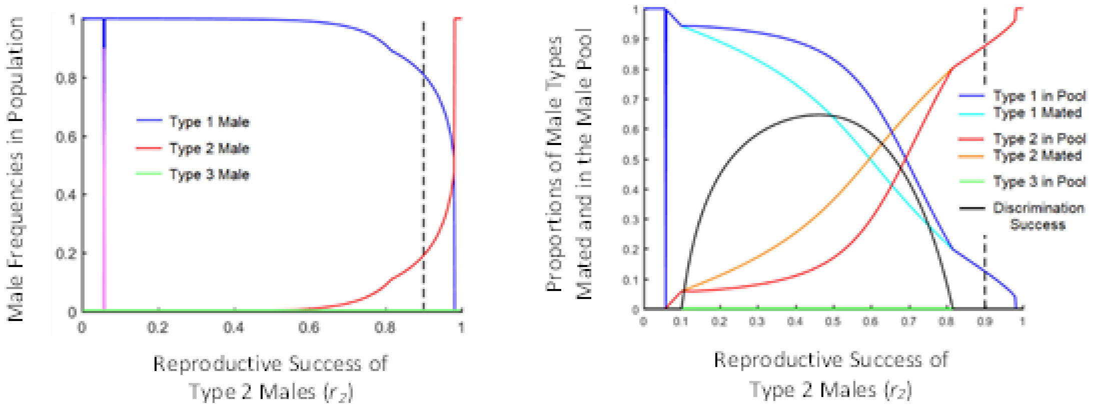
(c) Time spent in the male pool is low for pure type 1, increases with r_3 for the shifting mating proportions in the interval of the stable 1-3 mixture, and then is maximal for pure type 3. There is no discrimination in the absence of type 2 males.

(d) The fitness magnitudes are consistent with the three ESS intervals: type 1, types 1 and 3, and type 3. For the mixed ESS, the green line covers the blue line.

Human Type 2 Male Reproductive Success under Default Parameters (a-d) and Exploratory Type 2 and Type 3 Parameters (e-f)

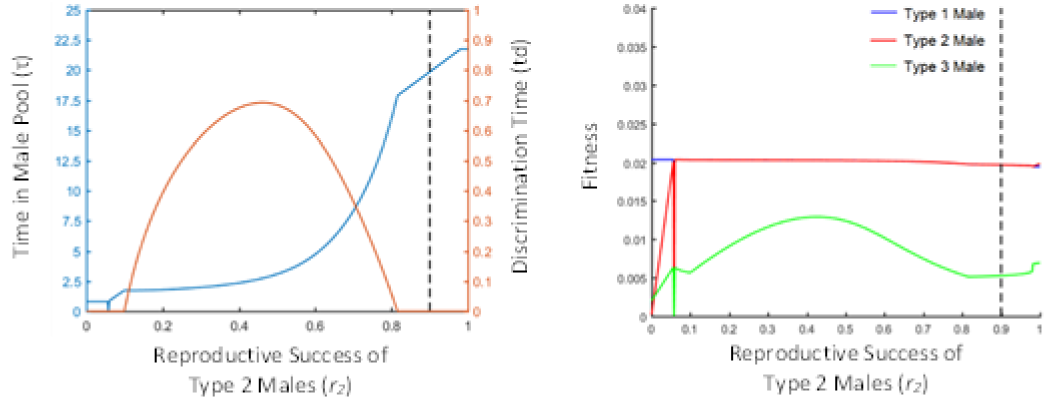
(a) Male Frequencies in Population

(b) Male Types Mated



(c) Time in Discrimination and in Pool

(d) Male Fitness



(e) Male Types Mated under High Coercive Fertilization Rate

(f) Male Frequencies in Population with Similar Type 2 and 3 Parameters

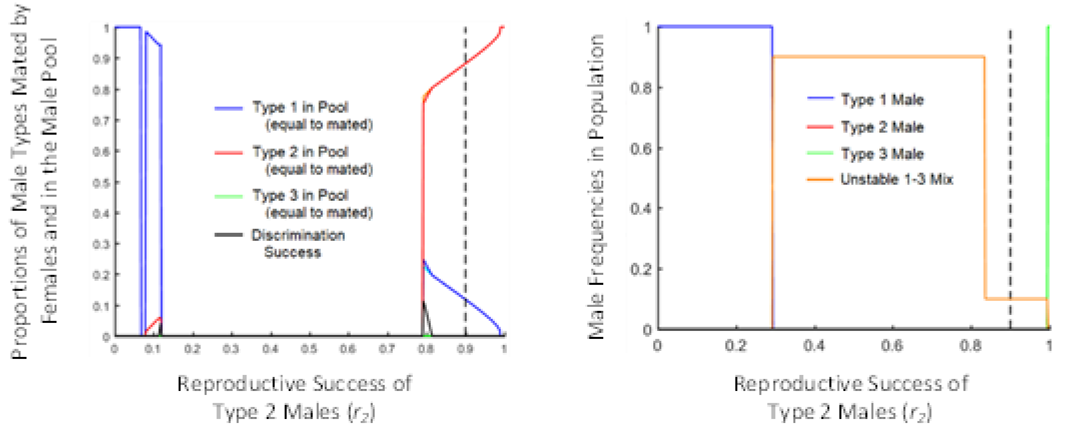


Figure 3.5. Humans, with parameters as in Table 2.2 in panels (a)-(d), and with altered parameters in panels (e) and (f).

Results produce a stable mixture of male types 1 and 2 for the default magnitude of r_2. The default magnitude of $r_2 = 0.9$ is indicated by the vertical dashed line. The type 3 reproduction parameter $r_3 = 0.9r_2$ along the abscissa (vertical dashed line).

(a) On this frequency graph, type 1 males dominate for r_2 magnitudes below the disappearance of discrimination above 0.81, above which discrimination ceases. For r_2 magnitudes below about 0.06, pure type 1 is the ESS; there is a very short interval around $r_2 = 0.06$ with an unstable mix of types 1 and 2, which appears as a vertical spike on panels (a)-(d); for $0.06 < r_2 < 0.1$, there is a stable mix of male types 1 and 2, with no discrimination; and for $0.1 < r_2 < 0.81$, the stable mix of types 1 and 2 persists, but with active discrimination by females in favor of type 1. For $0.81 < r_2 < 0.98$, including the default magnitude $r_2 = 0.9$, there is again a stable combination of types 1 and 2 without discrimination. For $r_2 > 0.98$, the ESS is pure type 2.

(b) Here, M_1 and M_2 are the proportions of males mated by females of types 1 and 2; p1 and p2 are the proportions of these two types in the male pool, illustrating the discrimination bias when compared against M_1 and M_2. The proportion of encounters in which the two types were successfully discriminated is the black line d.

(c) The optimal discrimination time td increases with r_2 over the discrimination interval. The waiting time τ is lowest for pure type 1 and increases with the proportion of type 2.

(d) Fitnesses are consistent with the regions most clearly indicated in panel B. For $0.06 < r_2 < 0.98$, the red type 2 line coincides with and covers the blue type 1 line.

(e) In this case, $\gamma_3 = 0.4$ instead of the human default value $\gamma_3 = 0.08$, with all other parameters at default. Several new regions appear, but the default outcome is unchanged. For $0< r_2 < 0.068$, the ESS is pure type 1. Within $0.068 < r_2 < 0.080$, there is an unstable mixture of all three male types. For $0.080 < r_2 < 0.120$, the ESS is the stable mixture of types 1 and 2. Between $r_2 = 0.120$ and 0.792 is another unstable mix of all three male types. For $0.792 < r_2 < 0.990$ is another stable mixture of types 1 and 2 containing the default magnitude of r_2; for $0.990 < r_2 < 1$, pure type 2 is the ESS.

(f) With $\gamma_2 = 0.061$ and $t_2 = 0.5$ instead of the default magnitudes $\gamma_2 = 0.44$ and $t_2 = 1$, the pattern is completely altered. For $0 < r_2 < 0.294$, pure type 1 is the ESS; but for $0.294 < r_2 < 0.836$, there is an unstable mixture of types 1 and 3, dominated by type 1, indicated by the orange line at 0.9. For $0.836 < r_2 < 0.996$, there is still an unstable mixture of types 1 and 3, but now dominated by type 3, indicated by the orange line at 0.1 and containing the default magnitude of $r_2 = 0.9$. For $0.996 < r_2 < 1$, the ESS is pure type 3.

3.5 DISCUSSION

The species-specific implementations of the model are not intended as rigorous tests. Their purpose is to determine whether a simple, reproductive game among optimally choosy females and three types of males differing in commitment to reproductive liaisons captures some of the key features and patterns found in nature. Overall, we found general agreement and gained some insight into each system, suggesting ways to follow up in future empirical or theoretical work. We summarize for each system below.

In the absence among related species of the territoriality characteristic of Japanese water striders, pairing seems unlikely, and female avoidance of males (as commonly observed in water striders—Krupa et al. 1990, Arnqvist 1992) may result in ubiquitous coercion (see the Results for this species). In nature, Japanese water strider mating behavior fluctuates based on seasonal timing. Early in the season, females mate with males displaying courtship behavior (type 2) but do not oviposit. In mid-season, males begin defending territories and courting females, which oviposit while type 1 males defend them from other males. Late in the season, coercive males begin mating opportunistically with females that are ovipositing without a male guarding them (Hayashi 1985). However, the chance of fertilization when mating at the time of oviposition is unknown. Since larger males are frequently type 1, smaller males are type 3, and medium-sized males vary their strategy throughout the breeding season (Hayashi 1985), coercive mating may have a low fertilization rate in this species, and coercion is a viable option only for males that cannot defend a territory. More exploration of this system is clearly warranted.

In scorpionflies, type 1 males should dominate the population for all realistic parameters. These results are unsurprising, as males aggressively fight for arthropod nuptial gifts (Thornhill 1980(a)) and resort to salivary masses or coercion only when they can provide neither of these (Thornhill 1980(b)). To calculate the mortality rates of the different types of males, we explored two possibilities based on two hypotheses. The first hypothesis is that coercive scorpionflies avoid the high risk of mortality associated with defending arthropods in spider webs (spiders result in 65% of adult scorpionfly mortality) (Thornhill 1980(b)). The second is that coercive scorpionflies would have a higher rate of mortality because of increased male-male competition for reproductive opportunities (Thornhill 1981). We therefore ran the model twice, once with type 1 males having the lowest mortality and type 3 the highest, and again reversing type 1 and type 3 mortality rates. If type 1 scorpionfly males have the highest mortality rates, type 2 males dominate over type 1, which is not supported empirically. Evidence indicates that type 1 males are always preferred, and our results suggest that this may be, in part, due to the limited reproductive lifetime of type 3. In defending arthropods, type 1 males may be in areas where predatory spiders may attack more often. But Thornhill (1981) showed that large male scorpionflies are less likely to be killed by spiders than smaller males, so these males may be able to afford a strategy too risky for the others.

For all realistic parameters in guppies, males should always attempt to mate consensually using S-displays and only resort to coercion if this fails. These results are consistent with observations that males only resort to coercion in nature when females are unreceptive to S- displays (Magurran and Nowak 1991). Opportunistic coercion may thus be associated with very limited prospects for being chosen by a female and when the cost of attempted mating is low.

This strong preference for type 2 males is seen in both high and low predation environments, which differ in sex ratios and the chances of each type of reproduction successfully fertilizing eggs. In both environments, the reproductive success of type 2 males would have to drop substantially for type 3 to invade; this is especially true in high predation environments, requiring a reproductive success of just over half that of low predation environments for type 3 invasion (low predation – 0.126, high predation – 0.072). Alternatively, if unchosen males could isolate and subject females to repeated gonopodial thrusts, this might raise $\gamma_3 > \gamma_2$ and allow this coercive type to stably persist. More attention to the frequency of success of this coercive strategy and the fertilization frequency would be valuable for understanding its role here.

Unpaired mallard ducks establish pairs in the fall and generally retain the partner across many breeding seasons, though only females provide care for young. Coercive mating, which apparently accounts for most or all extra-pair mating, and extra-pair paternity itself, are well documented, with approximately 14% of offspring unrelated to the social male parent (Denk 2005). This is generally consistent with the stable combination of male types 1 and 3 found by the model. If the extra-pair coercion parameter k_{13} is raised from 0.14 to 0.18, the default becomes pure type 3, which suggests that active resistance by females may help keep the fertilization parameter γ_3 low enough to prevent a complete type 3 take-over. A female-biased sex ratio ensures that not all coercive matings must be extra-pair, because not all females will be tied up in long-term pairing, improving the competitiveness of coercers. Empirical work should address the role of resistance, the magnitude of the coercion parameter, and whether individuals pursue a consistent stable mixture of strategies.

For chimpanzees, the model finds that type 1 males in consortships should always be favored with the default parameter magnitudes, but in fact consortships are uncommon in nature. Aggressive male-male competition, not explicitly included in the model, and strict social policing could account for this discrepancy, as noted in Results. When a female chimpanzee nears estrus, she is followed by multiple males. Pairing to form consorts is solicited by males with particular females, but other males frequently intervene by keeping a potentially consorting pair from leaving the group. Consorts are initiated successfully only when the consorting male grooms the female and successfully leads her away from the group (her participation is consensual – Tutin 1979). So while it is always beneficial for a male to engage in a consortship, other males have an incentive to intervene and thus retain potential access to the female. This and further intervention to greatly reduce the incidence of coercion (i.e., policing) may account for the prevalence of non-coercive opportunistic mating (type 2) in nature.

For humans, the stable mixture of types 1 and 2 becomes pure type 1 if the reproductive lifetime of type 1 males more than slightly exceeds that of females, but we expect these lifetimes to coincide because of long-term pairing fidelity rather than because of physiological constraints on reproductive lifetime, which are generally less severe in males. Coercion persists if type 2 relationships last no longer than type 3 with $r_2 < r_1$. Better estimates of key parameters, the reproductive lifetimes λ, and the r values would considerably improve our confidence in the results obtained here. It has been postulated that offspring-rearing help provided by grandmothers and other members of close-knit communities (DeLeire and Kalil 2002) may remove the need for extensive male contributions of time and other resources. This would imply that $r_2 = r_1$ and thus that pure type 2 males constitute the ESS (Figure 3.5a-d). This result is consistent with an expected shift to low-commitment paternity when such male contributions are not required. In the case that type 2 males closely resemble type 3 in having only a very brief (though consensual) pairing interval, the resulting much reduced fertilization parameter γ_2 =0.061 shifts the outcome to favor coercers in an unstable mixture with type 1 at the default r_2 magnitude. Thus, when a consensual mating type focuses only on very short-term relationships, this can facilitate the persistence of coercers in the system.

3.6 GENERAL CONCLUSIONS

We have shown that a simple game-theoretic mating model based on choosy females and three male types differing in response to individual reproductive liaisons can produce persistence of all possible individual male types and combinations of types, though the combinations may be unstable. In some circumstances, females will spend time at the expense of reproduction on discriminating between types, mating with the more desirable type and rejecting the less desirable type; but female choice and male competition often result in single male types and some stable combinations in which spending time on discrimination is non-optimal. This framework incorporates many key features of mating games in nature and encouraged us to compare model outcomes to observed natural patterns for diverse taxa that fit the assumptions relatively well.

In varying the parameters of interest, we found that relative magnitudes across male strategies of the parameters for fertilization rate given mating γ_i and reproductive success given fertilization *ri* played the most prominent role in the emergence of male coercion. Varying the magnitudes of other parameters generally contributed less to the persistence of male strategies, though unbalanced sex ratios resulting from sex-specific differences in reproductive lifetime also shifted outcomes in some cases (e.g., guppies, scorpionflies). Better documented assessments of the success of alternative male mating behaviors (e.g., for guppies and Japanese water striders) and of the effectiveness of female resistance against coercion (e.g., mallards) would be particularly valuable in making more robust predictions about the emergence of male coercion.

For some species, some of the model's parameters can be found in the published literature, particularly the six focal species investigated here. In four of these six species (Japanese water striders, scorpionflies, guppies, and chimpanzees), female mate choice tends to result in evolutionarily stable male strategies of one dominant type. These outcomes are biased by females through their effect on fertilization and reproduction parameters γ_i and r_i toward high investment in reproduction by males (generally type 1, but type 2 when pairing intervals are particularly short and type 1 is not found). In another case (humans), male types 1 and 2 form a stable mixture. The coercive male type persists in stable combination in the mallard duck system.

Coercion (type 3) is observed but relatively uncommon across taxa in nature. The model suggests one possible explanation for this: coercion may tend to be evolutionarily unstable, and that instability may be facilitated by female resistance and social policing. Usually, coercion is associated with a reduced chance of fertilization (sometimes greatly reduced, though humans [Gottschall and Gottschall 2003] and some birds [D.F. Westneat, personal communication] appear to be exceptions) and commonly with a reduced reproductive success per fertilization.

The potentially offsetting advantages—bypassing female mate choice, reduced investment in offspring after mating, reduced exposure to predators—have not been shown to be especially important in the systems of interest here. Coercion may tend to be the "best of a bad job"; when choice-related mating prospects are unusually bleak, this may be the best possible response, though we do not directly address this in our model (see Luttbeg 2004). (Note that the fitness of type 3 in humans is only modestly below that of types 1 and 2 at the default magnitude in Figure 3.5d, perhaps keeping coercers within range when opportunities arise.) When male quality is only partially correlated with strategy and is detectable by females, a scenario not addressed in the present study, lower quality males may be the most likely to resort to coercion—despite evidence to the contrary in humans, where coercive males typically report more sexual partners than non- coercive males (Kanin 1985, Malamuth et al. 1991, Lalumière et al. 1996). While coercion could be, and in human studies often is, explained as pathological, the focus here is on evolutionary explanations and the ecological conditions that contribute to the emergence of coercion.

Conclusions concerning coercion lacking an evolutionary perspective will likely be incomplete and applications of such less effective. To the extent that coercion is heritable and a liability for males through effective resistance or policing, avoidance of mating with such males would be favorable because sons would be coercive and pay such costs (Pradhan and van Schaik 2009). However, if heritable coercion is effective at increasing the mating rate, then it should be tolerated and possibly even sought by females (Kokko 2005). Even if evolutionarily unstable, coercion might be a "spillover" consequence of maximizing mating opportunities, for which males are strongly selected (Johnson 2001, Johnson and Sih 2005). The fertilization probability γ_i may be positively related to insistence for type *i* males, creating a trade-off that merits investigation in future work.

We included no cost of policing in our model but note that if there is a significant cost, then a society in which coercers exist in the absence of policing may cycle between adequate and inadequate policing. As coercers appear, policing may increase to eliminate them at a cost, as coercers are eliminated, policing diminishes to reduce the cost, and coercion may reappear, and so on. Policing cycles may be detectable in human societies and perhaps some other primates.

3.7 TESTABLE HYPOTHESES AND FUTURE DIRECTIONS

We have identified several avenues for building on the model in future work, including additional focus on female resistance (Kokko et al. 2003), policing, and a possible trade-off between fertilization success and male insistence that may result in coercion as a spillover strategy. Many of the ways forward would involve structuring the model around a more accurate depiction of a particular species (e.g., incorporating condition-dependence, male-male aggression into male strategies in chimpanzees, or allowing for best-of-a-bad-job opportunistic coercion in humans). More detailed information about the array of male strategies to be found in individual populations would be particularly valuable and may result in a broader array of discrete strategies or a continuous distribution along a strategy axis. Our hope is that the more general model presented here will spark follow-up analyses that cede as little generality as possible in exchange for the deeper insights about particular species that may come from more mechanistic approaches and greater biological realism.

Our examination of focal systems has suggested testable hypotheses and other avenues for future research in understanding their mating systems. Coercion may be a viable strategy in guppies if type 3 males concentrate their reproductive efforts on the same female in an environment where she can be sequestered, thereby increasing coercive fertilization rates to surpass type 2 males. In our model, consorts are always favored in chimpanzees; we hypothesize that male-male aggression and social policing account for the dominance of short-term consensual mating, and we propose future models incorporate competition where appropriate.

We predict that coercion is more frequent in Japanese water striders when habitat conditions impede a territorial male's ability to isolate and defend females, resulting in extensive extra-pair paternity (high k_{13}); more data on fertilization rates associated with the alternative strategies would be valuable in understanding this system.

Female resistance to coercion should be detectable in mallards via mechanisms to reduce fertilization success in coercive matings. Though difficult to test, we hypothesize that scorpionflies avoid extrapair copulation because, in doing so, the type 2 and 3 males would have higher reproductive success (via k_{12} or k_{13}) and potentially stabilize in the population. In human societies, we predict a positive relationship between the frequency of very brief consensual relationships (and the accompanying low fertilization rate) and coercive relationships.

By applying a game-theory approach to a wide range of model systems in which coercive strategies appear, we found that the fertilization rate and reproductive success given fertilization are the most significant predictors of sexually coercive behavior. In several species, these values can be mediated through social policing and female reproductive decisions. A greater understanding of these values and their application may allow greater insight into the prevention of sexually coercive behavior in humans.

Reflection

As outlined in Chapter 1, sexual coercion in humans takes many forms. At minimum, it can present as both a fast and a slow mating strategy that emerges in a context-dependent way. The parameters associated with the type 3 male most accurately reflects the coercion that is associated with a fast mating strategy, with males investing in high mating effort by returning to the mating pool as quickly as they can. However, the model does not account for in-pair coercion, which is a substantial source of coercion in humans. This type of coercion emerges primarily in response to perceived paternal uncertainty, which is included in the model, so it might be possible that the model could be adjusted to account for this, adding a layer of complication and nuance that might be revealing. But the model does include a factor representative of shifting context. The element of social policing allows for the incorporation of an immediate, tangible consequence to the choice to engage in coercion, allowing the model to reflect the influence of broader social convention and the acceptability of coercive behaviors. And because coercion emerged or disappeared from the human model in response to social policing, this might provide biological evidence for the use of social avenues in addressing sexual coercion.

In our conclusion, we identified two possibilities for coercion in humans. The first is that it might emerge when males are deprived of mating prospects. However, as previously illustrated, this is not supported by the available evidence. Thus, I propose that it is more likely the result of the second possibility: that for type 3 males, coercion “might be a ‘spillover’ consequence of maximizing mating opportunities”, one that emerges most often in men with specific developmental experiences and whose social context indicates there is low cost for doing so.

CHAPTER 4. IN THE EYE OF THE BEHOLDER: RELATIONSHIP- AND FERTILITY-MODERATED PREFERENCES FOR POTENTIAL MALE FACE-TRAITS

4.1 ABSTRACT

Many of the biosocial developmental factors that influence facial structure also influence behavioral tendencies related to dominance, trust, and threat, and this relationship may allow women to use facial cues to make reproductive decisions. In this study, I explore whether female preferences vary based on her perception of a man's likelihood of engaging in different kinds of behavior, as assessed through facial cues, as well as how these preferences change in response to fertility and interest in a new sexual partner. Women rated images generated at extreme ends of seven characteristics associated with female mate preferences, including facial attractiveness, short- and long-term relationship potential, and forms of antisociality, including general antisociality and the Dark Triad. Female preferences were, for the most part, in the predicted direction. However, contrary to expectations, women showed preference for "poor" (not "good") long-term partners and "high" (not "low") psychopathy. Further, while the results were heavily moderated by the woman's interest in new sexual partners, they were generally not influenced by the menstrual cycle. Results support the hypothesis that women may use male facial cues as a proxy for behavioral tendencies, indicate the potential for confirmation bias in fertility-based research, and suggest several avenues of exploration.

4.2 INTRODUCTION

Dominance behaviors are used to navigate social conflicts and as such carry adaptive significance. In humans, these behaviors can manifest as prosocial or antisocial, and they emerge under the influence of biosocial developmental factors, including that of testosterone. Because testosterone also influences male-typical facial dimorphisms, women may be able to use facial cues to make reproductive decisions, distinguishing between men who vary in personality-correlated facial structures in ways that indicate optimal choices. These decisions may also vary in response to changes in the woman's menstrual cycle-regulated fertility and to their own relationship status. In this study, I explore the preferences women have for dominance-related face-traits in response to these contextual elements.

4.2.1 Sociobiology and Dominance Behavior

While group living conveys a variety of benefits, it also carries costs (Alexander 1974 [review], Earley and Dugatkin 2010, Clutton-Brock and Huchard 2013 [review]). Many of these costs are associated with the demands of establishing social hierarchies – such as allocating responsibilities, identifying group members, and communicating information quickly and accurately – and as group size and complexity increases, so do these demands. Various adaptations have emerged in response, including the use of dominance behaviors to resolve social conflicts. In primates, dominance contests often require face-to-face interactions, and they usually result in a "winner" and a "loser," with the winner gaining social status and the associated benefits (Mazur 1985, Van Honk et al. 2014 [review]). In humans, dominance status is associated with reproductive success in both indigenous and Western cultures (Kaplan and Hill 1985, Mulder 1987, Hawkes et al. 2001, Smith 2004 [review], Gurven and Von Rueden 2006 [review], Hopcroft 2006, Von Rueden et al. 2011); with increased intramarital fertility and lower infant mortality (Von Rueden et al. 2011); and with wealth, income, and education, which are independently associated with reproductive success in men (Hopcroft 2006, Weeden et al. 2006, Fieder and Huber 2007, Nettle and Pollet 2008).

Dominance behaviors can be prosocial or antisocial. Prosocial behaviors are those associated with the maintenance of the social group; those who engage in prosocial behaviors have greater social influence and success in balancing the costs of group living (see Milinski et al. 2002, Hawkes and Bird 2002, Smith 2004 [review], Hardy and Van Vugt 2006, Willer 2009, Jaeggi and Gurven 2013). Antisocial behaviors, on the other hand, are those that are disruptive to the group, and include various forms of criminality, aggression, and violence. All kinds of dominance behaviors emerge from the interaction of genetic, environmental, and social factors that combine to influence the development of behavioral patterns most likely to be adaptive in that particular environment. Indeed, both the developmental factors and behavioral patterns associated with pro- and antisociality align with those associated with slow and fast life history strategies, respectively (Figueredo et al. 2006, Del Giudice 2018, 2020), and the factors associated with antisociality seem to prime the individual toward patterns optimal in harsh and unpredictable environments (summarized below, see Table 1.1 for full details and references).

Mechanistically, the divergence of prosocial and antisocial behaviors occurs primarily as a result of testosterone- and cortisol-related factors. Indeed, even though testosterone is most commonly known for its effect on male-typical sexual dimorphisms (T'Sjoen et al. 2019 [review]), particularly for masculinized facial structure (Fink and Penton-Voak 2002, Bulygina et al. 2006, Thordarson et al. 2006, Weston et al. 2007, Toma et al. 2008, Marečková et al. 2011, Whitehouse et al. 2011), testosterone's impact on dominance behavior is such that it may be considered primarily a strategic social status-seeking hormone (Hirschenhauser and Oliveira 2006 [review], Eisenegger et al. 2011 [review], Terburg and van Honk 2013 [review], Van Honk et al. 2014 [review], Geniole and Carré 2018 [review]). Different forms of antisociality emerge from the influence of other related factors. A general tendency toward antisociality is associated with parental rejection and the concentration of the sex hormone binding globulin (SHBG) responsible for transporting testosterone. Aggression seems to emerge primarily in response to the imbalance of testosterone and cortisol – specifically that of high testosterone and low cortisol. Conditions of chronic stress can amplify aggressive responses, as these increase the production of vasopressin, a cortisol-stimulating hormone independently associated with increased aggression. The type of aggression that appears – proactive (instrumental) or reactive (explosive) – depends upon the degree of control that the prefrontal cortex has over the amygdala, control that is weakened through long-term testosterone exposure. And violent behavior seems to emerge in response to decreased androgen sensitivity. However, criminality seems to have little association with these factors (apart from the aforementioned behaviors); instead, the tendency toward criminal behavior is heavily influenced by the presence of childhood trauma. Similarly, while both sexual activity and violence are both independently related to testosterone, sex-related violence seems primarily unrelated to testosterone.

Antisocial behavior can present in consistent patterns, or personalities. Three of these personalities – Machiavellianism, narcissism, and psychopathy – are collectively termed the Dark Triad. These "Dark personalities" emerge in response to a mix of biological and environmental factors (Table 4.1) and share tendencies such as the use of aggression, callousness, and manipulation to achieve goals (Paulhus and Williams 2002, Furnham et al. 2013 [review], Jonason et al. 2013, Lee and Ashton 2014 [review], Semenyna and Honey 2015, Muris et al. 2017 [review], Koehn et al. 2019 [review], Jonason and Sherman 2020, Schreiber and Marcus 2020 [review], Truhan et al. 2021). However, they differ in distinctive ways. Generally speaking, Machiavellianism is associated with cunning and subtle manipulation, narcissism with excessive self-obsession, and psychopathy with self-indulgent malice. These personalities also demonstrate different patterns of aggression. Machiavellianism demonstrates both proactive and reactive aggression (van Lier 2015), narcissism exclusively demonstrates reactive aggression (Bobadilla et al. 2012, van Lier 2015), and psychopathy demonstrates either or both, depending on how the psychopathy manifests. There are two intersecting aspects to psychopathy – callous-unemotionality (CU) and impulsivity-antisociality (IA) – and each aspect is characterized by proactive and reactive aggression, respectively. Thus, individuals with psychopathic traits vary with regards to the degree that they embody both aspects (Skeem et al. 2007, Bobadilla et al. 2012, van Lier 2015, Yildirim and Derksen 2015(a) [review], Neumann et al. 2015, Porter et al. 2018, Bronchain et al. 2020, Harrison 2021).

Because dominance behaviors and masculinized facial structure share developmental roots through the effects of testosterone, it may be possible to learn to associate the likelihood of engaging in certain behaviors with face traits. This ability may be of particular importance in complex fission-fusion primate groups that have frequent contact with unknown individuals, a dynamic that would act as a strong selection pressure for the ability to rapidly detect sources of potential threat, particularly when those sources could not be easily faked. Indeed, an ability to associate dominance tendencies with facial characteristics may help explain the dependence of face-to-face interactions for dominance contests in primates.

Table 4.1. Biosocial developmental factors associated with the Dark Triad.

Identified Contributing Factors	**Machiavellianism**	**Narcissism**	**Psychopathy**
Heritability			
Additive Genetic Effects	0.31	0.59	0.64
Environmental Factors			
Shared	0.39	0.00	0.04
Non-Shared	0.30	0.41	0.32
CITATIONS: All: Onley et al. 2013, Vernon et al. 2018, Schermer and Jones 2020			
Biological Factors			
Testosterone		X	X
Estradiol			X
Cortisol		X	X
Dopamine		X	X
Serotonin			X
Oxytocin			X
CITATIONS: Narcissism – Konrath and Bonadonna 2014 [review], Pfattheicher 2016, Dane et al. 2018, Borraz-Leon et al. 2019, Miles et al. 2019. Psychopathy – van Honk and Schutter 2006 [review], Blanchard and Lyons 2010, Meyer-Lindenberg et al. 2011 [review], Montoya et al. 2012 [review], Yildirim and Derksen 2012(b) [review], Brune 2012 [review], Yildirim and Derksen 2013 [review], Herpers et al. 2014 [review], Yildirim and Derksen 2015(a) [review], Yildirim and Derksen 2015(b) [review], Choy et al. 2018 [review], Fragkaki et al. 2018 [review]			
Environmental Factors			
Disordered Childhood Attachment			X
Parental Protection and/or Overcontrol			
Presence of Risk Factors			X
e.g., Trauma, Social Rejection			
CITATIONS: Psychopathy – Gao et al. 2010, Brune 2012 [review], Meyer-Lindenberg et al. 2011 [review], Yildirim and Derksen 2012(b) [review], Yildirim and Derksen 2015(a) [review], Blanchard et al. 2016(b), Fragkaki et al. 2018 [review]			

Indeed, there is evidence that humans and chimpanzees may have the ability to associate static facial features with behavioral tendencies if they share underlying developmental factors (Humans – Todorov et al. 2015 [review], Todorov 2017 [review], Todorov and Oh 2021 [review]; Chimpanzees – Kramer et al. 2011). Moreover, social judgments made based on these associations – known as face-traits – tend to be consistent, rapid, and accurate (Todorov et al. 2015 [review], Todorov 2017 [review], Todorov and Oh 2021 [review]), and are less variable than social judgments made based on dynamic features (Todorov and Porter 2014, Hehman et al. 2015). Much of this research has relied on composite images, in which images of individuals who score similarly on a specific metric are merged into one image, or on computer-generated or -manipulated faces. These techniques have allowed the researchers to isolate facial cues associated with accurate judgments (Oosterhof and Todorov 2008, Kramer and Ward 2010, Todorov et al. 2010, Jones et al. 2012), many of which, like testosterone, share developmental roots with factors also expected to influence behavior: for example, muscle tone, skin tone and texture, and resemblance to facial expressions are influenced by nutrition, sleep deprivation, environmental stressors, and the repetition of those facial expressions (Todorov 2017 [review]). This research also suggests that accuracy in these face-trait judgments emerges at rapid speed – shorter than 50 ms and faster than conscious awareness; in fact, deliberate, intentional judgments tend to decrease accuracy (Bar et al. 2006, Ballew and Todorov 2007, Borkenau et al. 2009, Todorov et al. 2009, Kramer and Ward 2010, Todorov et al. 2010, Jones et al. 2012, Todorov et al. 2013).

The detection of face-traits seems limited to specific kinds of social signals – those related to dominance, trust, and threat, which is unsurprising given the importance of identifying potentially harmful strangers. Evidence suggest that dominance and trustworthiness comprise 80% of face-trait social judgments (Fiske et al. 2007 [review], Oosterhof and Todorov 2008, Sutherland et al. 2013, Walker and Vetter 2016, Messer and Fausser 2019, Todorov and Oh 2021 [review]) and that the judgments of these are reliable and accurate across cultural and interracial groups (Walker et al. 2011, Short et al. 2012, Ma et al. 2015, Sutherland et al. 2018, Todorov and Oh 2021 [review]), and judgments of trustworthiness seem particularly accurate (Todorov et al. 2009, Todorov et al. 2010, Stirrat and Perrett 2010, Todorov et al. 2013, Rule et al. 2013). Dimensions of these two characteristics have been mapped onto 2D and 3D faces to generate validated models that reliably represent varying degrees of these traits (Oosterhof and Todorov 2008, Todorov et al. 2013, Walker and Vetter 2016, Todorov and Oh 2021 [review]).

It seems as though threat detection may be the primary driving force of face-trait detection (Oosterhof and Todorov 2008, Walker and Vetter 2016), and testosterone may be the primary mediator, given its influence on both broad, masculinized facial features and on dominance, and particularly antisocial, behaviors. Indeed, facial width-to-height ratio (fWHR) is associated with dominance, aggression, threatening behavior, and the likelihood of both holding explicitly racially prejudiced beliefs, all of which have also been accurately identified from face-traits (Dominance fWHR – Geniole et al. 2015 [review, meta-analysis]; Threat: Identification – Oosterhof and Todorov 2008, Todorov et al. 2013; fWHR – Geniole et al. 2015 [review, meta-analysis]; Aggression: Identification – Carré et al. 2009; fWHR – Carré et al. 2009, Carré and McCormick 2008, Geniole and McCormick 2015, Haselhuhn et al. 2015 [meta-analysis]; Explicit racism: Hehman et al. 2013). This general threat-detection tendency may include traits associated with the Dark Triad.

Ratings of composite images of high and low scoring individuals for different Dark Triad traits generally show an aversion to those who score high (Images generated in Holtzman 2011, used as is in Lyons et al. 2015, Marcinkowska et al. 2015, 2016, Lyons and Blanchard 2016, Lyons and Simeonov 2016; Morphed with unique images in Brown et al. 2017, Brewer et al. 2018, Brewer et al. 2019, McElroy et al. 2020, Alper et al. 2021). Other studies have used their own images and show similar findings (Gordan and Platek 2009, Giacomin and Rule 2018, Shiramizu et al. 2019). However, it is important to note that any preferences with regards to images associated with the Dark personalities is most likely due not to the identification of a specific personality but instead to shared underlying developmental factors associated with general threat potential detection.

While both face-traits and our ability to detect them seem to be biologically mediated, the actual associations that are formed develop through learning and experience. The ability to perceive trustworthiness seems to emerge around 7 months (Jessen and Grossmann 2016), and the ability to predict the outcome of dominance dynamics emerge between 10 and 15 months (Thomsen et al. 2013, Mascaro and Csibra 2014), with child-adult agreement appearing between 3 and 6 years old (Cogsdill et al. 2014, Cogsdill and Banaji 2015, Charlesworth et al. 2019). Having repeated, high-quality social interactions with diverse people during development seems crucial to accuracy (Freeman and Ambady 2011, Freeman et al. 2020). The lack of early-age interracial socialization seems to result in a poor ability to discern other-race face-traits (Lee et al. 2017, Qian et al. 2017, Over and Cook 2018). This may result in an overgeneralization of other-race faces as a potential threat, thereby explaining a variety of race-related trends in facial perception (MacLin and Malpass 2001, Hugenberg and Bodenhausen 2003, Baron and Banaji 2006, Dotsch et al. 2008, Stanley et al. 2011, Strachan et al. 2017, Charbonneau et al. 2020).

4.2.2 Human Mating Behavior

The evolution of human mating behavior has been shaped by the same forces as other species. Of particular concern are those forces that influence sexual conflict, specifically the different ways that men and women invest in their offspring (Labuda et al. 2010, Marlowe and Berbesque 2012). Based on the identified patterns, the expected trend in humans is that of a female mate choice system that prioritizes male mates who can offset the higher per-offspring reproductive investment made by the female. This choice would be mediated by various socio-environmental factors including but not limited to resource availability, the type of relationship she is pursuing, and available alloparental support.

Evidence supports this prediction. Women tend to be more selective than men in both their sexual behavior and choice of sexual partner. Further, they show a universal and historical preference for men who can offset her higher per-child reproductive investment, namely those with high social status and financial security (Buss 1989, Kenrick et al. 1990, 1993, Singh 1995(b), Schmitt and Shackelford 2001 [review], Li et al. 2002, Schmitt 2005 [cross-cultural], Shackelford et al. 2005 [cross-cultural], Penke and Asendorpf 2008, Valentine and Li 2012 [review], Conroy-Beam et al. 2015, Schmitt and Jonason 2015 [cross-cultural], Buss and Schmitt 2016 [review], Buss 2016 [review], 2017 [review], Csajbók and Berkics 2017, Buss and Schmitt 2019 [review]; Walter et al. 2020 [cross-cultural], Thomas et al. 2020 [cross-cultural]). Exceptions to this trend are consistent with relevant socioenvironmental factors and demonstrate trade-off decisions between direct and indirect benefits (Marlowe 2000, Brown et al. 2009, Schacht and Kramer 2019 [review, cross-cultural], Fortunato 2018).

In response to female choice, males can engage in different mating strategies. These strategies often develop in response to the same developmental factors as dominance behaviors, including those associated with pro- and antisociality, and thus tend to align with fast and slow reproductive strategies – faster male strategies are associated with investment into mating behavior whereas slower strategies with investment into parenting behavior (Booth and Dabbs 1993, Mazur et al. 1994, Bogaert and Fisher 1995, Storey et al. 2000, Fleming et al. 2002, Gray et al. 2002, McIntyre et al. 2006, Peters et al. 2008, Alvergne et al. 2009, Fisher et al. 2009, Muller et al. 2009, Edelstein et al. 2011, Pollet et al. 2011, Van Anders et al. 2012, Weisman et al. 2014, Puts et al. 2015, Das and Sawin 2016, Gray et al. 2017, Polo et al. 2019, Klimas et al. 2019). Like with dominance behaviors, these mating strategies are bidirectionally mediated by testosterone (Mazur and Michalek 1998, Archer 2006, Kuzawa et al. 2009, Alvergne et al. 2009, Gettler et al. 2011(b), Puts et al. 2015, Roney and Gettler 2015), with low testosterone associated with increased parenting investment (Fleming et al. 2002, Kuzawa et al. 2009, Muller et al. 2009, Gettler et al. 2011(a), Perini et al. 2012, Gettler et al. 2015, Gray et al. 2017, Saxbe et al. 2017). The mating behavior of Dark personalities suggest tendencies toward high mating investment (Jonason et al. 2011, Furnham et al. 2013 [review], Westhead and Egan 2015, Jonason et al. 2017) and, combined with developmental factors, indicates that they may represent specialized fast strategies (Jonason et al. 2009, 2010, Jonason et al. 2016).

Some forms of sexually coercive behavior may be a fast mating strategy as well. Men who engage in sexual coercion often engage in behaviors associated with a high investment in mating effort (Kanin 1985, Malamuth et al. 1991, 1995, Lalumière and Quinsey 1996, Lalumière et al. 1996, Malamuth 1998 [review], Abbey et al. 2006, McKibbin et al. 2008 [review], Westerlund et al. 2010, Camilleri and Stiver 2014 [review]). Additionally, fast strategies and sexually coercive behavior seem to emerge from similar developmental influences (Malamuth et al. 1991, 1995, Malamuth 1998, Ellis 1998 [review], Abbey et al. 2006, Yost and Zurbriggen 2006, Westerlund et al. 2010, Camilleri 2012 [review], Barnes et al. 2013, Ciardha and Ward 2013 [review], Tharp et al. 2013 [review], Camilleri and Stiver 2014 [review], Långström et al. 2015 [cross-cultural, longitudinal], Ward and Beech 2016). Additionally, there is overlap between men with Dark personalities and men who engage in sexually coercive behavior (Reise and Wright 1996, Yost and Zurbriggen 2006, Mouilso and Calhoun 2012, Lee et al. 2013, Figueredo et al. 2015, Westhead and Egan 2015, Jonason et al. 2017, Koehn et al. 2019 [review], Jonason and Sherman 2020, Zeigler-Hill et al. 2016), though not all coercers have Dark personalities: coercers often lack general tendencies toward callousness, manipulation, and the acceptance of non-sexual forms of domination and violence (Malamuth 1981, Malamuth et al. 1986, Malamuth 1998, Rice et al. 1990, Prentky and Knight 1991, Lalumière and Quinsey 1996, Hare 1996, Brown and Forth 1997, Lisak and Roth 1988, Paulhus and Williams 2002, Abbey et al. 2006, Camilleri et al. 2009, Woodworth et al. 2013, Lee et al. 2013, Brown et al. 2015, Westhead and Egan 2015).

These relationships may allow women to use facial structure, and masculinity in particular, as a cue to a man's probable investment into mating/parenting effort as well as his tendencies toward antisocial behavior. Thus, we might expect a female preference for masculinity to reflect these factors. Indeed, this seems to be the case: women show no marked preference for facial masculinity (Slight preference for masculinity – Johnston et al. 2001, DeBruine et al. 2006; No preference – Singh 1995(b), Swaddle and Reierson 2002, Penton-Voak and Chen 2004, Boothroyd et al. 2008, Scott et al. 2010, Geniole et al. 2015 [review], Kandrik 2017; Preference for femininity – Perrett et al. 1998, Rhodes et al. 2000) – they associate masculinity with being cold, unemotional, dishonest, uncooperative, and being a poor parent (Perrett et al. 1998, Kruger 2006) and with the Dark Triad (Lyons et al. 2015). Instead, women prefer traits associated with being a good long-term partner (Buss 1989, Buss 1994, Scheib 1994, Kenrick et al. 1990, 1993, Hill and Hurtado 1996, Scheib 2001, Valentine and Li 2012 [review], Moore et al. 2013, Conroy-Beam and Buss 2016, Farrelly et al. 2016, Shyte et al. 2016, Csajbók and Berkics 2017, Ehlebracht et al. 2018) and having high prestige (Snyder et al. 2008) over those associated with dominance. They show a preference for dominance only when it is accompanied by prosocial behaviors and attitudes (Jensen-Campbell et al. 1995, Brown et al. 2021) and the absence of antisocial ones (Sadalla 1987, Lyons and Blanchard 2016), and they show a distinct aversion to faces and behaviors associated with the Dark Triad which they associate with masculinity (Faces, All dark personalities – Lyons et al. 2015, Lyons and Blanchard 2016, Brewer et al. 2019, but see Carter et al. 2014; Behaviors, Psychopathy – Rauthman and Kolar 2013, Blanchard et al. 2016(a); Behaviors, Narcissism and Machiavellianism – Rauthman and Kolar 2013)

These preferences generally hold true in short-term contexts as well (Simpson and Gangestad 1992, Muggleton and Fincher 2017, Ehlebracht et al. 2018, Brown et al. 2019), though to a lesser extent. There does seem to be an increased preference for masculinity and dominance, particularly for less sexually restricted women (Simpson and Gangestad 1992, Gangestad and Simpson 2000 [review], Little et al. 2002, Frederick and Haselton 2007, Snyder et al. 2008, Penke and Asendorpf 2008, Valentine and Li 2012 [review], Valentine et al. 2014, Marcinkowska et al. 2015, Buss and Schmitt 2016 [review], Buss and Schmitt 2019 [review]). The aversion to Dark personalities holds in short-term contexts as well (Lyons et al. 2015, Blanchard et al. 2016(a), Brewer et al. 2018, Brewer et al. 2019, but see Aitken et al. 2013 and Jonason et al. 2015), though there may be some exceptions – specifically those associated with resource-availability (Marcinkowska et al. 2015, Lyons and Simeonov 2016), whether the women themselves have Dark personalities (Jonason et al. 2011, Jonason et al. 2015, Blanchard et al. 2016(a), Lyons and Blanchard 2016), and their use of contraceptives (preference for narcissists while not on contraceptives, strong aversion to Machiavellian while on contraceptives – Marcinkowska et al. 2015). Overall, the expectation that women would not show a particular preference for masculinity is supported. The evidence suggests that the negative effects of high levels of masculinity may have kept the potential for runaway selection with regards to displays of masculinity in check.

In addition to shifts in mate choice preferences under different relationship contexts and socioenvironmental conditions, it has been proposed that a woman's mate choice preferences change in response to changes in her fertility. This hypothesis derives from patterns in non-human primates which show fertility-mediated shifts in mating behavior, a behavior that has been documented even in species with concealed ovulation (Michael and Zumpe 1970, Wallen et al. 1984, Garcia et al. 2021 [review]). This suggests that there may be some degree of hormonally-mediated reproductive optimization involved, with women changing their reproductive behavior over their menstrual cycles in a fitness-enhancing way.

The human menstrual cycle consists of three non-overlapping periods: the follicular phase, ovulation (essentially instantaneous), and the luteal phase (Barbieri 2014 [review]). The follicular phase begins with the onset of menses. During this phase, follicle-stimulating hormone (FSH) and luteinizing hormone (LH) act to cause the primordial follicle in the ovary to grow and produce estradiol. As estradiol levels rise, the further production of FSH and LH are inhibited, and the chance of conception increases with changes in the cervix. The rising level of estradiol eventually reaches a threshold and begins a chain reaction – it causes a surge in LH and FSH which acts on the follicle and, approximately 24-36 hours later, causes ovulation. Fertilization by sperm can only occur within the day after ovulation, but because sperm can survive in the reproductive tract for five days, the human fertile window comprises the last five days of the follicular phase and the day of ovulation (Wilcox et al. 1995). The luteal phase begins after ovulation and is characterized by the release of progesterone from the corpus luteum, the structure that was formerly the ruptured follicle. Progesterone prevents the production of LH (and FSH) which in turn causes the corpus luteum to slowly break down, causing progesterone levels to decrease. If conception and implantation occur, the implanted blastocyst releases human chorionic gonadotropin (hCG). This rescues the corpus luteum and ensures the continued production of progesterone and the maintenance of the endometrium throughout pregnancy. If the egg is not fertilized, progesterone and estradiol levels continue to drop, and the endometrium will eventually shed, causing menses and the beginning of the next cycle.

While the menstrual cycle is commonly conceived as being 28 days long, this is neither medically normal nor reliable. Fertile menstrual cycles between 19 and 60 days long have been documented (Wilcox et al. 2000, Fehring et al. 2006, Jukic et al. 2007), and nearly one-third of women have more than 7 days of variation with each successive cycle (Fehring et al. 2006). This variability poses a unique complication in human fertility research as it makes fertility difficult to pinpoint. There are three general methods of identifying when ovulation, and thus the fertile window, occurs: (1) estimation methods that assume certain consistencies in cycle phases and length, (2) fertility-awareness based methods that track specific physiological changes, and (3) medically-confirmed methods that use hormonal assays or sonographs to confirm ovulation. Estimation methods are the least invasive and expensive, but they rely on consistent across-women and within-woman phases of the cycle. And while the general pattern of the menstrual cycle is consistent across most women, the timing and length of each phase is not. Therefore, estimates of fertility for research and medical use have a high chance of being inaccurate; indeed, no method has been found to have an accuracy greater than 30% (Blake et al. 2016). Fertility-awareness based methods are more accurate, though they are generally used for contraceptive purposes and thus are inadvisable for use in research. Medically-confirmed methods are the most accurate (Collins et al. 1979, World Health Organization 1980, Li et al. 1989, Guida et al. 1999, Guermandi et al. 2001). However, they are not only more expensive, but they increase the likelihood that participants become aware of the purpose of the study and thus subconsciously affect the results of the study.

Identifying consistent fertility-mediated trends in humans has been difficult for several reasons, including the use of incomparable methodology, inconsistent result reporting, and the impact of any pre-existing beliefs that the participants may have about their behavior and the menstrual cycle. However, several areas of behavioral fertility have been investigated, and fertility-mediated changes in sexual partner preferences is one of the most explored avenues. Lines of investigation have included changes in a woman's opinion toward her mate's attractiveness, her interest in in-pair and extra-pair mating, her ability to discriminate between potential mates, and her preferences for masculinity, mate variety, and signals of apparent health. Another area that has been explored is the degree to which fertility might influence a woman's behavior in response to potential risks or harm, including those related to potential sexual partners (Table 4.2).

However, despite shifts in sexual partner preferences being one of the most studied areas of behavioral fertility, the inconsistency in methodology along with inadequacy in fully reporting results has made it difficult to identify consistent trends. The most consistent patterns indicate both fertile and luteal effects. Most of the fertile effects seem to center on mate discrimination and harm avoidance: fertile women show an increased speed in mate discrimination (Macrae et al. 2002, Johnston et al. 2003, Brinsmead-Stockham et al. 2008, Rule et al. 2011), particularly when assessing potential mating threats (Garver-Apgar et al. 2007, Masataka and Shibasaki 2012); disgust toward aberrant sexual behavior (Fessler and Navarrete 2003); avoidance of perceived risky situations and people (Chavanne and Gallup 1999, Bröder and Hohmann 2003, Guéguen 2012); and paranoia toward out-group members (Brinsmead-Stockham et al. 2008, Navarrete et al. 2010, McDonald et al. 2011). Thus, it may be that the higher cost of mating while fertile in comparison to other parts of the cycle might cause women to be more discriminatory. And while this effect is expected to be directed primarily at men, it may also be part of a larger threat-avoidance heuristic. The luteal effects seem to center on partner-based preferences, including an increase in their preferences for apparent health (Jones et al. (2005(a)(b)), an increase in their desire for relationship commitment from their partners (Jones et al. 2005(a)), and a decrease in their interest in masculinity (Jones et al. 2005(a), Harris 2011), including for both long- and short-term mates (Puts 2006). These effects might occur as a byproduct of progesterone and its importance in pregnancy maintenance and which might result in both physiological and behavioral changes. These preferences might indicate an increased wariness of disease, of men who might harm her or the fetus, and desire to maintain a relationship with the father of the fetus. Indeed, repeated sexual intercourse with the father of the fetus decreases the risk of preeclampsia (Robillard et al. 2008; see also Smith et al. 1997, Kho et al. 2009, Saftlas et al. 2013, Triche et al. 2014), as sperm seems to act as an antigen that aids the mother in the immunoregulation needed to regulate placental invasion (Robertson and Sharkey 2001, Robertson et al. 2003, Dekker and Robillard 2005, Robertson et al. 2013, Martinez-Varea et al. 2014).

Table 4.2. Trends associated with menstrual cycle shifts in sexual partner preferences and behaviors associated with the perception of potential harm.

Sexual Partner Preferences

Area of Findings	*Trend*	*Summary*	*Reference*
Apparent Health			
	Potential luteal effect	Consistent findings for a luteal effect for an increased preference for apparent health	Jones et al. 2005(a), 2005(b)
In-Pair / Extra-Pair			
	Inconclusive	Findings indicate a fertility-mediated increase toward extra-pair, usually under extremely specific conditions, along with one toward in-pair and all men. Further, many results were unreported, and there was a high potential for a priming effect.	Gangestad et al. 2002, Pillsworth et al. 2004, Gangestad et al. 2005, Pillsworth and Haselton 2006, Haselton and Gangestad 2006, Gangestad et al. 2010(b), Gangestad et al. 2014
Long-term / Short-term Mates			
	Inconsistent	Some indicate a fertility-mediated shift in preferences for short-term men, but not always in expected direction, and many had high priming potential. Others found luteal effects for preferences for increased commitment and decreased masculinity in long-term men.	Penton-Voak et al. 1999, Gangestad et al. 2004, Puts 2005, Jones et al. 2005(a), Puts 2006, Haselton and Miller 2006, Gangestad et al. 2007, Garver-Apgar et al. 2007, Little et al. 2007, Durante et al. 2012
Masculinity / Femininity			
Bodies	Inconclusive	Increased effect of fertility but under specific contexts, accompanied by high degree of priming.	Little et al. 2007
Faces	Potential luteal effect	Most studies found no effect except after altering the phase of cycle determination or using visual inspection of the data. Other studies found a decreased preference for masculinity with the luteal phase.	Penton-Voak and Perrett 2000(b), Johnston et al. 2001, Jones et al. 2005(a), Harris 2011, 2012, Jones et al. 2018
Mate Attractiveness			
Vision Cue	Inconsistent	A few found a fertility-mediated shift, but most found no effect.	Koehler et al. 2002, Fisher et al. 2004, Gangestad et al. 2004, Anderson et al. 2010
Odor Cue	Inconclusive	Most studies report an association with scent attractiveness rating and fertility; however, findings indicate similar non-fertile, control, and contraceptive findings, and some results indicate errors in reporting.	Gangestad and Thornhill 1998, Thornhill and Gangestad 1999, Thornhill et al. 2003, Garver-Apgar et al. 2008
Preference Importance	Inconclusive	Results indicated increased preference with fertility, but high priming potential	Gangestad et al. 2010(a)
Mate Discrimination			
General	Potential for fertile effect	Results indicate increased speed in mate discrimination and disgust toward aberrant sexual behavior, though one altered the phase of cycle determination method	Macrae et al. 2002, Fessler and Navarrete 2003, Johnston et al. 2003, Brinsmead-Stockham et al. 2008, Rule et al. 2011
Mating Threat Context	Inconclusive	Findings indicate increased paranoia regarding potential sexual coercion, though likely proxy-dependent	Garver-Apgar et al. 2007, Masataka and Shibasaki 2012
Variety			
	Inconclusive	Findings suggest the possibility of an increase in variety, though dependent upon the specific proxy used	Thornhill et al. 2003, DeBruine 2005, Faraji-Rad et al. 2013

Table 4.2. (continued)

General Harm Avoidance			
Area of Findings	*Trend*	*Summary*	*Reference*
Risky Activities			
	Potential fertile effect	Findings indicate an aversion to potentially harmful or dangerous situations	Chavanne and Gallup 1999, Bröder and Hohmann 2003
Potentially Dangerous Men			
	Potential fertile effect	Results indicated women increased their avoidance of men who seemed dangerous	Guéguen 2012
In-Group/Out-Group Bias			
	Potential fertile effect	Findings suggest increased paranoia of those outside of their group	Brinsmead-Stockham et al. 2008, Navarrete et al. 2010, McDonald et al. 2011

Inconsistent: Mixed directional effects, such that significant findings found in opposing direction either with respect to the characteristic or the phase of cycle.

Inconclusive: Evidence is relatively weak, findings sufficiently scattered, or potential for priming is high

Potential for: Results tend to show a consistent direction

4.2.3 Study Question:

This project aims to investigate human female mate choice optimization in the context of relationship status, the menstrual cycle, and male facial structures as a proxy for various dominance-related traits. These traits include those related to general attractiveness, relationship potential, and antisociality (See *Methods: Survey Design and Procedure* for details about these images).

Question 1. Female preferences for and discrimination between men.

Facial structure may be associated with aspects of personalities (face-traits) that may be relevant to mating decisions, and women may be able to assess individuals based on these face-traits as being suitable for different kinds of relationships (or relationship-avoidance) accordingly. Using images constructed to be high or low on several different axes of appearance or personality traits, I assessed if these images elicited the predicted responses from subjects. I predict that subjects will consistently rate images differently under different relationship contexts (types of ratings). Specifically, I predict that ratings of attractiveness and hookup interest will be higher for images with high facial attractiveness than low, that ratings of short-term interest will be higher for images constructed for high short-term potential than for low, and that ratings of long-term interest will be higher for images constructed for high long-term potential than for low. Further, I predict that they will rate the images constructed to reflect a preference for low general antisocial potential than the high images regardless of context.

Question 2. Female relationship and image preferences

Women invest more into each individual offspring than men due to the associated costs of pregnancy and childbirth and are thus generally more discriminatory with regards to mating behavior. In particularly, women are expected to show a general preference for men who demonstrate qualities that indicate they are willing and able to help offset this investment by providing direct benefits, namely in the form of being willing to engage in a long-term relationship. If facial features can indicate these tendencies, I predict women will have higher ratings in the Attractiveness and Long-term Interest contexts for images formed with attributes indicating good long-term mates over poor long-term mates.

Question 3. Effect of Relationship status

Female mate choice preferences may shift in response to their relationship status. Specifically, women who are in a committed, monogamous relationship may view other men as generally less desirable as a type of relationship-maintenance behavior. Further, women who are single and not interested in a relationship may also exhibit a decreased interest in men. Thus, I expect participants who are not looking for new partners to rate images lower than women who are looking. I expect this to be true for each of the four types of responses.

Question 4. The effect of the menstrual cycle on image preference and discrimination

Because the chances of conception vary across the menstrual cycle, the consequences for engaging in sexual behavior vary accordingly. Consequently, female mate choice preferences may shift across the menstrual cycle so as to maximize reproductive fitness. Evidence suggests that menstrual cycle effects in sexual partner preferences include both fertile and luteal effects. The fertile phase may be associated with increased preferences in partner variety accompanied by increased partner discrimination, particularly against men who may represent sexual threats, as the cost of sexual coercion when fertile is higher than it is at other points in their menstrual cycle. Further, the luteal phase may be associated with increased interest in men who represent good long-term partners and with decreases in those who represent good short-term partners. Thus, I predict that women who are in their luteal phase will show less interest in men who are rated as high short-term partners, and greater interest in men rated as high long-term partners, than women who are in the other phases of their menstrual cycle. I also predict that women who are in their fertile phase will show an increase in their discrimination against the images of men who score high on the general antisocial potential images as compared to women who are not fertile.

Question 5. Fertility-mediated shifts based on relationship status

A woman's relationship status may affect any existing fertility-mediated shifts in sexual partner preferences. Specifically, evidence suggests women may show an increase in sexual partner variety with fertility as a means of increasing the genetic variation of their offspring. However, women who are, in general, not interested in other sexual partners, either because they are in a committed and monogamous relationship or because they are not currently seeking a relationship, may show none of these effects. Thus, I predict that women who are looking for a sexual partner (single, casually dating, or in an open relationship) will show a fertility-mediated increase in the ratings given to men who represent good short-term partners whereas women who are not looking for new partners will show no fertility-mediated increase.

4.3 METHODS

4.3.1 Participant Recruitment

My study population consisted of English-speaking, cisgender, heterosexual, female students at the University of Kentucky between the ages of 18-25. I began recruiting participants in the fall of 2018. All recruitment occurred through email after requesting and receiving email addresses from the registrar's office of students who met the criteria. I sent two reminders to those who had not completed the survey weekly. Email invitations described the survey and directed participants to an online consent form followed by the survey. After participants completed the first survey, they were sent a second, nearly-identical survey approximately two weeks later. A total of 528 participants completed the first survey, and 278 completed the second.

4.3.2 Phase of Cycle Classification

Survey responses were categorized into four phase of cycle designations customized to each participant's menstrual cycle (Figure 4.1). Using each participants' reported first date of their last menstruation and average length of cycle, I calculated the anticipated date of their next menses. Ovulation was estimated by counting backwards 12 days from this date (see Fehring et al. 2006), and the fertile window was determined to begin 6 days prior to ovulation (days -17 through -12, inclusive). The luteal phase was determined to be the 6-day window beginning 3 days after ovulation and ending 3 days before the anticipated date of ovulation. Menses was determined by adding the reported typical length of menstruation to the first day of their last menses. Remaining days were categorized as Other.

Surveys were excluded from analysis if they indicated an irregular or very irregular menstrual cycle, a last day of cycle greater than 32 days, the use of hormonal contraceptive, or reported invalid, incomplete, or incomprehensible menstrual cycle information. In total, 544 surveys were excluded, leaving 814 surveys in the final analysis.

4.3.3 Survey Design and Procedure

After consenting to the study and providing contact information and permissions, the participants were directed to the survey (see Appendix E for the complete survey). The first survey contained three parts: (1) basic questions about their menstrual cycles, sexual activity, and hormonal contraceptive use, (2) questions concerning composite images of men, and (3) basic demographic information, including relationship status, gender identity, sexual orientation, race, age, and ethnicity. The second survey contained only parts (1) and (2).

4.3.3.1 Part 1: Phase of Cycle

Menstrual cycle questions consisted of the following:

- How long does your menstrual cycle (from the start of one period to the start of the next) typically last?
- How long does menstruation typically last (length of menstrual bleeding)?
- How regular are your cycles? (Range: Six-point Likert, Very irregular to Very regular)
- When was the first day of the start of your last cycle? (When was the last day that your period started?)
- Are you using any hormonal contraceptives?
    - If Yes: What kind of hormonal contraceptive are you using?

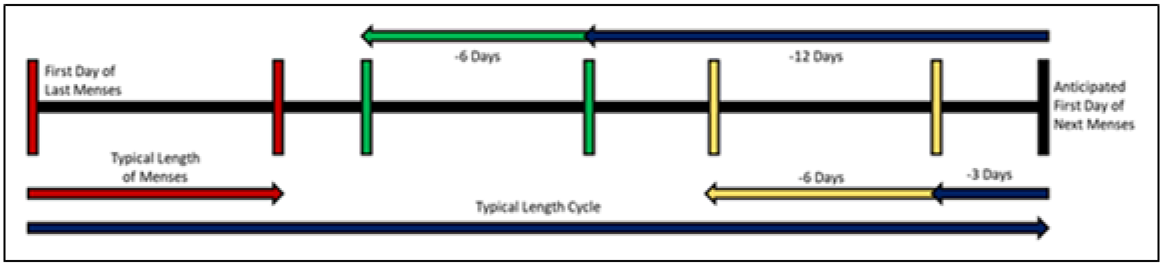


Figure 4.1. A graphical depiction of the fertility-determination method.

Participants provided the first date of their last menses (left red bar) and their average cycle length (black arrow on bottom) which I used to estimate when their next cycle would be likely to begin (right black bar). Ovulation was estimated by counting backwards 12 days (center green bar) and the fertile window included ovulation and the five previous days (top green arrow, between green bars). The luteal phase was determined to be the 6-day window between the estimated day of ovulation and the anticipated day of next menses (bottom yellow arrow, between yellow bars).

4.3.3.2 Part 2: Image Assessment

Participants rated expression-neutral composite images of men, generated with respect to specific characteristics, for relationship-related attributes. The images were taken from Holtzman 2011 and were generated from facial pictures of individuals who were scored on various characteristics using self- and peer-reported metrics. The highest and lowest ten images were merged into a composite image representing the high and low ends of each characteristic. I organized a total of fourteen images divided into two sets: one set represented high and low levels of general attractiveness and relationship potential, and the other set represented high and low levels of traits associated with harm. See the survey in Appendix E for the images as presented with post-distribution identification of image type.

The first set of images, referred to as Attractiveness/Mating Potential images (AMP), included images generated with respect to facial attractiveness, short-term partner quality, and long-term partner quality. The facial attractiveness images were created based on the ratings of 50 unknown same-sex observers. Short- and long-term partner images consisted of the images of individuals who were rated on an author-created 33-item inventory for short- and long-term relationships. It should be noted that these metrics were prototypical and have not been validated through external means, though they were consistent with other metrics used at the time (N.S. Holtzman, personal communication).

The second set of images, referred to as General Antisocial Potential (GAP) images, included high and low scorers for antisociality and the Dark Triad: Machiavellianism, narcissism, and psychopathy. The GAP images were scored using widely accepted and validated inventories for each of the personality traits in question, including (but not limited to) the Mach-IV (Machiavellianism), the Narcissistic Personality Inventory-40, and the Self-Report Psychopathy Scale (Holtzman 2011).

Participants were provided with each image successively and were asked to rate each on attractiveness and their potential for different relationship types. Specifically, they were asked to indicate on a six-point Likert scale the degree to which they agreed or disagreed (strongly to somewhat) with the following statements:

- I find this person very attractive.
- I would be interested in a one-time hookup with this person.
- I would be interested in a short-term romantic relationship with this person.
- I would be interested in a long-term romantic relationship with this person.

I did not define the differences between short-term and long-term relationships. I felt as though this would add additional complications; I did not want participants to be overly concerned with the precise length of time they would want to spend with any one individual. Instead, I relied on their own intuitive understanding of the terms, accepting that they likely fell into that of a short-term relationship being one in which they would not want to extend the relationship into long-term intimate relationship involving family, vacations, and extended commitment, and a long-term relationship being one that they would.

A specific limitation with regards to the survey design was that I was unable to adequately randomize the order of the images across all participants; the images were randomly organized in the survey, but participants did not receive the survey with the images in different orders (see the order of the images presented in Appendix E). Thus, the accuracy of the ratings given to images toward the end of the survey could have been affected by survey fatigue. However, more than three-quarters of the participants completed the survey in less than 10 minutes, and the median response time was just over 6 minutes, so I believe that this effect would be relatively minimal. However, this should be tested explicitly.

4.3.3.3 Part 3: Demographics

Following the survey, participants were asked age, racial, ethic, and marital history demographic questions. They were also asked to complete one question describing their current relationship status:

- Which option best describes your current relationship status?
- Single: Looking
- Single: Not Looking
- Dating: One or more casual partners
- Committed: Closed Relationship / Monogamous
- Committed: Open or Poly Relationship
- Other

The options indicating “Single: Not Looking” and “Committed: Closed Relationship / Monogamous” were categorized as “Not Looking” whereas the other options as “Looking.”

4.3.4 Data Analysis

Linear mixed models were used for all predictions. The dependent variable was the rating given and was modelled assuming a Gaussian distribution. An ordinal regression using a generalized linear mixed model was attempted; however, the analysis was unexpectedly complex and could not be completed within a reasonable amount of time. Depending on the hypothesis, fixed effects included image type, menstrual cycle phase, and relationship status as well as their interactions. All models included the interaction between participant and survey set as a random-effect. See Table 4.3 for models and Table 4.4 for definitions of model factors. Analyses were completed using the mixed procedure in SPSS 28.0 (IBM SPSS Statistics, 2021); the Satterthwaite approximation method to calculate degrees of freedom; the restricted maximum likelihood (REML) method to estimate variance parameters; and the Fisher’s least significant difference for calculating p-values, which were adjusted for multiple comparisons. The full syntax for the analyses can be found in Appendix F.

Table 4.3. The models and data subsets for study questions and predictions. Model factors are defined in Table 4.4.

Prediction 1. Female preferences for and discrimination between men	
Facial Attractiveness Images; Attractiveness and Hookup Interest Ratings	
Model	*Rating = Context + Level + Context*Level + AssignedID*SurveySet*
Subsets	Data was subsetted to include only Facial Attractiveness images (Axis) and ratings of Attractiveness and Hookup interest (Context)
Long-term Partner Images, Long-term Interest Ratings	
Model	*Rating = Level + AssignedID*SurveySet*
Subsets	Data was subsetted to include only Long-term images (Axis) and ratings of Long-term interest (Context).
Short-term Partner Images, Short-term Interest Ratings	
Model	*Rating = Level + AssignedID*SurveySet*
Subsets	Data was subsetted to include only Short-term images (Axis) and ratings of Short-term Interest (Context).
General Antisocial Potential Images, All Ratings	
Model	*Rating = Context + Axis + Level + Context*Axis + Context*Level + Axis*Level + Context*Axis*Level + AssignedID*SurveySet*
Subsets	Data was subsetted to include only General Antisocial Potential images (Axis).
Prediction 2. Female long-term relationship interest and image preferences	
Model	*Rating = Context + Level + Context*Level + AssignedID*SurveySet*
Subsets	Data was subsetted to include only Long-term images (Axis) and ratings of Attractiveness and Long-term interest (Context).
Prediction 3. Effect of relationship status	
Model	*Rating = Context + LookStat + Context*LookStat + AssignedID*SurveySet*
Subsets	Data was not subsetted for any of the model factors.
Prediction 4. The effect of the menstrual cycle on image preference and discrimination	
Luteal Status on Short-term and Long-term Partners	
Model	*Rating = Axis + LutStat + Axis*LutStat + AssignedID*SurveySet*
Subsets	Data was subsetted to include only Short-term and Long-term images (Axis) and ratings of Attractiveness (Context).
Fertile Status on General Antisocial Potential Images	
Model	*Rating = Axis + FertStat + Axis*FertStat + AssignedID*SurveySet*
Subsets	Data was subsetted to include only General Antisocial Potential images (Axis) and ratings of Attractiveness (Context).
Prediction 5. Fertility-mediated shifts based on relationship status	
Model	*Rating = Context + LookStat + Context*LookStat + AssignedID*SurveySet*
Subsets	Data was not subsetted for any of the model factors.

Table 4.4. Definitions of model factors.

Context of Rating (Context)	
Attractiveness	AttRate
Hookup Interest	HookRate
Long-term Interest	LongRate
Short-term Interest	ShortRate

Image Types (ImageType)		**Axis**	**Level**
High Facial Attractiveness	HFA	FA	High
Low Facial Attractiveness	LFA	FA	Low
High Long-term Potential	HLT	LT	High
Low Long-term Potential	LLT	LT	Low
High Short-term Potential	HST	ST	High
Low Short-term Potential	LST	ST	Low
High Antisocial	HAS	AS	High
Low Antisocial	LAS	AS	Low
High Machiavellianism	HMA	MA	High
Low Machiavellianism	LMA	MA	Low
High Narcissism	HNA	NA	High
Low Narcissism	LNA	NA	Low
High Psychopathy	HPS	PS	High
Low Psychopathy	LPS	PS	Low

Menstrual Cycle Phase (Phase)	**Fertile Status (FertStat)**	**Luteal Status (LutStat)**
Other	Not Fertile	Not Luteal
Menstrual	Not Fertile	Not Luteal
Fertile	Fertile	Not Luteal
Luteal	Not Fertile	Luteal

Relationship Status (RelShip)	**Looking Status**
Single: Not Looking	Not Looking
Single: Looking	Look
Dating: One or more casual partners	Look
Committed: Open or Poly Relationship	Look
Committed: Closed Relationship / Monogamous	Not Looking
Other	Look

Random Effects	
Individual Participants	AssignedID
Survey Set (1 or 2)	SurveySet

4.4 RESULTS

For simplicity in communication in the Results and in the Discussion, I periodically refer to the images generated with respect to each characteristic as that characteristic (e.g., “High Short-Term” image vs. “image generated with respect to High Short-Term potential”). This should not be interpreted as conflating the characteristic and the image constructed from that characteristic.

4.4.1 Question 1: Female preferences for and discrimination between men

My prediction was that women would rate High and Low images differently and that these ratings would be in a direction appropriate for the type of image. Specifically, for the Attractiveness and Mating Potential Images (AMP), I predicted that ratings of Attractiveness and Hookup interest would be higher for High Facial Attractiveness than Low, ratings of Short-term Interest would be higher for images constructed for High Short-Term potential than for Low, and ratings of Long-term Interest would be higher for images constructed for High Long-term potential than for Low. Also, I predicted that women would rate the images constructed to reflect a preference for Low General Antisocial Potential (GAP) than the High images regardless of context.

For the AMP images, these predictions were supported, except for images generated with respect for Long-term potential – women rated Low images higher than High ones (Table 4.5; Figure 4.2a). Similarly, for the GAP images, these predictions were supported for the images generated with respect to Antisociality, Machiavellianism, and Narcissism. However, for the Psychopathy-generated images, women rated High images greater than they rated Low images. This pattern held for all rating contexts (Table 4.6; Figure 4.2b).

4.4.2 Question 2: Female relationship and image preferences

I predicted that women would rate the images generated with respect to Long-term images in such a way so as to indicate preference for Long-term mates, rating High images greater than Low images for ratings of Attractiveness and Long-term Interest.

This prediction was also not supported: the general direction was opposite of what was predicted, with women showing a preference for images constructed for Low Long-term potential. When broken down by rating type, the difference between the High-Low pairs for ratings of Attractiveness was not significant (Table 4.7; Figure 4.3).

Table 4.5. Differences in ratings given to High and Low AMP images.

Mixed model results indicate that women demonstrated a significant and substantial preference for the High versions of all images except for Long-term images in which they preferred Low. (Context = context of rating, Level = high/low images, df = degrees of freedom, F = F-statistic, *p* = p-value, EMM = estimated marginal means, SE = standard error)

Type III Tests

		df			
Model	Fixed Effects	Num	Den	F	*p*
Facial Attractiveness					
	Intercept	1	804.7	5720.0	<0.001
	Context	1	2413.0	497.1	<0.001
	Level	1	2413.0	664.3	<0.001
	Context * Level	1	2413.0	47.6	<0.001
Long-term					
	Intercept	1	804.3	4076.2	<0.001
	Level	1	802.8	24.1	<0.001
Short-term					
	Intercept	1	804.7	4200.9	<0.001
	Level	1	804.2	14.1	<0.001

Pairwise Tests

Model	Rating	High Image		Low Image		
		EMM ± SE	df	EMM ± SE	df	*p*
Facial Attractiveness						
	Attractiveness	3.4 ± 0.0	2074.1	2.3 ± 0.0	2074.1	<0.001
	Hookup Interest	2.4 ± 0.0	2078.1	1.8 ± 0.0	2074.1	<0.001
Long-term						
	Long-term Interest	2.5 ± 0.0	1296.9	2.7 ± 0.0	1297.8	<0.001
Short-term						
	Short-term Interest	2.6 ± 0.0	1288.7	2.4 ± 0.0	1289.6	<0.001

Table 4.6. Differences in rating types of the High and Low GAP images.

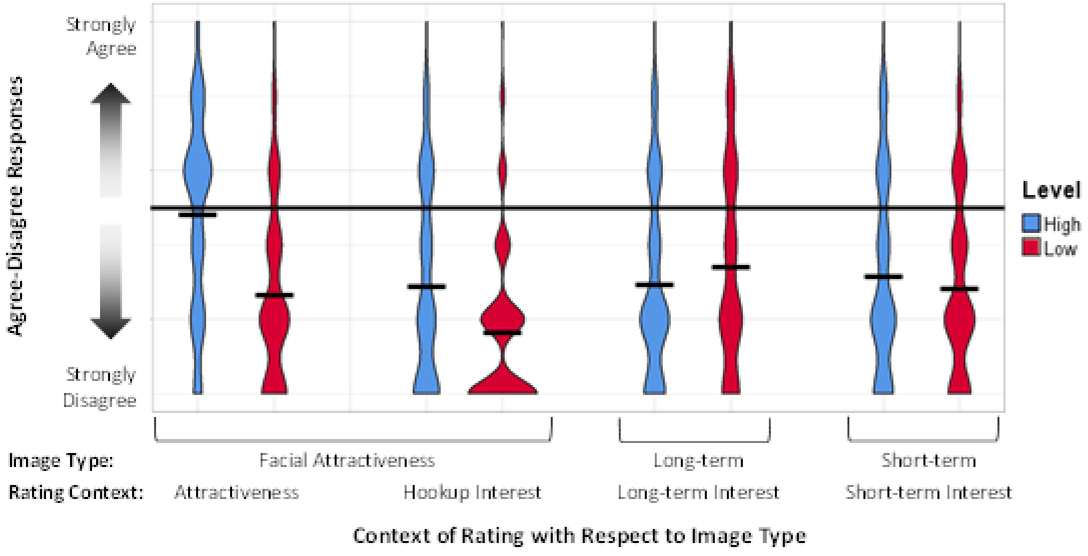
Mixed model results indicated women showed significant and substantial preference for the Low versions of all the images except for those generated with regards to Psychopathy, for which they showed preference for High images. Pairwise comparisons restricted to relevant hypotheses for brevity. (Context = context of rating, Level = high/low images, df = degrees of freedom, F = F-statistic, *p* = p-value, EMM = estimated marginal means, SE = standard error)

Type III Tests

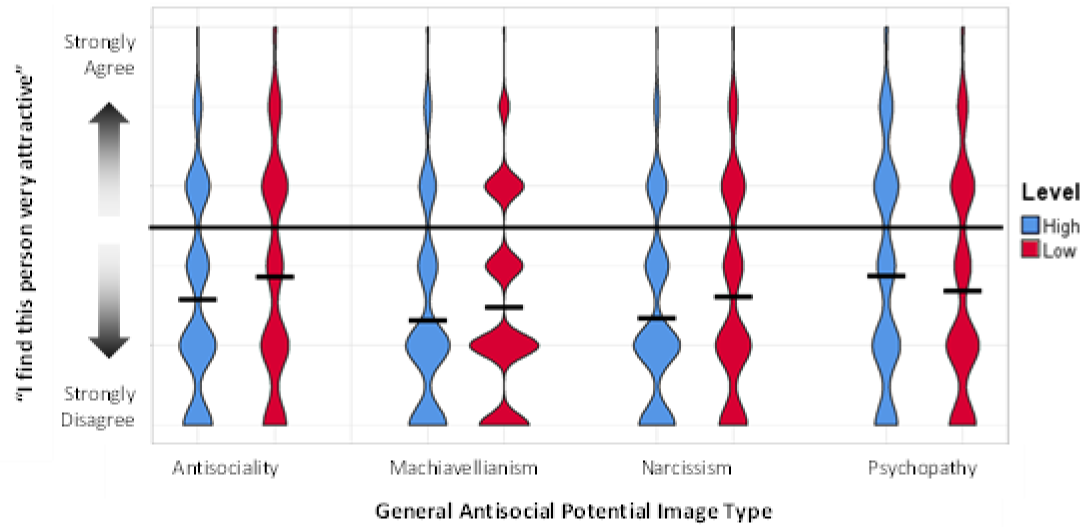
	df			
Fixed Effects	Num	Den	F	*p*
Intercept	1	805.0	6442.01	<0.001
Context	3	24919.0	850.76	<0.001
Axis	3	24919.2	276.07	<0.001
Level	1	24919.2	140.57	<0.001
Context * Axis	9	24919.0	2.33	0.013
Context * Level	3	24919.0	6.41	<0.001
Axis * Level	3	24919.2	97.17	<0.001
Context * Axis * Level	9	24919.0	3.02	0.001

Selected Pairwise Comparisons

	High Image		Low Image		
	EMM ± SE	df	EMM ± SE	df	*p*
Attractiveness Ratings					
Antisociality	3.0 ± 0.0	2883.57	3.3 ± 0.0	2883.56	<0.001
Machiavellianism	2.6 ± 0.0	2880.12	2.9 ± 0.0	2880.12	<0.001
Narcissism	2.6 ± 0.0	2880.12	3.0 ± 0.0	2887.02	<0.001
Psychopathy	3.4 ± 0.0	2880.12	3.1 ± 0.0	2883.57	<0.001
Hookup Interest Ratings					
Antisociality	2.2 ± 0.0	2883.57	2.4 ± 0.0	2883.57	<0.001
Machiavellianism	2.0 ± 0.0	2880.12	2.1 ± 0.0	2880.12	0.036
Narcissism	2.0 ± 0.0	2880.12	2.2 ± 0.0	2883.57	<0.001
Psychopathy	2.4 ± 0.0	2880.12	2.3 ± 0.0	2883.57	<0.001
Long-term Interest Ratings					
Antisociality	2.6 ± 0.0	2887.02	2.9 ± 0.0	2897.42	<0.001
Machiavellianism	2.3 ± 0.0	2890.47	2.5 ± 0.0	2887.01	0.009
Narcissism	2.3 ± 0.0	2887.01	2.6 ± 0.0	2890.47	<0.001
Psychopathy	2.8 ± 0.0	2880.12	2.7 ± 0.0	2890.47	0.001
Short-term Interest Ratings					
Antisociality	2.5 ± 0.0	2883.57	2.8 ± 0.0	2883.57	<0.001
Machiavellianism	2.3 ± 0.0	2883.56	2.5 ± 0.0	2880.12	0.003
Narcissism	2.4 ± 0.0	2887.01	2.6 ± 0.0	2883.57	<0.001
Psychopathy	2.9 ± 0.0	2880.12	2.7 ± 0.0	2883.57	<0.001



(a) The Relationship-Context Ratings of Images Generated with Respect to Attractiveness and Mating Potential



(b) Attractiveness Ratings of Images Generated with Respect to General Antisocial Potential

Figure 4.2. Violin plots of ratings given to High and Low images generated with regards to (a) Attractiveness and Mating Potential (AMP) and (b) General Antisocial Potential (GAP).

Black bars denote means, and black stars pairs that differ significantly. All High/Low pairs were significantly different from each other.

(a) For AMP images, women demonstrated substantial preference for the High versions of all images except for Long-term images in which they preferred Low. Preferences for Long-term images and Short-term images shows similar, but reversed patterns, such that the High Short-term images and Low Long-term images are preferred over their counterparts (all *p*s < 0.001).

(continued)

(b) For GAP images, women showed substantial preference for the Low versions of all images except for those generated with regards to Psychopathy, for which they showed preference for High images (all *p*s ≤ 0.001 except for High/Low Machiavellianism: Hookup Interest, $p = 0.036$; Long-term Interest, $p = 0.009$, Short-term Interest, $p = 0.003$).

Table 4.7. Differences in Attractiveness and Long-term Interest Rating types for High and Low Long-term partner images.

Mixed model results indicate women showed significant and substantial preference for Low Long-term images, but when broken down by rating type, this finding held only for Long-term Interest ratings, not for Attractiveness ratings. (Context = context of rating, Level = high/low images, df = degrees of freedom, F = F-statistic, *p* = p-value, EMM = estimated marginal means, SE = standard error)

Type III Tests

Fixed Effects	df Num	Den	F	*p*
Intercept	1	804.4	5818.9	<0.001
Context	1	2409.7	208.7	<0.001
Level	1	2411.3	23.6	<0.001
Context * Level	1	2409.7	5.3	0.022

Selected Pairwise Comparisons

	EMM ± SE	df	EMM ± SE	df	*p*
Context					
Attractiveness Rating	3.1 ± 0.0	1128.7			<0.001
Long-term Interest Rating	2.6 ± 0.0	1129.1			
Level					
High	2.7 ± 0.0	1128.8			<0.001
Low	2.9 ± 0.0	1129.3			
Context * Level	High Image		Low Image		
Attractiveness Rating	3.0 ± 0.0	1798.0	3.1 ± 0.0	1798.0	0.070
Long-term Interest Rating	2.5 ± 0.0	1798.0	2.7 ± 0.0	1799.8	<0.001
	<0.001		<0.001		*p*

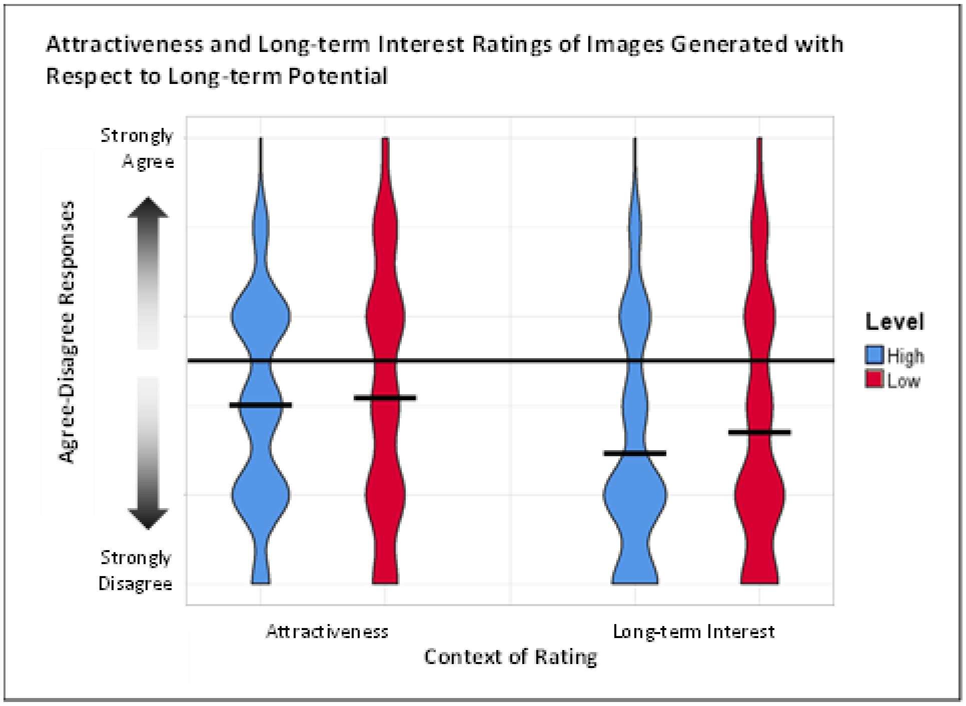


Figure 4.3. Violin plots of Attractiveness and Long-term Interest Rating types for High and Low Long-term Partner Images.

Black bars denote means, and black stars pairs that differ significantly. Women showed significant and substantial preference for Low Long-term images when they were rated for Long-term relationships (*p* < 0.001), not for Attractiveness (*p* = 0.070).

4.4.3 Question 3: Effect of relationship status

I predicted that participants who were not looking for new partners would rate images lower than women who were looking, regardless of context of rating.

This prediction was supported. Women who were looking for potential partners rated images higher than women who were not, regardless of Context (Table 4.8; Figure 4.4).

4.4.4 Question 4: The effect of the menstrual cycle on image preference and discrimination

I predicted that women who were in their Luteal phase would show less interest in men who were rated as High Short-term partners, and greater interest in men rated as High Long-term partners, than women who were in the other phases of their menstrual cycle. I also predicted that women who were in their Fertile phase would show an increase in their discrimination against the images of men who score high on the General Antisocial Potential Images as compared to women who were Not Fertile.

Neither prediction was supported. Luteal status had no effect on overall preferences, nor on either High Long-term or High Short-term image rating (Table 4.9; Figure 4.5a). Further, there were no significant differences between ratings given to the images designed with attributes indicating General Antisocial Potential when subjects were Fertile versus Not Fertile (Table 4.10; Figure 4.5b).

4.4.5 Question 5: Fertility-mediated shifts based on relationship status

I predicted that women were are Looking for a sexual partner (single, casually dating, or in an open relationship) would show a Fertility-mediated increase in the ratings given to men who represent good Short-term partners whereas women who were Not Looking for new partners will show no Fertility-mediated increase.

This prediction was not supported. While women who were Fertile gave higher ratings than Non-Fertile women to images constructed with attributes of High Short-term potential, this effect was driven by a significant difference in the Not Looking group, not the Looking group. For these women, Fertile women rated the images higher than the Non-Fertile ones (Table 4.11; Figure 4.6).

Table 4.8. Differences in rating types based on Looking status.

Mixed model results indicate women whose relationship status indicated an interest in new partners rated images significantly and substantially higher than others. (Context = context of rating, df = degrees of freedom, F = F-statistic, *p* = p-value, EMM = estimated marginal means, SE = standard error, HU = Hookup Interest, LT = Long-term Interest, ST = Short-term Interest, NS = non-significant)

Type III Tests

Fixed Effects	df Num	df Den	F	*p*
Intercept	1	804.0	7101.6	<0.001
Context	3	44264.0	1264.6	<0.001
LookStat	1	804.0	29.6	<0.001
Context * LookStat	3	44264.0	39.3	<0.001

Pairwise Comparisons

	EMM ± SE	df	HU	LT	ST	*p*
Context						
Attractiveness Rating	3.0 ± 0.0	911.2	<0.001	<0.001	<0.001	
Hookup Interest Rating	2.2 ± 0.0	911.3		<0.001	<0.001	
Long-term Interest Rating	2.6 ± 0.0	911.5			0.658	
Short-term Interest Rating	2.6 ± 0.0	911.3				
Looking Status						
Looking	2.7 ± 0.0	804.0				<0.001
Not Looking	2.4 ± 0.0	804.0				

Context * Looking Status	Looking		Not Looking		*p*
Attractiveness Rating	3.1 ± 0.0	911.2	2.9 ± 0.0	911.3	<0.001
Hookup Interest Rating	2.3 ± 0.0	911.4	2.1 ± 0.0	911.3	<0.001
Long-term Interest Rating	2.8 ± 0.0	911.5	2.4 ± 0.0	911.5	<0.001
Short-term Interest Rating	2.8 ± 0.0	911.2	2.4 ± 0.0	911.3	<0.001

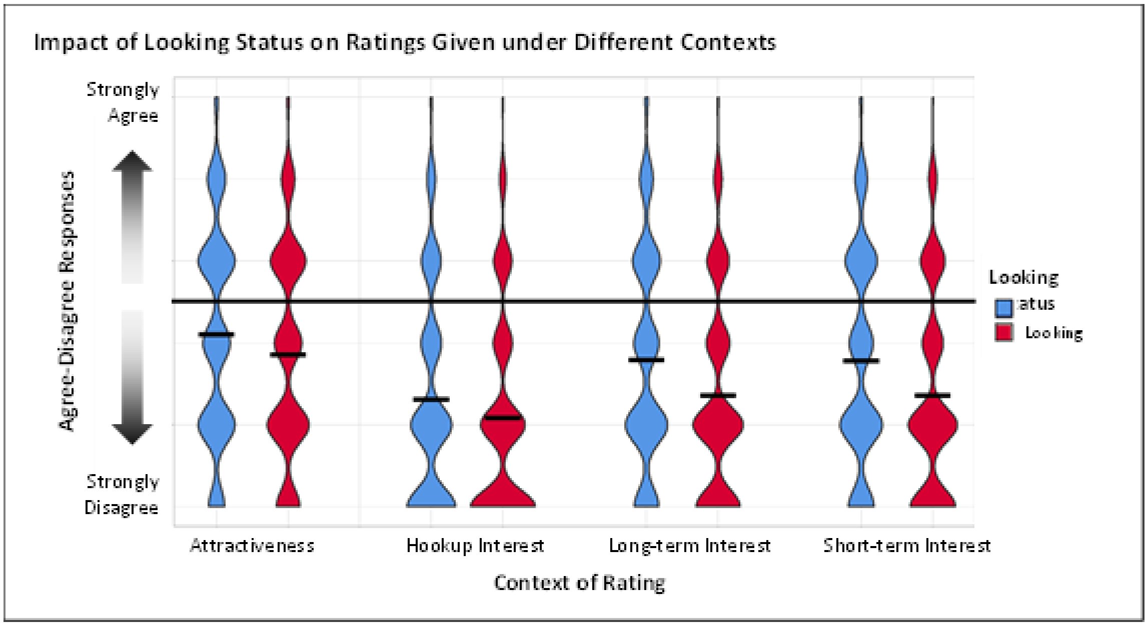


Figure 4.4. Violin plots of Rating types for those Looking and Not Looking for other potential partners.

Black bars denote means, and black stars pairs that differ significantly. Women whose relationship status indicated an interest in new partners rated images significantly and substantially higher than others (all *p*s < 0.001).

Table 4.9. Effect of Luteal status on ratings to High Long-term and Short-term Images. For analysis, only Attractiveness ratings were used. Mixed model results indicate there was no effect of Luteal status on the ratings. (df = degrees of freedom, F = F-statistic, *p* = p-value, EMM = estimated marginal means, SE = standard error)

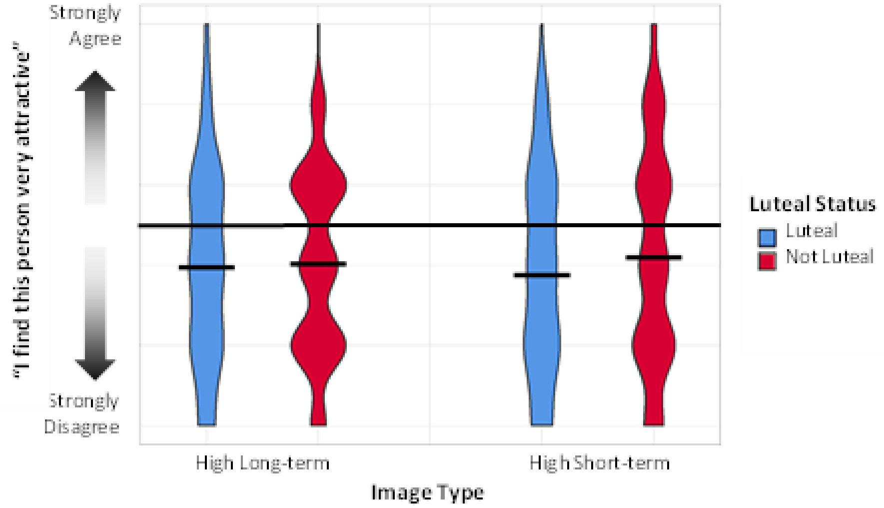
Type III Tests

Fixed Effects	df Num	Den	F	*p*
Intercept	1	802.7	3492.532	≤0.001
Image	1	801.9	0.012	0.911
Luteal Status	1	802.7	1.702	0.192
Image * Luteal Status	1	801.9	1.650	0.199

Selected Pairwise Comparisons

	EMM ± SE	df			
Image					
High Long-term	3.0 ± 0.1	1389.7			0.911
High Short-term	3.0 ± 0.1	1389.7			
Luteal Status					
Luteal	2.9 ± 0.1	802.5			0.192
Not Luteal	3.1 ± 0.0	803.5			
Image * Luteal Status	Luteal		Not Luteal		
High Long-term	3.0 ± 0.1	1389.5	3.0 ± 0	1390.5	0.702
High Short-term	2.9 ± 0.1	1389.5	3.1 ± 0	1390.5	0.073
	0.446		0.143		

(a) Attractiveness Ratings given to High Short-term and High Long-term Images in Response to Luteal Status



(b) Attractiveness Ratings given to High General Antisocial Potential Images in Response to Fertility Status

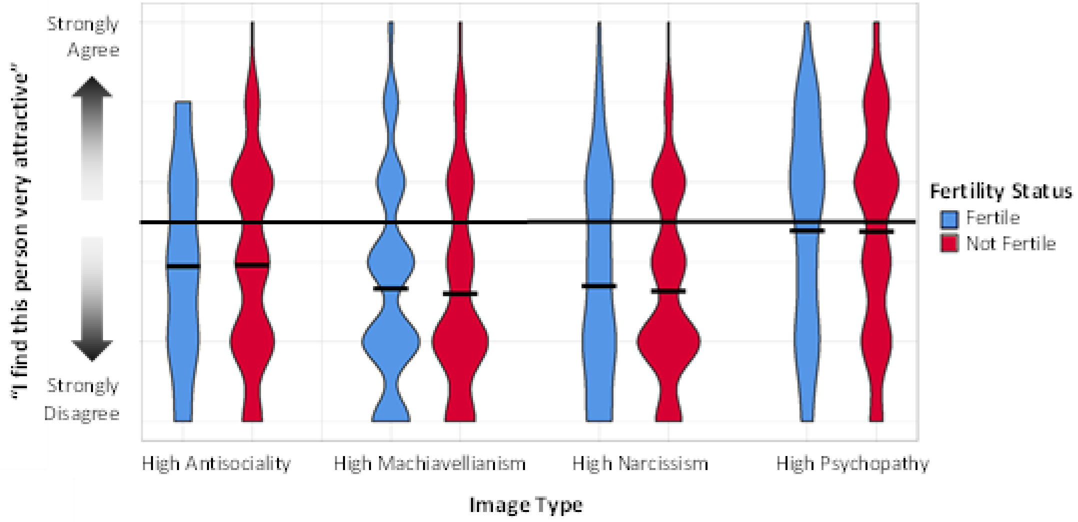


Figure 4.5. Violin plots of Attractiveness Ratings given by (a) Luteal and Not Luteal women to High Long-term and High Short-term Images and (b) Fertile and Not Fertile women to the General Antisocial Potential Images.

Black bars denote means. There was no effect of either Luteal status or Fertile status on the ratings (all *p*s > 0.073).

Table 4.10. Effect of Fertility status ratings given to GAP Images.

For analysis, only Attractiveness ratings were used. Mixed model results indicate the Fertile status of the women did not influence the ratings given to the GAP images. (df = degrees of freedom, F = F-statistic, *p* = p-value, EMM = estimated marginal means, SE = standard error, MA = Machiavellianism, NA = narcissism, PS = psychopathy)

Type III Tests

Fixed Effects	df Num	Den	F	*p*
Intercept	1	803.8	3833.7	<0.001
Axis	3	2410.9	79.1	<0.001
Fertility Status	1	803.8	0.1	0.746
Axis * Fertility Status	3	2410.9	0.3	0.846

Selected Pairwise Comparisons

	EMM ± SE	df	MA	NA	PS	*p*
Axis						
Antisociality	3.0 ± 0.1	1705.9	<0.001	<0.001	<0.001	
Machiavellianism	2.6 ± 0.1	1705.6		0.598	<0.001	
Narcissism	2.7 ± 0.1	1705.6			<0.001	
Psychopathy	3.4 ± 0.1	1705.6				
Fertility Status						
Fertile	2.9 ± 0.1	803.8				0.746
Not Fertile	2.9 ± 0.0	803.9				

Axis * Fertility Status	Fertile		Not Fertile		*p*
Antisociality	2.9 ± 0.1	1705.6	3.0 ± 0	1707.6	0.878
Machiavellianism	2.7 ± 0.1	1705.6	2.6 ± 0	1705.6	0.574
Narcissism	2.7 ± 0.1	1705.6	2.6 ± 0	1705.6	0.584
Psychopathy	3.4 ± 0.1	1705.6	3.4 ± 0	1705.6	0.924

Table 4.11. Fertility status and Looking status on ratings.

For analysis, only High Short-term images and Attractiveness ratings were used. Mixed model results indicate women whose relationship status indicated an interest in new partners did not show a fertility-mediated difference in their ratings. However, women who were Not Looking did. (df = degrees of freedom, F = F-statistic, *p* = p-value, EMM = estimated marginal means, SE = standard error)

Type III Tests

Fixed Effects	df Num	df Den	F	*p*
Intercept	1	801.0	2542.6	<0.001
Looking Status	1	801.0	5.2	0.023
Fertility Status	1	801.0	2.8	0.097
Looking Status * Fertility Status	1	801.0	1.3	0.263

Selected Pairwise Comparisons

	EMM ± SE	df	*p*
Looking Status			
Looking	3.3 ± 0.1	801.0	0.023
Not Looking	3.0 ± 0.1	801.0	
Fertility Status			
Fertile	3.2 ± 0.1	801.0	0.097
Not Fertile	3.0 ± 0.1	801.0	

Looking Status * Fertility Status	Fertile		Not Fertile		
Looking	3.3 ± 0.2	801.0	3.2 ± 0.1	801.0	0.714
Not Looking	3.2 ± 0.2	801.0	2.8 ± 0.1	801.0	0.040
	0.525		<0.001		*p*

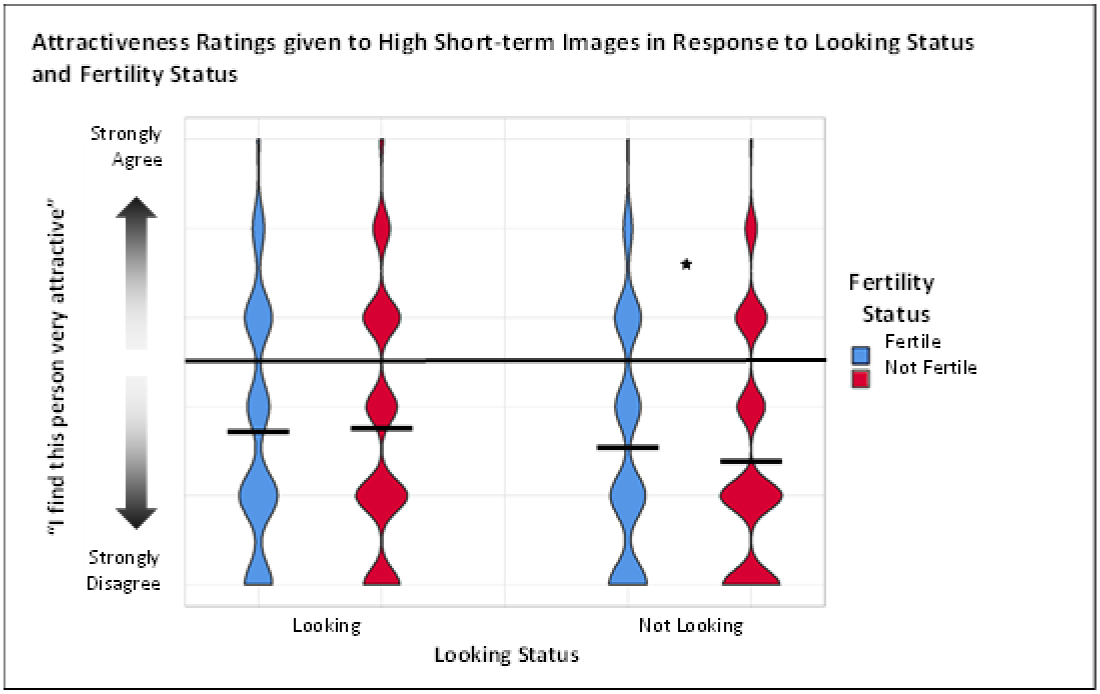


Figure 4.6. Violin plots of Attractiveness Ratings given to General Antisocial Potential Images by Fertile and Not Fertile Women who differ in Looking Status.

Black bars denote means, and black stars pairs that differ significantly. Women whose relationship status indicated an interest in new partners did not show a fertility-mediated difference in their ratings (p = 0.714). However, women who were Not Looking did (p = 0.040), with Non-Fertile women rating images significantly lower than Fertile women (p = 0.040).

4.5 DISCUSSION

This study explored women's mating choices in context of their fertility, their relationship status, and the potential type of mate that each man represented. The results of the study indicate several interesting findings with regards to the use of and detection of face-traits; female mating preferences, particularly in response to fertility and relationship status; and study design. However, a discussion of the results of the study should begin with a recognition of generally applicable caveats and limitations.

4.5.1 General Limitations

One general limitation of this study is its exclusive reliance on facial images. This was a deliberate choice as doing so might allow for the perception of face-traits that might represent deception-proof cues of potential dominance- and threat-related related behaviors. They also reflect a modern aspect of dating culture – the use of dating apps with the faces of potential partners being presented and "swiped" on.

However, the use of these faces as proxies for specific personality traits have limitations, the primary being that they should not be considered perfect correlates of the traits themselves. The use of these proxies relies on a series of assumptions that connect real faces to face-traits that develop under specific hormonal influences; that in turn connect to dominance-, trust-, and threat-related behaviors; that in turn connect to personality traits and mating tendencies; and that finally connect to metrics used to assess individuals on these traits and tendencies. Thus, the degree to which these assumptions are met influences the degree to which the proxies are reliable, and caution should be taken when drawing conclusions regarding direct associations between them. Therefore, it should be emphasized that the identification of a trend in the expected direction is not proof that these images perfectly capture the characteristics in question or that women are perceiving the characteristics attributed to them. A more thorough and detailed method of validation that tests each assumption is needed before we could assert either.

A fundamental concern of the Holtzman images is the methods used in their construction, specifically the metrics employed. While the metrics used to generate the General Antisocial Potential images have been well-validated, the ones used to generate the Attractiveness and Mating Potential images have not been and thus warrant closer attention. The facial attractiveness images were rated by 50 men – not women – and thus do not necessarily reflect female mate choice preferences. While it is reasonable to assume that male and female ratings would generally agree, there may be some specific elements, such as those associated with masculinity, that might result in divergent assessments. The metrics used for both the short- and long-term images also deserve attention. These metrics were prototypical to the study, and, while they were consistent with other metrics used at the time (N.S. Holtzman, personal communication), there is no available evidence that the questions included would be sufficient to capture dominance-related behaviors and thus that their images reflect dominance-related face-traits.

Another factor that should be considered with regards to the construction of the Holtzman images is the potential for cross-classification within the subjects. The male composites were created from the images of 33 individual men, and the author admits in the original 2011 paper that there was a high degree of cross-classification for the low-scoring Dark Triad images (the same 5 men for all images). And while he also states that the rates for the other images were much lower (and are available upon request), it is possible that the cross-classification of specific combinations – such as between men with high facial attractiveness and psychopathy, an often recognized combination – could help explain some of patterns found in these results.

A final factor to consider with regards to the Holtzman images concerns the methods employed in their validation and replication. In the original study, the images were validated using a forced-choice design: the high and low images were presented next to each other as a set, and participants were given a description of the characteristic for which they were designed and then asked to indicate which image best represented that characteristic as well as their own confidence in that selection. All other studies that I have found that have used these images have similarly relied on a forced-choice design, presenting the images in pairs and asking participants to choose between the images (Holtzman originals: mating preferences – Lyons et al. 2015, Marcinkowska et al. 2015, 2016, Lyons and Blanchard 2016, Lyons and Simeonov 2016. New morphs: mating preferences – Brown et al. 2017, Brewer et al. 2018, Brewer et al. 2019, Alper et al. 2021; Boss preferences – McElroy et al. 2020). Thus far, I found no evidence, aside from the results of this study, that these characteristics, based on images alone, could be detected outside of a forced-choice design – that they could be spontaneously detected in a "real world" scenario. This might be particularly important when assessing men as potential mates or threats; judgments in these contexts are not conducted in settings where women would choose between two men at opposite ends of a spectrum. They are generally assessed individually without cues to the characteristics in question.

Another reason the images may not perfectly represent the characteristics of interest is the degree to which root biosocial conditions influence both the characteristic and facial structure. For example, while we would expect psychopathy to be detected under a threat-detection heuristic, many of the biosocial influences responsible for its development would not be expected to influence facial structure in substantial ways (e.g., oxytocin, dopamine and serotonin receptor biases). Indeed, this may contribute to the ability of psychopathic individuals to integrate easily into society; there are no reliable face-traits associated with it. Similarly, the relationship between testosterone – specifically, its *presence* and its *absence* – and both short- and long-term mating strategies, respectively, might make these identifying these strategies from images more difficult. Any threat-detection heuristic might be attuned to identifying the presence of testosterone more than its absence, and, thus, when presented with images outside of a forced-choice design, it might be more difficult for women to accurately identify which is which. Similarly, mating strategies and testosterone are dynamic and shift in response to social cues. Thus, an individual's past testosterone exposure may not reflect their current testosterone levels, making it a weak predictor of mating strategy.

Other limitations of this study come from aspects unrelated to the composition of the images. One is the ability of the assessor to associate a characteristic with a face-trait, assuming that such a link exists. As previously discussed, the ability to accurately detect face-traits develops over time as a function of increased exposure to varied faces and personalities. It is thus possible that those in this demographic have not yet had the experience necessary to detect certain characteristics if they have had limited experience with individuals who have those characteristics and face-traits. This might be particularly relevant for the psychopathy-related images, as the callous-unemotional aspect of psychopathy is also connected to an ability to integrate and blend into society. Thus, any aversion to threat-related face-traits associated with psychopathy may take longer time to develop and may be dependent upon the concentration of psychopathic traits in the population.

4.5.2 Image Discrimination and Mate Choice Preferences

Predictions 1 and 2 centered on the degree to which women were able to discriminate between the images in ways that corresponded with predicted mate choice preferences. In general, the results indicate that women do show preferences toward the images that represent physically attractive men and/or those who are good relationship partners and preferences away from those representing a potential threat – though there are two exceptions that will be discussed below. These findings add general support to the existence of a relationship between some aspects of personality and facial characteristics, particularly when they are related to dominance and in the context of female mate preferences. Further, they provide the first evidence that at least some of the Holtzman images can be used outside of a forced choice design in ways that align predictably with the characteristics used to generate them, though additional testing is warranted.

There are a few noteworthy findings. One concerns the ratings giving to the high facial attractiveness images. These ratings, while higher than all other images (except for high psychopathy), was still given relatively "neutral" ratings (an average of 3.4 with 3 being "somewhat disagree" and 4 "somewhat agree" to finding the man attractive, Table 4.6). This may be an artifact of the aforementioned limitation regarding their construction – that these images were generated by ratings of men, and not women, and thus might not actually represent female mate preferences.

There were two other noteworthy – and unexpected – findings, with their having received ratings opposite of what was expected. For images generated with respect to long-term partners and ratings of long-term interest, women indicated a preference for low scoring images instead of high. And for the images generated with respect to psychopathy, women indicated a preference for high scoring images instead of low for all types of ratings. As discussed above, these could be due to various limitations in the study design or image construction, but there may be other reasons.

One explanation for women indicating a preference for poor long-term partners over good ones is that the prediction reflected inaccurate expectations for the mating preferences of this demographic. Specifically, this prediction was predicated on evidence that female mate choice is biased toward resource-provisioning males due to their higher per-offspring reproductive demands. However, shifts in both resource availability and in sociosexuality (particularly with regards to reproductive control) would be expected to shift these preferences. Indeed, shifts in female preferences have been documented over the past several decades, particularly in cultures associated with egalitarian sociosexual expectations (Muggleton and Fincher 2017). The population represented in this study – female college students between 18-25 – would be expected to reflect these shifting preferences. It is already recognized that university populations do not reflect universal behavior (Henrich et al. 2010), and care must be taken in extrapolating research results from these populations onto other demographics. Thus, it is possible that a population of generally educated and sexually unrestricted women who are increasingly less likely to need male resource provisioning will have different mate preferences than others when it comes to long-term partners. This possibility is supported by the results of Prediction 2: when women rated the same images for attractiveness, there was no difference in the ratings given to the low-scoring and high-scoring images. Thus, it may be that this preference for low long-term images may be specific toward ratings related to long-term relationships.

At the same time, I suspect that it is unlikely that the unexpected results with respect to the psychopathy-related images is due to any generalized shifts in mating preferences of the demographic. While assortative mating among those with the Dark Triad has been documented, the likelihood of the vast majority of this demographic being similarly psychopathic is low. However, there is evidence that the general aversion to the Dark triad may shift in response to resource availability, a pattern that is consistent with the factors that influence the emergence of Dark personalities. Thus, it may be that this preference has emerged due to the perceived availability of resources for the women in this demographic. Little is known about how this preference would be expected to shift, however, and a great deal of work is needed before this could be proposed as a probable explanation. Thus, I suspect that this unexpected finding is more likely to be related to the aforementioned limitations, namely the potential for cross-classification with high facial attractiveness, the particularly varied biosocial developmental factors behind the emergence of psychopathy, and the possibility that this demographic lacks the experience necessary to identify any face-traits associated with psychopathy.

4.5.3 Mate Choice Optimization, Relationship Status, and Fertility

The last three predictions explored mate choice optimization dynamics in response to the influence of relationship status and the menstrual cycle. Prediction 3 focused on the effect of relationship status; prediction 4 on the effects of the fertile window and the luteal phase; and prediction 5 on both relationship status and the menstrual cycle. In this discussion, I address the results of both parts of Prediction 4 first, and then I address Predictions 3 and 5 together.

The first part of prediction 4 was that women would show a luteal-mediated preference for long-term partners, and it was based on previous research that identified two progesterone-mediated trends: an aversion to masculinity (facial – Jones et al. 2005(a), vocal – Puts 2006) and an increase in feelings of relationship commitment for women in a relationship (Jones et al. 2005(a)). My prediction was not supported – there was no effect of the luteal phase. This may be due to the aforementioned limitations of the study, namely the lack of a comparison image (such as those found in a forced-choice design scheme) or a poor proxy for a long-term partner due to inadequate metrics for assessing long-term partners or the lack of a strong relationship between facial structure and long-term mating strategies.

However, assuming that these images do adequately capture long-term potential, there may be another explanation. It is possible that luteal shifts exist, but that they are more specific than what was captured in the design of the study. The shift in feelings of relationship commitment documented in Jones et al. (2005(a)) might indicate a preference for a long-term partner, but it might also indicate a preference for *their specific* long-term partner, not a long-term partner in general (the women in the Jones et al. study were partnered). If this is the case, women may show no marked preference for the images of men who *generally* represent good long-term partners, instead only showing a preference for *her* partner. Indeed, this is what we might expect if progesterone acts as a cue of pregnancy and the need to engage in relationship-maintenance behaviors (see Robillard et al. 2008).

The second part of prediction 4 was that women would show a fertility-mediated aversion to images of men who might represent potential threats, and it was based on research that suggests fertile women show increased harm avoidance and mate discrimination tendencies. However, I found no such effect. One possible explanation is that the judgments were not being made in a realistic context, a design element that might act to minimize any "real-time" effect of the menstrual cycle on the judgments. Previous studies that have documented a fertility-effect of threat-avoidance were designed to capture real-time decision-making, assessing intuitive reactions to realistic "while fertile" scenarios. My study design merely rated images for relationship potential while the women were fertile (or not) – it did not indicate that the women would have any interactions with the men in the images at that moment. Thus, there was no immediate threat to avoid.

Another explanation may be that my method of fertility determination was flawed. Estimated methods of fertility determination are highly inaccurate, and while I used one of the more accurate methods (backwards counting using reported length, approximately 35% - Black et al. 2016), it would still be expected to miss a significant portion of the fertile window for most participants. Thus, it is possible that a fertility-mediated shift in preferences for these images exists, and the methodology that I used was unable to capture it.

Predictions 3 and 5 explored the effect of relationship status, with prediction 5 examining this within the context of the menstrual cycle. Prediction 3 compared the ratings given to all images and found that women who were open to a new sexual partner rated images significantly higher than those who were not. This result is unsurprising.

Prediction 5 explored the attractiveness ratings given to the images representing good short-term partners within the context of fertility, and it expected to find a fertility-mediated increase in the ratings given by women who are open to a new relationship partner but not by women who were not. This finding would have indicated support for a fertility-mediated mate choice optimization effect.

The results found the opposite effect. Fertile women rated images higher than non-fertile women *only* if they were *not* interested in a new partner. There are two possible mechanisms driving this finding – an increase in ratings due to fertility, and/or a decrease in ratings due to non-fertility. Each possibility is addressed below.

If this finding is driven by fertility, the lack of the same trend emerging for women open to new relationships suggests that this effect emerges in response to relationship status, which was that of a committed, monogamous relationship for the majority of the women. Importantly, none of the women were on oral contraceptives, and all were enrolled in a university program. Taken together, it can be surmised that these women were likely to be both sexually active and motivated to avoid pregnancy, and therefore likely using other forms of contraceptives – including rhythm-based methods and/or methods associated with menstrual tracking apps – that often teach about menstrual-based patterns in mood and sexuality. It is possible, then, that, in comparison to the looking group, these participants may have been more aware of and had pre-existing beliefs regarding their fertility, beliefs that may include an increased interest in attraction to other men. If so, this result may be the effect of fertile belief and not fertility, particularly since I used an estimated method of fertility determination which women using rhythm-based methods often use.

This explanation is supported by the results of Prediction 3, which found that, across all rating types, women who are looking for a new partner rate images higher than those who are not. In these results, the fertile women who are not looking rated the images comparably to both fertile and non-fertile women who were. That suggests there was an *increase* in the ratings given by this group. Further exploration into these dynamics is needed.

Still, it is also possible that this finding is driven by the non-fertile group, not looking group, with their having rated these images lower than the other three groups. If so, this might be evidence for a luteal-based relationship-maintenance effect and a potential manifestation of a "relationship commitment" effect. Such an effect might exist as a by-product of pregnancy-related and progesterone-mediated relationship-maintenance behaviors that might aid in preeclampsia prevention (Robillard et al. 2008). This would be consistent with evidence that women who are in relationships show a luteal-based increase in their desire for relationship commitment (Jones et al. 2005(a). However, this idea has been generally under-studied and so little is known about potential luteal effects, and much more work is needed.

4.5.4 Future Directions

This study reveals several avenues for which future work is needed. One avenue is a need to improve the proxies available for this research. The creation of composite images is influenced heavily by both the metrics used and the population from which the participants were sampled, a factor that includes both racial composition as well as the relative extremity of the ultimate scores. Future research would benefit from the creation of images generated from larger sample sizes with minimal, if no, cross-classification; that represent diverse racial, ethnic, and gender groups; were created using well-validated metrics with clearly defined boundaries for their use (e.g., creating male-, female-, and all-rated images of facial attractiveness); and were validated through both forced-choice and non-forced-choice designs.

Further, it might be beneficial to create a series of proxies tied more directly to the face-traits in question. As discussed, the use of the Holtzman Dark Triad images is predicated upon the assumption that face-traits associated with dominance, trust, and threat underly the facial structures of these individuals. However, this assumption may not hold true, particularly for the psychopathy images. It is thus important to expand the exploration of mate preferences using image assessments using different kinds of images, such as those tied directly to accurate and reliable face-traits that have been computer generated. While these faces may not reflect "real" faces, they would allow for direct testing of the degree to which face-traits influence mate choices. Until then, research conducted using these images should be cautious in overgeneralizing their conclusions.

Another general avenue for future work is the exploration of how more cryptic threat-related traits might be learned. Of particular interest is the unexpected psychopathy-related result which would have been expected to be identified and avoided under a general threat-avoidance heuristic. It is possible that the weaker influence of testosterone on the emergence of psychopathy may aid in the ability of some psychopaths to remain concealed and that more time and/or experience is needed to form face-trait associations than these women may have had, if it is even possible with the biosocial developmental factors associated with it. This may have considerable implications on mating decisions, particularly for a younger demographic actively pursuing relationships.

Another general avenue of work that is needed is an expansion of menstrual-cycle research. This includes the influence of immediate socioenvironmental factors in shifts in mate preferences. Female mate preferences should be heavily influenced by the availability of resources, and thus factors such as socioeconomic condition, perceived social stability, majors and career plans, and familial relationships (particularly with female family members) should be incorporated into these studies. Further, I recommend that research into menstrual-cycle mediated threat-avoidance behaviors should explore the degree to which "real time" decisions affect responses – for example, whether fertility affects the likelihood of engaging in a risky behavior now or planning for one in the future. The current study could be repeated with the inclusion of a "real-time" context which might reveal interesting dynamics.

One area of much-needed investigation is into the existence of luteal-phase shifts in sexuality and/or partner preferences. One of the primary roles of progesterone is to maintain pregnancy, and this may include the inducement of behaviors that increase the likelihood of carrying a fetus to term, such as increased sexual activity with any sexual partner who might be the father of any potential offspring. Unfortunately, little has been done to explore this possibility. Instead, research has focused primarily on fertility, and it has done so while using the luteal phase as the comparison window. This makes it difficult to discern whether any difference is attributable to fertility or to progesterone. Thus, future research should prioritize the use of methods that minimize this complication, including looking at trends across-the-cycle as opposed to specific windows of time, and investigating behavioral shifts that occur during early pregnancy.

In addition to areas of exploration, future research should control for the effect of fertility belief. While effort can be taken to avoid priming participants to the nature of the study, this is not always possible, particularly when using medically-confirmed methods of fertility determination. Still, regardless of the method used, menstruating participants are continually aware of their menstrual cycles, if for no other reason than to keep track of when menstruation is likely. However, many participants are not only aware of how their behavior and preferences might shift throughout their cycles, but they may also track them using the same methods of estimation that are used in research. Thus, while efforts to blind participants to the nature of the study can be taken, they do not ensure that participant beliefs are not influencing their responses. Thus, I emphasize the importance of controlling for these effects by the use of careful study design that assesses, incorporates, and controls for participant beliefs.

Finally, I recommend that future studies be mindful of the diverse lives and identities of our participants. Current relationship dynamics play a crucial role In mate choice research, but prior research has often placed participants into inflexible categories (e.g., “in a relationship” v. “single”) that neither accurately reflect the participants’ relationships nor appropriately align with the research interest. Providing a diverse range of relationship dynamics is not only inclusive to our participants and their lives, but allows us to explore mate choice dynamics more accurately. Similarly, care should be taken to be deliberate and cautious in how we use these images, particularly with regards to assumptions regarding their universality. For one, as discussed, these images are less reflective of the characteristic in question than they are of the assessment used and population sampled to generate them. For another, the images make assumptions about gender and sexual identity that neither reflect all of our participants nor the population in general. Thus, care should be taken to use these images within heterosexual cisgender contextual ratings – and they should not be interpreted as “a standard” of attractiveness or “ideal” relationship dynamic.

CHAPTER 5. BELIEVING MAKES IT SO: SEXUALITY IS RELATED TO FERTILITY BELIEF, NOT FERTILITY

5.1 ABSTRACT

Recent research into fertility-mediated shifts in human sexuality suggests that women experience fertility-mediated increases in sexual desire and behavior, shifts that had not been found in previous research. In this study, I investigate the degree to which sexuality shifts in response to fertility while accounting for participant beliefs regarding fertility. Participants provided daily urine samples and answered daily questions regarding their sexuality, happiness, and fertility belief for at least one menstrual cycle. Results indicated that hormonally-confirmed fertility had no influence on sexuality: instead, happiness influenced sexual desire, and sexual desire influenced hypothetical sexual response. Further, even though participants were well-informed about the menstrual cycle, they were unable to predict their own fertility accurately, believing they could get pregnant for most of their cycle. Instead of conception probability, sexual desire seemed to be a primary driver of fertility belief. Finally, I explored the effect that using estimated methods of fertility determination would have on these findings. Using a total of 36 estimated fertile/non-fertile pairings, estimated methods resulted in significance between fertility and sexual desire 89% of the time, sexual response 78% of the time, and fertile belief 69% of the time (compared to 17%, 0%, and 0% using hormonal methods, respectively). These results suggest that fertility belief, not fertility itself, may be driving some of the documented fertility-associated shifts and that the use of proper controls for fertility belief and confirmation bias is needed in future research.

5.2 INTRODUCTION

Fertility-mediated shifts in sexual behavior have been documented in many primate species, including some with concealed ovulation. Such shifts have been proposed to occur in humans, and evidence from the last 20 years generally supports this idea. However, rarely have these studies taken into consideration the beliefs that the participants themselves may have about the menstrual cycle. This study seeks to explore the relationships between fertility, fertility belief, and sexuality, testing the degree to which fertility influences sexuality, the factors that influence fertility belief, and the potential impact that using estimated fertility may have on results, given that women themselves have beliefs about their own menstrual cycles.

5.2.1 Human Fertility

The human menstrual cycle is a series of complex hormonal and physiological changes that regulate fertility, conception, and pregnancy. It can be generally divided into three phases: the follicular phase, ovulation (essentially instantaneous), and the luteal phase (see Barbieri 2014 [review]). The follicular phase begins with menstruation and is characterized primarily by elevated levels of estradiol, which is produced by the combined effects of FSH and LH on the growing ovarian follicle. During this phase, estradiol acts on the endometrium and the cervix to increase the chances of successful implantation and conception, respectively, and it inhibits the further production of FSH and LH. This continues until the levels of estradiol in the blood reach a threshold that results in a surge of LH and FSH that causes the oocyte within the follicle to mature, the follicle to weaken, and, approximately 24-36 hours later, the successful release of the oocyte, a phenomenon known as ovulation. Fertilization can only occur within the day of ovulation, but because sperm can survive in the reproductive tract for five days, the human fertile window comprises the last six days of the follicular phase. Conception probability without respect to survivability increases steadily throughout the 6-day fertile window (0.1, 0.16, 0.14, 0.27, 0.31, and 0.33 [ovulation] – Wilcox et al. 1995), but risk of embryo loss increases with oocyte ageing, resulting in survivable conception probabilities that peak on the fourth and fifth days of the 6-day window (0.04, 0.13, 0.08, 0.29, 0.27, and 0.08 [ovulation] – Wilcox et al. 1998). After ovulation, the luteal phase begins, a phase that is characterized primarily by progesterone, which is produced by the corpus luteum, the structure formerly known as the follicle. Progesterone acts to maintain the endometrium in preparation for pregnancy and to inhibit the further production of LH and FSH. In absence of LH, the corpus luteum degrades, and without the implantation of an embryo (and the subsequent production of human chorionic gonadotropin, hCG), the levels of progesterone and estradiol drop which triggers the start of menstruation. If fertilization and implantation does occur, the resulting production of hCG maintains the corpus luteum, and the production of progesterone, throughout pregnancy.

The length of the menstrual cycle varies considerably among women and within the same woman. While the average menstrual cycle is generally considered to last approximately 28 days, this merely represents the mean across highly variable fertile cycles. Only 13-15% of women have a 28-day cycle (Johnson et al. 2018, Bull et al. 2019), and fertile cycles have been documented to range from 19 days to 60 days (Wilcox et al. 2000, Fehring et al. 2006, Jukic et al. 2007). Indeed, over 40% of women experience more than 7 days of variation with each successive cycle (Fehring et al. 2006). This variation is largely driven by the variation in the length of the follicular phase; while the follicular phase lasts an average of 16.5 days, it varies by more than 7 days in one-third of women, and 95% of women experience a follicular phase that lasts between 10 to 22 days. As this phase precedes ovulation, this variation in timing makes the timing of ovulation vary in response as well. In contrast to the follicular phase, the luteal phase is more consistent, since it is dependent upon the relatively consistent decay of the corpus luteum: it lasts an average of 12.4 days (12.4 days – Fehring et al. 2006; 13 days – Wilcox et al. 2001, Trussell et al. 1998; 13.4 days – Baird et al. 1991; 14 days – Dixon 1980, Bull et al. 2019), and only 9% of women experience more than 7 days of variation, with 95% experiencing luteal phases of between 9 and 16 days (Fehring et al. 2006).

There are three general methods of predicting or identifying ovulation and, consequently, fertility: (1) estimation methods, which assume certain consistencies in cycle phases and general length; (2) fertility awareness-based methods, which track changes in mood and various physiological symptoms; and (3) medical diagnostic methods, which use medical tests to track changes in hormone levels or the ovaries. Estimation methods are the least invasive and least expensive, but they rely on consistent across-women and within-woman phases of the cycle. As a result, these methods are highly inaccurate: in general, no method has been found to have an accuracy of greater than 30% (Blake et al. 2016). Fertility-awareness based methods are customized to the individual and track physiological markers known to vary with fertility (Dunson et al. 2001, Manhart et al. 2013, Duane et al. 2016), but they are invasive, dependent heavily upon participant self-reports, and introduce a strong priming effect to the results. Medical diagnostic methods are the most reliable, but they are also the most costly and invasive (Guida et al. 1999, Guermandi et al. 2001).

5.2.2 Fertility Awareness and Belief

While it has been generally accepted that women are unable to tell when they are fertile (Burley 1979), efforts to assess this have been confounded by the effects of sex education, cultural beliefs, and access to technology. Research investigating fertility awareness among Indigenous peoples has indicated that, while respondents generally understood that sex causes pregnancy, they were not aware of the period of the cycle in which that is most likely to occur (Marlowe 2004).

Comparatively, Westernized, industrialized, and educated populations show high knowledge of fertility, with a 2014 survey of the general US population indicating that 75% of women know that maximum fertility occurs mid-cycle (Lundsberg et al. 2014). This awareness of fertility is higher in white and educated populations (Swift and Liu 2014) and has been helped by movements to normalize menstruation (Hunter 2016, Weiss-Wolf 2017, Hodge 2019, Bobel and Fahs 2020). It has been further assisted by the wide-spread use of menstrual tracking apps, used by nearly half of women in some populations internationally (Gambier-Ross et al. 2018, Ali et al. 2020, Ford et al. 2020). These apps not only track and report physiological, mood, mental, and behavioral changes in response to menses and fertility (Ali et al. 2020), but many of them educate their users on what they can expect during different phases of their cycles (Gambier-Ross et al. 2018, Ali et al. 2020).

And yet, both women who are educated regarding their fertility and menstrual tracking apps demonstrate a consistent inability to accurately identify fertility. Before the use of apps, studies assessing fertility identification primarily recruited women who actively tracked their fertility, often to conceive, and who reported high confidence in their knowledge of fertility. Still, the fertility predictions of these women were highly inaccurate, missing ovulation between 73 and 87% of the time (Blake et al. 1997, Sievert and Dubois 2005, Zinaman et al. 2012, Hampton et al. 2012), presumably due to a dependence on information from unreliable sources (Peterson et al. 2012). The same inaccuracy is common with many menstrual tracking apps, which rely heavily on inaccurate estimation methods or unreliable physiological cues (Duane et al. 2016, Ali et al. 2020). As a result, these apps – including those specifically advertised for contraception – demonstrate high inaccuracy in predicting fertility (Duane et al. 2016).

Because women enter research studies with their own beliefs about their menstrual cycles and the behavioral and physiological shifts that accompany them, it is possible that their beliefs may influence the results. Indeed, the strong potential for bias is one reason that it is notoriously difficult to collect and analyze human subject data (Popovic and Huecker 2021). Unfortunately, researchers studying behavioral fertility rarely, if ever, take into consideration the preexisting beliefs women have about their own fertility. Further, the study design of many experiments may act to prime participants to think about their menstrual cycles before or during data collection; participants are often asked to report information about their menstrual cycles before answering a survey, complete daily journals that include menstrual information and the behavior of interest, schedule data collection around their menstrual cycles, or take hormonal assays that coincide with the middle of their menstrual cycles. Even collecting samples for an entire menstrual cycle may prime participants to associate what they are tracking with changes in their cycles if they start and stop the study in response to menses. These effects can also be compounded by recruitment procedures: much of this research suffers from an overreliance on white, educated, technology-savvy university students, often enrolled in courses related to biology, reproduction, and/or human behavior, and often specifically target women who are both not on hormonal contraceptives and in a relationship. Indeed, as some authors have stated, these women show stronger ovulatory effects (Haselton et al. 2007) – a finding that is unsurprising, as these women would be expected to be likely to be more familiar with fertility awareness-based methods of contraception.

Even if researchers managed to avoid priming participants to the nature of the study, if the women are using fertility estimation to track their own cycles, then any beliefs that the women may have about what they should or should not be experiencing at that moment in time may influence their results. This is particularly the case if the researchers are using the same methods of estimation that the women use to track their own cycles and when the variable of interest is one that the participant believes should fluctuate in response to her cycle. A woman's belief about her menstrual cycle exists outside of the research lab.

5.2.3 Fertility and Sexuality

Most mammals, including all estrous species and most menstrual species, undergo periods of estrus. Estrus is the term used to describe the distinct behavioral and physiological changes associated with sexual receptivity and peak fertility. Some primates have evolved the ability to conceal these periods of peak fertility. This phenomenon, known as concealed ovulation, allows for extended sexual receptivity and for females to engage in sexual behavior throughout their cycles (Sillén-Tullberg and Møller 1993, Garcia et al. 2021 [review]), though many species still show fertility-mediated peaks in sexual behavior (Michael and Zumpe 1970, Wallen et al. 1984, Garcia et al. 2021 [review]).

Even though humans have concealed ovulation, it has been proposed that humans demonstrate fertility-mediated peaks in sexual behavior. Research into fertility-mediated changes in human sexual behavior – and particularly sexual desire and sexual behavior – had begun by at least 1937 with particular interest increasing in the 1970's (Table 5.1).

Before 2000, there was no evidence of an association between sexual desire and the menstrual cycle (Hart 1960, Englander-Golden et al. 1980, Stanislaw and Rice 1988, Schreiner-Engel et al. 1989, Slob et al. 1996). Instead, the evidence pointed to cultural and cognitive factors as a primary driver for menstrual-cycle-related sexual desire. While these studies usually involved methods of fertility determination that were invasive, they also often specifically excluded participants who used fertility-awareness based methods of contraception or deliberately controlled for beliefs regarding fertility. In one of the earliest studies, conducted before hormonal contraceptives were widely available, Hart (1960) documented an increase in desire that corresponded with the "safe period" that women could have sex without conceiving. This suggested that sexual desire was a result of either a self-fulfilling prophesy (might help avoid sex during fertility) or a conditioned response (accustomed to having sex during that time). The results of Stanislaw and Rice (1988) also point to an effect of confirmation bias. They studied women who were using family planning methods of contraception that taught that increased sexual desire was associated with fertility, and using the same method of fertility tracking as the women, they found that these women did report increased desire with increased fertility. Similarly, Slob et al. (1996) found that learned behavior was the likely driver behind fertility-associated increases in subjective (but not objective) measures of sexual arousal. Finally, and notably, Englander-Golden et al. (1980) examined the effect of being aware of a study's intention had on the reported results. They found strong evidence that a woman's beliefs regarding her fertility and what she should be experiencing at different points had a strong influence on what she reported having experienced.

Similarly, there was little evidence to support fertility-mediated sexual behavior, not just desire, before 2000. The earliest studies found no effect of the menstrual cycle at all (James 1971, Morris et al. 1977, Udry and Morris 1977) except a potential increase in sexual behavior immediately after menstruation, proposed to being due to having avoided sexual behavior during menses (Spitz et al. 1975). Later research began exploring whether fertility affected specific types of sexual behavior (e.g., autosexual or allosexual behavior, initiation of allosexual behavior, etc.; Adams et al. 1978, Matteo and Rissman 1984, Hedricks et al. 1987, Harvey 1987), and the results generally showed no consistent pattern. From these studies, the only result that was found more than once was that of a potential increase in female-initiated sexual behavior; however, the two studies that reported this finding were conducted when the "rhythm method" of contraception was becoming more common, and both studies relied on exploratory, non-standard methods of both fertility estimation and phase-of-cycle determination (Matteo and Rissman 1984, Harvey 1987), making this finding tentative.

After 2000, research into sexual desire and behavior began to report fertility-mediated changes. Like the pre-2000 research, they often utilized invasive methods of fertility determination with participants knowing precisely when they were fertile. However, unlike pre-2000 research, these studies rarely included methods of controlling for beliefs regarding fertility and sexuality. Further, and particularly for sexual behavior, many of the studies relied on unique, non-standard methods of phase-of-cycle determination and comparison, making it difficult to compare results across studies and to identify consistent patterns.

Table 5.1. Studies examining fertility-mediated shifts in sexual desire and behavior, divided into pre- and post-2000.

Area of Findings	**Trend**	**Summary**	**References**
Sexual Desire / Interest			
Pre-2000	No effect	No hormonal influence on sexual desire. Results indicate a strong relationship between sexual desire and other factors, namely confirmation bias, conditioned effects, and self-fulfilling prophesies.	Hart 1960, Englander-Golden et al. 1980, Stanislaw and Rice 1988, Schreiner-Engel et al. 1989, Slob et al. 1996
Post-2000	Inconclusive	Findings suggest a potential decrease in desire with menses and an increase with fertility (specifically, a marked increase in for partnered women in sexually satisfying relationships, and an increase in the emotional content and sexual arousal of fantasies). Importantly, most methods involved invasive fertility tracking, with participants knowing exactly when they were fertile and that the study involved both sex and their menstrual cycles.	Gangestad et al. 2002, Bullivant et al. 2004, Pillsworth and Haselton 2004, Haselton and Gangestad 2006, Pillsworth and Haselton 2006, Röder et al. 2009, Brown et al. 2011, Dawson et al. 2012, Roney and Simmons 2013
Sexual Behavior			
Pre-1980	No effect	Results show no consistent effect of menstrual cycle. Later research reported a potential mid-cycle effect on female-initiated sexual behavior, though with the utilization of non-standard methods of fertility determination.	James 1971, Spitz et al. 1975, Morris et al. 1977, Udry and Morris 1977, Adams et al. 1978, Matteo and Rissman 1984, Hedricks et al. 1987, Harvey 1987
Post-2000	Inconclusive	Results suggest a strong influence of the menstrual cycle on sexual activity: a decrease in allosexual activity with menses, and an increase in both general and female-initiated sexual behavior with fertility (but not male- or mutually-initiated). However, these studies relied heavily on both nonstandard methods of phase of cycle comparison and highly invasive methods of fertility determination such that the participants knew both precisely when they were fertile and the purpose of the study.	Burleson et al. 2002, Gangestad et al. 2002, Wilcox et al. 2004, Bullivant et al. 2004, Brown et al. 2011, Roney and Simmons 2013, Caruso et al. 2014

Inconsistent: Mixed directional effects, such that significant findings found in opposing direction either with respect to the characteristic or the phase of cycle
Inconclusive: Evidence is relatively weak, findings sufficiently scattered, or potential for priming is high
No effect: Evidence does not point to an effect of fertility; other factors may be involved
Potential for: Results tend to show a consistent direction

At least eight studies have investigated fertility effects on general sexual desire. The earliest of these studies found no effect of the menstrual cycle on sexual desire, regardless of relationship status, even with participants completing questionnaires only after receiving a positive LH test from an in-lab urine test (Gangestad et al. 2002). In contrast, later studies often found an effect: one found an effect for “mated” women (undefined – Pillsworth et al. 2004), two for women in a relationship (Bullivant et al. 2004, Haselton and Gangestad 2006), one for only women with high relationship sexual satisfaction (Pillsworth and Haselton 2006), and two for women in general (Röder et al. 2009, Roney and Simmons 2013); only one study has reported no effect of fertility (Brown et al. 2011). Further, many of these studies compared fertility to other phases of the menstrual cycle in ways that makes it difficult to discern if fertility was actually responsible for any effect. Both the luteal phase and menses have been associated with decreased desire (luteal – Roney and Simmons 2013, menses – Brown et al. 2011) and yet are common phases used in comparison (luteal/progesterone – Haselton and Gangestad 2006, Pillsworth and Haselton 2006; menses – Bullivant et al. 2004; both – Röder et al. 2009). Further, Bullivant et al. (2004) found an effect of fertility when compared against *maximum* fertility. Importantly, most of these studies took no effort to blind participants to the nature of the study, having participants complete menstrual cycle questions before completing a one-time survey on sexual desire (Pillsworth et al. 2004) or having them complete daily, in-depth questionnaires documenting their menstrual cycles and sexual desire (Haselton and Gangestad 2006, Röder et al. 2009). Three studies required participants to confirm a positive LH test while providing, or in order to provide, data (Bullivant et al. 2004, Pillsworth and Haselton 2006, Brown et al. 2011). Only one study took efforts to decouple the menstrual cycle information from that related to sexuality, having participants provide daily saliva samples in addition to completing detailed questionnaires (Roney and Simmons 2013).

In addition to general sexual desire, two studies have examined desire in context of sexual fantasies, and both reported an effect of fertility (Bullivant et al. 2004, Dawson et al. 2012). However, they also had strong priming effects, requiring participants to record their daily fantasies along with taking, testing, and reporting the results of at-home urine tests; in one, participants also recorded vaginal secretions, cervical mucus, and basal body temperature (Bullivant et al. 2004).

Similarly, the more recent research into sexual behavior also indicates a relationship with fertility. I have found five studies that have examined the effects of fertility on general sexual behavior, and all but one reported an effect. All five used hormonal methods of fertility determination, but only two collected the information in a manner that might blind the participants to the specific phase of the cycle of interest (daily saliva – Roney and Simmons 2013; daily urine – Wilcox et al. 2004). The other three studies made no attempt to blind participants to the focus on fertility, requiring participants to test urine in the lab setting until a positive LH was detected before completing the study (Gangestad et al. 2002); recording daily characteristics of vaginal secretions, cervical mucus, basal body temperature, and the results of at-home LH urine tests (Bullivant et al. 2004); and undergoing weekly blood tests and a sonograph to confirm ovulation (Caruso et al. 2014). Further, none of the studies attempted to blind the participants regarding the outcome of interest, instead asking participants to record or recollect detailed sexual behavior either daily or when they reported to the lab. Finally, none of the studies used standard methods of comparison window determination, instead opting to develop their own methods (fertile vs. non-fertile, fertile vs. days-to-fertile – Gangestad et al. 2002; fertile vs non-bleeding-non-fertile days – Wilcox et al. 2004; generated an algorithm that divided the cycle into six phases – Bullivant et al. 2004; divided the cycle into four phases – Caruso et al. 2014; compared changes in response to hormonal profiles across the cycle – Roney and Simmons 2013). The only study that did not find an effect of fertility on sexual behavior collected urine samples across the cycle and compared across-the-cycle changes in sexual behavior directly to the hormones present (Roney and Simmons 2013).

In addition to general sexual behavior, three of these studies explored patterns in the initiation of sexual activity; as before, Bullivant et al. and Gangestad et al. reported fertility effects, but only with female-initiated sexual behavior, and, also as before, Roney and Simmons found none. Similarly, three studies have explored autosexual and allosexual behavior, two of which reported increases in autosexual activity with fertility. However, these two studies have similar methodological concerns, including failing to blind participants to the subject of interest and using physiological methods that communicated the timing of fertility to participants (self-reported positive LH urine tests – Brown et al. 2011; daily basal body temperature and cervical mucus – Burleson et al 2002). The third study, again Roney and Simmons (2013), found no effect.

At the surface level, these studies would seem to indicate an effect of fertility on sexuality. However, these studies may instead be pointing to an effect of fertility belief. The early research that accounted for beliefs about the menstrual cycle found no effect of fertility and instead found that patterns of sexuality were associated with beliefs and attitudes regarding sexuality and the menstrual cycle. That the later studies failed to take into consideration pre-existing beliefs of the participants while using methods that may have acted to prime participants to recall those beliefs during the study further must be considered.

5.2.4 This Study

The present study explored the relationships between fertility, sexuality, and belief. Specifically, I tested the hypothesis that fertility increases sexuality, while accounting for fertility belief, and the hypothesis that women cannot consciously and intuitively identify when they are fertile. I used hormonal ovulation tests combined with daily journaling reports to determine the degree to which fertility affected participants' fertility belief, sexual desire, and hypothetical sexual behavior. To test for the existence of an association between fertility and sexuality, I predicted that the participants (1) would show increased sexual desire and proclivity to sexual behavior when fertile. To test for whether ovulation, and thus fertility, was concealed from women, I predicted that the participants (2) would not be able to predict their own fertility accurately. I also explored which factors might explain fertile belief.

Finally, I explored this data using common methods of estimating fertility. I tested each method of estimation with regards to (a) their accuracy in capturing the hormonally confirmed fertile window and the degree to which they correlated with reported (b) sexual desire and response and (c) fertile belief. As this was primarily exploratory and descriptive in nature, I made no statistical predictions.

5.3 METHODS

5.3.1 Research Participants

We recruited cisgender women enrolled at the University of Kentucky during the fall of 2018, contacted through emails acquired by the office of the registrar. Recruited women were between the ages of 18 to 35 and were naturally cycling (not using hormonal contraceptives, not pregnant, and without known reproductive disorders), and they had the option of participating in the full study (urine collection and journaling) or just the journaling. Interested participants were asked to complete a consent form and to provide basic demographic information. After completion, participants were assigned a random research ID which was used to code all identifying information. They were then directed to a second survey where they provided information about their menstrual cycles as well as a baseline survey to assess their general knowledge regarding menstruation and ovulation. Upon completion of the study, participants were asked to complete this baseline survey a second time to determine if answers changed.

5.3.2 Daily Journaling

The journaling component lasted for at least one full menstrual cycle and up to two full menstrual cycles. Participants notified the PI upon the start of menstruation, at which point they began receiving an email with a daily journaling link, sent between noon and 4:00 pm EST (no later than 6:00 pm given any errors), that they were to complete by the end of the day. The link directed them to complete a survey that asked the following questions:

1. What is your random ID?
2. Do you believe you are fertile today? (If you had unprotected sex with a man, could you get pregnant?)
3. Are you on your period?
4. Please rate the intensity of your sexual desire today
   (*6-point Likert scale: very weak to very intense*)
5. Based on how you feel today, which of the following are you most likely to do?
   (*Actively seek sex, Agree to sex if propositioned (offered), or Avoid (or reject) sex*)
6. How happy do you feel today?
   (*10-point Likert scale: extremely happy to extremely unhappy*).
   In data analysis, this score was reversed to reflect a more intuitive interpretation, with 10 being extremely happy and 0 being extremely unhappy.

Participants were encouraged to respond “intuitively” with regards to their fertile beliefs and not with regards to estimations or calculations. Participants who missed a journal entry could retroactively provide the information via the survey link, notifying the PI that this was from the previous day. Retroactively provided journal entries were only accepted if submitted for the previous day. Days with missing data were excluded from the analysis.

At the completion of two full menstrual cycles, after 30 days of not completing a journal entry, or after 100 days of consecutively completing a journal entry, participants were removed from the email list. For each month of completed questions, participants received $5 electronically (PayPal/gift card/etc.). They were required to complete the first cycle before proceeding to the second cycle, and individuals completing both cycles of journaling received a total of $10.

5.3.3 Urine Testing

Each cycle, participants who opted to provide urine were provided 10 specimen cups with instructions to collect samples starting from the end of their period until all cups are used. Samples were collected between 10 am and 8 pm (per Pregmate© ovulation kit instructions; see Baird et al. 1991 for first-morning urine sample validity) and stored in individual plastic bags within a larger gallon plastic bag in their personal refrigerator. Participants were asked to collect samples around the same time each day but were told that any sample collected at any time is better than none. If a participant missed a day of their collection, they were allowed to collect at the end of the original 10 days (Day 11, etc.). When they finished collecting samples for their cycle, they contacted the PI who retrieved the samples for testing, confirming the dates that the samples were collected. Individuals who completed both cycles of urine collection were placed in a drawing to win one of three $50 gift cards.

Samples were tested upon arriving to the lab using a Pregmate© ovulation kit. Positive test results indicate the presence of the LH surge associated with ovulation which is expected to occur within the next 24-48 hours, as per kit instructions. Results were photographed and recorded in a lab log, and samples were discarded immediately after testing.

5.3.4 Phase of State Classification

For Predictions 1 and 2, I used hormonally-determined fertility and thus restricted all analyses to cycles that detected a positive LH surge. Several factors were included when determining the fertile window and assigning conception probabilities. The concentration of LH increases sharply approximately 24-36 hours before ovulation and is often detectable in the blood stream for several days (Direito et al. 2013). Because participants could collect a sample immediately preceding an LH surge, this might result in the first LH positive sample being collected over 24 hours after the surge occurred, effectively collecting a positive LH sample on the day of ovulation. Therefore, ovulation estimations that utilize a shorter LH-to-ovulation window tend to be more accurate than those that utilize longer windows. Further, the probability of conception surviving to clinical detection is highest on the two days before ovulation (Wilcox et al. 1998), so using a shorter LH-to-ovulation window will be at low risk of excluding high conception days. Thus, I assigned the conception probabilities calculated in Wilcox et al. (1998) to the corresponding day in each cycle's fertile window, ending on the predicted day of ovulation (0.04, 0.13, 0.08, 0.29, 0.27, and 0.08). However, it should be noted that these estimates assume that all participants have the same conception probability, an assumption that is likely to be inaccurate.

I chose to compare the fertile window to the luteal phase using the luteal midpoint method. This method allowed for a comparison of equal-sized windows of time while also maximizing the chances of avoiding the confounding effects of either fertility or premenstrual/menstrual symptoms. In this estimation, I erred on the side of avoiding overlap with fertility as opposed to menstruation, as I were comparing results against the effects of fertility. Therefore, for short cycles and for cycles with odd-numbered days until menses, these cycles were shifted closer to the start of menses as opposed to fertility. However, it was be noted that any results that suggest an effect of fertility in this comparison could also be influenced by the high levels of progesterone during the luteal phase.

All cycles, both hormonally confirmed and not, were used to explore the effect that estimated fertility and type of comparison window would have on the reported results. In addition to the hormonally-confirmed method described above, six methods of estimation were used, most of which are commonly reported in the literature. Two of the methods I used were backwards-counting methods, counting 13 and 15 days backward from the start of menses (referred to as "-13" and "-15", respectively) to determine the estimated date of ovulation. The accuracy of this method varies with whether the start of menses is estimated or confirmed, and in this case, I used confirmed menses. Two other methods I used were forward-counting, counting forward from the start of menses of the current cycle to estimate the date of ovulation within the same cycle. One method is the particularly common "+14" method, estimating ovulation as exactly two weeks from menses. The other, referred to here as the "variable method," was derived from Wilcox et al. (2000) which estimated fertility probability in accordance with menstrual cycle length variability (Figure 5.1). I used this to determine the estimated date of ovulation for each cycle based on its confirmed length (< 28 days: +14; 28-29 days: +15; > 30 days: +17 ("+Var"). The final two methods I used were actuarial methods, which use population-based risk-of-conception data to estimate the point of highest fertility. The first method, known as the Jöchle method, was derived from reported conceptions from rape (Jöchle 1973, adapted into Baker and Bellis 1995). The second, the Wilcox method, and was derived from couples trying to conceive (Wilcox et al. 2001).

I also used six commonly-used methods to designate the comparison window. Three were luteal methods, including the midpoint method described above ("LM"). The other two count forward from the date of ovulation a set number of days to begin the luteal window (3 and 8, "L3" and L8", respectively). The other three methods were "non-fertile" methods ("NF"), which included all or most of the days outside of the fertile window in the comparison window, including menses. One method included all of the days entirely, while the other two excluded four and eight days around the fertile window ("NF4" and "NF8", respectively).

I paired the seven methods of fertility determination (one hormonal, six estimated) with each of the six methods of comparison window determination to create a total of forty-two combinations. An illustration of these methods can be seen in Figure 5.2, which present six methods of fertility estimation and three methods of luteal designation as assigned to a participant's cycle.

Table 5.2. Commonly-used methods of phase of cycle classification.

Day of Ovulation Fertile window comprises day of ovulation and 5 days preceding						
Hormonally Confirmed	**Estimated**					
	Backwards-counting (Luteal-phase dependent) Relies on next menses (current or estimated)		**Forward-counting** Relies on current menses			
			Follicular-phase dependent		**Actuarial Method** Population-based conception risk	
			Standard length	Variable based on cycle length *Wilcox et al. 2000*	Conception from reported rape *Jöchle et al. 1973*	Couples trying to conceive *Wilcox et al. 2001*
LH surge +1	-13 days	-15 days	+14 days	<28: +14 days 28-29: +15 days >30: +17 days	+12 days	+16 days

Comparison Window					
Luteal Comparable-sized window			**Non-Fertile** Collection of days outside the fertile window		
Backwards-counting Next menses	**Forward-counting** Current menses			**Fertile window buffer**	
Midpoint	+3	+8	All	± 2	± 4
Equidistant between fertile window and menses	Ovulation +3 days	Ovulation +8 days	All days	All days +2 and -2 from fertile window	All days +4 and -4 from fertile window

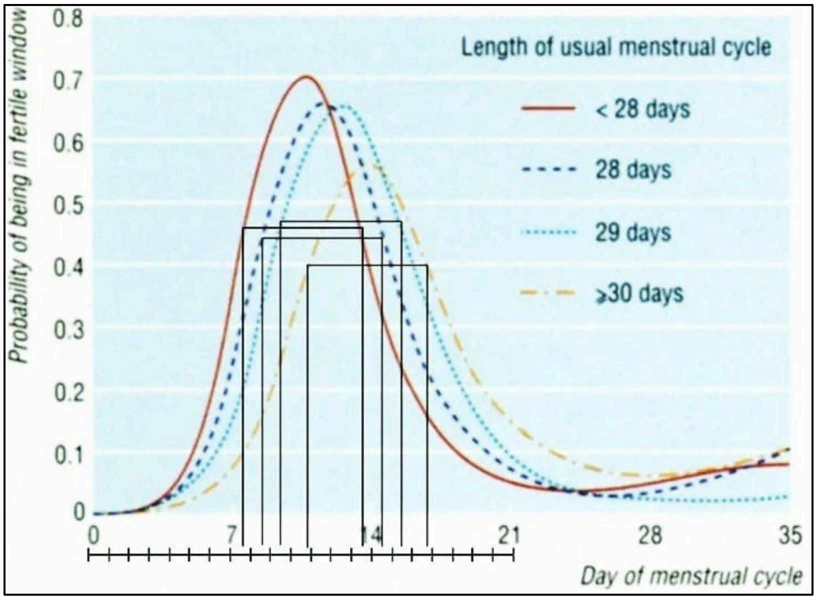


Figure 5.1. The estimated fertility window based on variation in length of menstrual cycle, from Wilcox et al. (2000).

5.3.5 Data Analysis

5.3.5.1 Preliminary Analysis: Within-Study Changes in Belief

The preliminary analysis examined changes to participants' answers to baseline menstrual cycle questions before and after the study. Their responses regarding their confidence in their knowledge, the average cycle length, average menses length, and estimated ovulation date were compared using paired t-tests. Their responses regarding (1) the hormones involved in menstruation and (2) the time of the menstrual cycle in which a woman is most likely to get pregnant were compared using linear mixed model analyses. The fixed effects of each model included the response of interest (either hormones involved in menstrual cycle or pregnancy likelihood), the survey (pre-study or post-study), and whether they sought new information during the course of the study (open response). Each model also included two interaction terms: the response of interest and the survey, and the response of interest, the survey, and whether they sought new information. Analyses were completed using the mixed procedure in SPSS 28.0 (IBM SPSS Statistics, 2021); the Satterthwaite approximation method to calculate degrees of freedom; the restricted maximum likelihood (REML) method to estimate variance parameters; and the Fisher's least significant difference for calculating p-values, which were adjusted for multiple comparisons (Bonferroni). The full syntax for the analyses can be found in Appendix G.

5.3.5.2 Predictions

Prediction 1 tested the effects of predictors on two outcomes, a woman's reported sexual desire and her hypothetical sexual response and was examined using generalized linear mixed models (the "Desire" and "Response" models); the structure of the models used can be found in Table 5.3. Fixed effects for both models included Conception Probability, Belief, and Happiness, and random effects included the interaction of Participant ID and Cycle ID to account for both repeated days of data collected and cycles in which participants participated. Further, Desire was included as a fixed effect for the Response model.

Prediction 2 explored the accuracy of participant beliefs and the factors that influenced those beliefs. Accuracy was calculated by comparing the days the participants believed they were fertile ("claimed fertile window") to their actual fertile window using one-sample, two-tailed t-tests with heteroscedastic variance. The factors influencing fertile belief was also explored using a generalized linear mixed model ("Belief" model; see Table 5.3 for full model structure). The Belief model was structured similarly to the Desire model, except for the use of a binomial distribution and the inclusion of Desire instead of Belief as a fixed effect.

The interaction terms included in each model was determined by model fit analyses (AIC method, Table 5.3) and indicated that 2-way interactions, but not 3-way interactions, were the best fit for all models. Reference options for the models were the lowest Desire score ("1") for the Desire model, "Avoid Sex" for the response model, and "Not Believe" for the Belief model. Notice that Belief and Desire were both tested as predictors of the other, as I did not want to presume whether increased sexual desire acted as a trigger for believing a participant was fertile or whether a belief in being fertile led to an increased sexual desire. Similar logic was used with regards to Response and Belief. Analyses were completed using the GENLINMIXED procedures in SPSS 28.0 (IBM SPSS Statistics, 2021); the Satterthwaite approximation method to calculate degrees of freedom; the restricted maximum likelihood (REML) method to estimate variance parameters; and the Fisher's least significant difference for calculating p-values, which were adjusted for multiple comparisons (Bonferroni). The full syntax for the models can be found in Appendix H.

The exploratory analyses regarding the different methods of fertility determination were conducted using a total of 42 fertile/comparison window combinations: the 1 hormonal method and 6 estimated methods of determining fertility as well as the 6 different comparison windows. For each participant's cycle, the percent of fertile window captured by each of the 6 methods of fertility estimation was calculated and compared using a one-way ANOVA. The correlations between fertility and sexual desire, sexual response, and fertile belief were calculated using Pearson correlation coefficients for all 42 methods.

The exploratory analyses regarding the different methods of fertility determination were conducted using a total of 42 fertile/comparison window combinations: the 1 hormonal method and 6 estimated methods of determining fertility as well as the 6 different comparison windows. For each participant's cycle, the percent of fertile window captured by each of the 6 methods of fertility estimation was calculated and compared using a one-way ANOVA. The correlations between fertility and sexual desire, sexual response, and fertile belief were calculated using Pearson correlation coefficients for all 42 methods.

5.4 RESULTS

5.4.1 Summary Statistics

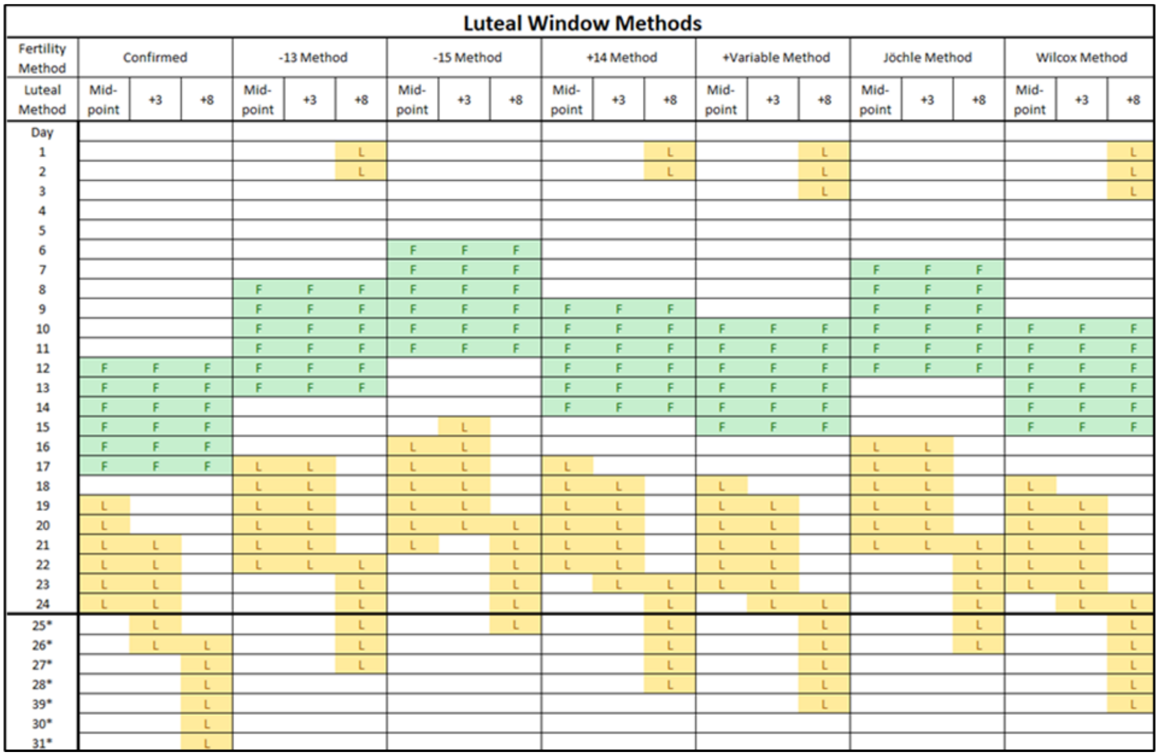
115 women consented in the original interest form; 50 went on to complete the menstrual cycle survey, receive an ID to begin journaling, and collect urine samples, if they opted to. See Figure 5.4 for a breakdown of participant retention, their type of participation, and how their cycles were ultimately included in the analysis. Overall, 25 participants contributed to the 41 cycles that were included in the analysis. All 41 cycles were included in the estimated analyses of exploratory analyses, but only the 23 cycles with confirmed fertility were included in the hormonal analyses of predictions 1 and 2. See Table 5.4 for a demographic and physical information breakdown of the participants.

Table 5.3. The structure of the models used in predictions 1 and 2.

Model fit analyses using Akaike's Information Criterion (AIC) indicated that two-way interactions for all models should be included.

Structure and Fit of Statistical Models

Outcome Variable	**Model Type**	**Distribution**	**Link Function**	**Fixed Effects**	**Interactions**	**AIC**
Sexual Desire						
	Generalized Linear Mixed Model	Multinomial	Logit	Probability	2-way	60833.29
				Happiness Belief	3-way	65444.92
Sexual Response						
	Generalized Linear Mixed Model	Multinomial	Logit	Probability	2-way	4198.86
				Happiness Belief	3-way	4265.28
				Desire	4-way	4857.71
Fertile Belief						
	Generalized Linear Mixed Model	Binomial	Logit	Probability	2-way	1385.19
				Happiness Desire	3-way	1385.26



Luteal Window Methods

Fertility Method	Confirmed			-13 Method			-15 Method			+14 Method			+Variable Method			Jöchle Method			Wilcox Method		
Luteal Method	Mid-point	+3	+8	Mid-point	+3	+8	Mid-point	+3	+8	Mid-point	+3	+8	Mid-point	+3	+8	Mid-point	+3	+8	Mid-point	+3	+8
Day																					
1						L						L			L						L
2						L						L			L						L
3															L						L
4																					
5																					
6							F	F	F												
7							F	F	F							F	F	F			
8				F	F	F	F	F	F							F	F	F			
9				F	F	F	F	F	F	F	F	F				F	F	F			
10				F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
11				F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
12	F	F	F	F	F	F				F	F	F	F	F	F	F	F	F	F	F	F
13	F	F	F	F	F	F				F	F	F	F	F	F				F	F	F
14	F	F	F							F	F	F	F	F	F				F	F	F
15	F	F	F					L					F	F	F				F	F	F
16	F	F	F				L	L								L	L				
17	F	F	F	L	L		L	L		L						L	L				
18				L	L		L	L		L	L		L			L	L		L		
19	L			L	L		L	L		L	L		L	L		L	L		L	L	
20	L			L	L		L	L	L	L	L		L	L		L	L		L	L	
21	L	L		L	L		L		L	L	L		L	L		L	L	L	L	L	
22	L	L		L	L	L			L	L	L		L	L				L	L	L	
23	L	L				L			L		L	L	L	L				L	L	L	
24	L	L				L			L			L		L	L			L		L	L
25*		L				L			L			L			L			L			L
26*		L	L			L						L			L			L			L
27*			L			L						L			L						L
28*			L									L			L						L
39*			L												L						L
30*			L																		
31*			L																		

Figure 5.2. Depiction of one cycle's fertile (F) and luteal (L) designations based on some of the methods in Table 4.2.

This cycle was the second cycle for this participant and a 24-day cycle. The "luteal" designations on days 1-3 for the +8 method came from the previous cycle that was 26 days long, thus designating menstrual days as luteal. Similarly, days 25-31 would have occurred at the beginning of this participant's third cycle.

5.4.2 Data Analysis

5.4.2.1 Preliminary Analysis: Within-Study Changes in Belief

The preliminary analysis examined changes to participants' answers to baseline menstrual cycle questions before and after the study. Their responses regarding their confidence in their knowledge, the average cycle length, average menses length, and estimated ovulation date were compared using paired t-tests. Their responses regarding (1) the hormones involved in menstruation and (2) the time of the menstrual cycle in which a woman is most likely to get pregnant were compared using linear mixed model analyses. The fixed effects of each model included the response of interest (either hormones involved in menstrual cycle or pregnancy likelihood), the survey (pre-study or post-study), and whether they sought new information during the course of the study (open response). Each model also included two interaction terms: the response of interest and the survey, and the response of interest, the survey, and whether they sought new information. Analyses were completed using the mixed procedure in SPSS 28.0 (IBM SPSS Statistics, 2021); the Satterthwaite approximation method to calculate degrees of freedom; the restricted maximum likelihood (REML) method to estimate variance parameters; and the Fisher's least significant difference for calculating p-values, which were adjusted for multiple comparisons (Bonferroni). The full syntax for the analyses can be found in Appendix G.

5.4.2.2 Predictions

Prediction 1 tested the effects of predictors on two outcomes, a woman's reported sexual desire and her hypothetical sexual response and was examined using generalized linear mixed models (the "Desire" and "Response" models); the structure of the models used can be found in Table 5.3. Fixed effects for both models included Conception Probability, Belief, and Happiness, and random effects included the interaction of Participant ID and Cycle ID to account for both repeated days of data collected and cycles in which participants participated. Further, Desire was included as a fixed effect for the Response model.

Prediction 2 explored the accuracy of participant beliefs and the factors that influenced those beliefs. Accuracy was calculated by comparing the days the participants believed they were fertile ("claimed fertile window") to their actual fertile window using one-sample, two-tailed t-tests with heteroscedastic variance. The factors influencing fertile belief was also explored using a generalized linear mixed model ("Belief" model; see Table 5.3 for full model structure). The Belief model was structured similarly to the Desire model, except for the use of a binomial distribution and the inclusion of Desire instead of Belief as a fixed effect.

The interaction terms included in each model was determined by model fit analyses (AIC method, Table 5.3) and indicated that 2-way interactions, but not 3-way interactions, were the best fit for all models. Reference options for the models were the lowest Desire score ("1") for the Desire model, "Avoid Sex" for the response model, and "Not Believe" for the Belief model. Notice that Belief and Desire were both tested as predictors of the other, as I did not want to presume whether increased sexual desire acted as a trigger for believing a participant was fertile or whether a belief in being fertile led to an increased sexual desire. Similar logic was used with regards to Response and Belief. Analyses were completed using the GENLINMIXED procedures in SPSS 28.0 (IBM SPSS Statistics, 2021); the Satterthwaite approximation method to calculate degrees of freedom; the restricted maximum likelihood (REML) method to estimate variance parameters; and the Fisher's least significant difference for calculating p-values, which were adjusted for multiple comparisons (Bonferroni). The full syntax for the models can be found in Appendix H.

5.4.3 Preliminary Analysis: Within-Study Changes in Belief

Menstrual cycle information and beliefs about the menstrual cycle in general are represented in Tables 4.5-4.8. Most participants tracked their cycles and more than half used mobile applications (Table 5.5). Participants expressed high confidence in their knowledge regarding the menstrual cycle and were relatively accurate regarding the average cycle length, menses length, and date of ovulation for a 30-day cycle. Paired t-tests found no significant differences between their responses on the pre- and post-study tests (Table 5.6).

Many of the participants were able to accurately identify hormones involved in the menstrual cycle before the study (Table 5.7). A linear mixed model revealed few differences in the pre- and post-study responses. The number of participants that identified progesterone as an involved hormone dropped significantly (73% to 34%, $p < 0.001$), but there was no significant difference in the other reported hormones. A few participants admitted to seeking new information about the menstrual cycle during the course of the study. Including this information in the model led to some slight differences with regards to responses that included estrogen, testosterone, and progesterone. Specifically, when asked if they sought new information during the study, participants who responded "no" were more likely to identify both estrogen and testosterone (n=19), "not really" were less likely to identify progesterone (n=1), "a little bit" were less likely to identify both progesterone and testosterone (n=2), and "yes" were more likely to identify estrogen (n=3). Overall, the study seemed to have little influence on what the participants reported knowing regarding these hormones, and the changes that were present did not represent a more accurate understanding of fertility.

Pre- and post-study analyses on when participants believed peak fertility occurred, which was defined as when pregnancy was most likely to occur, suggested that the study itself may have influenced beliefs. While there were no significant differences in the responses for each of the provided areas of the cycle (Table 5.8), when analyzed with respect to whether the participants sought new information, some nuances emerged. In the post-study survey, participants who answered "yes" to whether they sought more information (n=3) were more likely to report after-menses and the end-of-the-cycle as being associated with peak fertility. Participants who said they did not seek more information also showed changes, being more likely to indicate the middle of the cycle and being less likely to indicate both the end of the cycle and the "all points equal" option.

Table 5.3. The structure of the models used in predictions 1 and 2.

Model fit analyses using Akaike's Information Criterion (AIC) indicated that two-way interactions for all models should be included.

Structure and Fit of Statistical Models

Outcome Variable	Model Type	Distribution	Link Function	Fixed Effects	Interactions	AIC
Sexual Desire						
	Generalized Linear	Multinomial	Logit	Probability	2-way	60833.29
	Mixed Model			Happiness Belief	3-way	65444.92
Sexual Response						
	Generalized Linear	Multinomial	Logit	Probability	2-way	4198.86
	Mixed Model			Happiness Belief	3-way	4265.28
				Desire	4-way	4857.71
Fertile Belief						
	Generalized Linear	Binomial	Logit	Probability	2-way	1385.19
	Mixed Model			Happiness Desire	3-way	1385.26

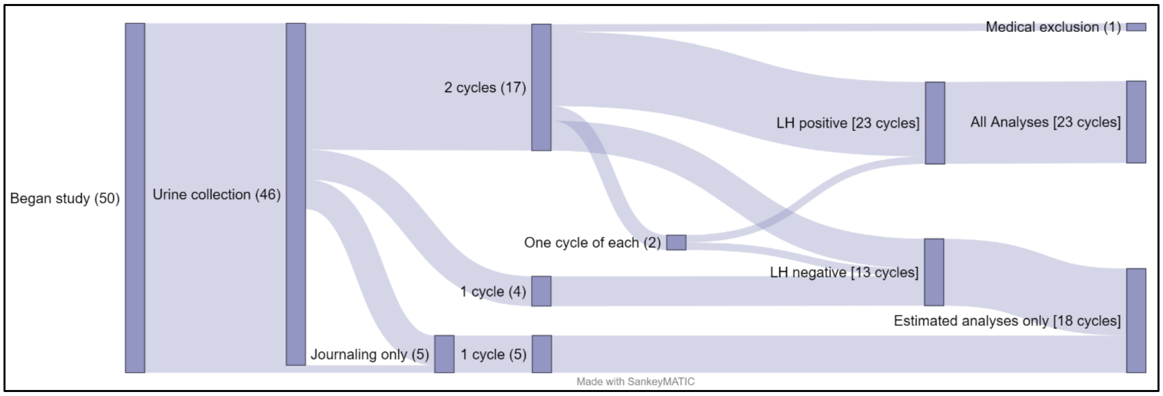


Figure 5.3. Participant retention, level of participation, and the contributed cycles' ultimate category of analysis (number of participants in parentheses).

A total of 26 participants completed the full study, but 1 had to be excluded from the analysis due to a revealed medical disqualification. Two participants contributed two cycles that each captured only 1 positive LH surge. Ultimately, 23 cycles were included in the hormonal analyses (predictions 1 and 2), and 41 in estimated analyses (exploratory analyses).

Table 5.4. Demographic breakdown of included participants (n=25).

Activity level, race, and ethnicity presented in %(#) format. *Indicates multiple selections allowed

Demographic characteristic	
	mean (range)
General	
Age (yrs)	25.7 (19-33)
Height (in)	64.5 (58.5-71)
Weight (lbs)	153.8 (96-258)
	% (#)
Activity Level	
Very active	12 (3)
Fairly active	60 (15)
Fairly sedentary	24 (6)
Sedentary	4 (1)
Race*	
White	60 (15)
Black or African American	28 (7)
Black or African American, White	4 (1)
Asian	8 (2)
Ethnicity*	
Caucasian	52 (13)
African	20 (5)
Black American	4 (1)
Caribbean	4 (1)
Mixed	4 (1)
South Asian	4 (1)
Latino/Hispanic	4 (1)
Middle Eastern	4 (1)
East Asian	4 (1)

Table 5.5. Participant personal menstrual information (n=25).

	Mean (range)
Cycle Length in Days	29.1 (25.5-35)
	% (#)
Variation	
1-2 days	52 (13)
3-4 days	36 (9)
5+	12 (3)
Tracking Method	
App	56 (14)
Calendar	16 (4)
None	16(4)
Mixed Methods (Write, App)	4 (1)
Memory	4 (1)
Predictable Dates	4 (1)
Unspecified	4 (1)

Table 5.6. Pre- and post-study differences in reported cycle knowledge.

Statistics included paired t-tests and paired samples correlations between the pre- and post-study questions on overall confidence in knowledge about the menstrual cycle as well as average cycle length, menses length, and ovulation date. All significance tests are two-tailed with an alpha of 0.05. Significant results are underlined for convenience. (EMM = estimated marginal means, SE = standard error, N = sample size, r2 = Pearson correlation coefficient, *p* = p-value)

Menstrual Cycle Knowledge: Pre- and Post-Study

		Pre-Study	Post-Study	t-test	Correlation	
	N	EMM ± SE	EMM ± SE	*p*	r_2	*p*
Confidence	25	7.48 ± 0.33	7.52 ± 0.25	0.866	0.711	<0.001
Cycle Length	24	28.24 ± 0.13	28.58 ± 0.19	0.111	0.191	0.360
Menses Length	24	5.44 ± 0.16	5.40 ± 0.16	0.731	0.000	<0.001
Ovulation Date	23	15.52 ± 0.75	15.13 ± 0.58	0.692	0.741	<0.001

Table 5.7. Differences in pre/post-study hormonal open responses.

P-values are two-tailed at a 0.05 significance level and were adjusted for multiple comparisons (Bonferroni) (mixed model analysis) (n=25 subjects with repeated measures). (df = degrees of freedom, Num = numerator, Den = denominator, F = F-statistic, *p* = p-value, EMM = estimated marginal means, SE = standard error, Ea = estradiol, T = testosterone, Pr = progesterone, F = follicle-stimulating hormone, L = luteinizing hormone, Ps = prostaglandins, G = GnRH)

Type III Tests

Fixed Effects	df Num	df Den	F	*p*
Intercept	1	21	15.76	<0.001
Hormone Type	7	191	77.43	<0.001
Survey	1	1915	4.15	0.042
New Info	3	21	1.18	0.342
Hormone Type * Survey	7	1915	5.98	<0.001
Hormone Type * New Info * Survey	42	1915	4.19	<0.001

Pairwise Tests

Hormone Type	EST	±	SE	df	Ea	T	Pr	F	L	Ps	G
Estrogen	0.67	±	0.05	41	‡	‡	†	‡	‡	‡	‡
Estradiol	0.01	±	0.05	41		†	‡	-	-	-	-
Testosterone	0.15	±	0.05	41			‡	†	†	†	†
Progesterone	0.53	±	0.05	41				‡	‡	‡	‡
FSH	0.02	±	0.05	41					-	-	-
LH	0.02	±	0.05	41						-	-
Prostaglandins	0.01	±	0.05	41							-
GnRH	0.01	±	0.05	41		-NS	* <0.05		† <0.01		‡ <0.001

	Pre-study	±		Post-study	±		df	*p*
Survey	0.20	±	0.05	0.16	±	0.05	23	0.042
Hormone Type * Survey								
Estrogen	0.61	±	0.06	0.72	±	0.06	72	0.072
Estradiol	0.01	±	0.06	0.01	±	0.06	72	1.000
Testosterone	0.19	±	0.06	0.11	±	0.06	72	0.160
Progesterone	0.73	±	0.06	0.34	±	0.06	72	<0.001
FSH	0.01	±	0.06	0.03	±	0.06	72	0.829
LH	0.01	±	0.06	0.03	±	0.06	72	0.829
Prostaglandins	0.01	±	0.06	0.00	±	0.06	72	0.829
GnRH	0.01	±	0.06	0.01	±	0.06	72	1.000
Hormone Type * New Info * Survey								
Estrogen								
No (19)	0.79	±	0.04	0.89	±	0.04	72	0.010
Not really (1)	0.00	±	0.18	0.00	±	0.18	72	1.000
A little bit (2)	1.00	±	0.13	1.00	±	0.13	72	1.000
Yes (3)	0.67	±	0.10	1.00	±	0.10	72	0.001
Estradiol								
No (19)	0.05	±	0.04	0.05	±	0.04	72	1.000
Not really (1)	0.00	±	0.18	0.00	±	0.18	72	1.000
A little bit (2)	0.00	±	0.13	0.00	±	0.13	72	1.000
Yes (3)	0.00	±	0.10	0.00	±	0.10	72	1.000

Table 5.7. (continued)

Testosterone								
No (19)	0.26	±	0.04	0.42	±	0.04	72	<0.000
Not really (1)	0.00	±	0.18	0.00	±	0.18	72	1.000
A little bit (2)	0.50	±	0.13	0.00	±	0.13	72	<0.000
Yes (3)	0.00	±	0.10	0.00	±	0.10	72	1.000
Progesterone								
No (19)	0.58	±	0.04	0.53	±	0.04	72	0.196
Not really (1)	1.00	±	0.18	0.00	±	0.18	72	<0.000
A little bit (2)	1.00	±	0.13	0.50	±	0.13	72	<0.000
Yes (3)	0.33	±	0.10	0.33	±	0.10	72	1.000
FSH								
No (19)	0.05	±	0.04	0.11	±	0.04	72	0.196
Not really (1)	0.00	±	0.18	0.00	±	0.18	72	1.000
A little bit (2)	0.00	±	0.13	0.00	±	0.13	72	1.000
Yes (3)	0.00	±	0.10	0.00	±	0.10	72	1.000
LH								
No (19)	0.05	±	0.04	0.11	±	0.04	72	0.196
Not really (1)	0.00	±	0.18	0.00	±	0.18	72	1.000
A little bit (2)	0.00	±	0.13	0.00	±	0.13	72	1.000
Yes (3)	0.00	±	0.10	0.00	±	0.10	72	1.000
Prostaglandins								
No (19)	0.05	±	0.04	0.00	±	0.04	72	0.196
Not really (1)	0.00	±	0.18	0.00	±	0.18	72	1.000
A little bit (2)	0.00	±	0.13	0.00	±	0.13	72	1.000
Yes (3)	0.00	±	0.10	0.00	±	0.10	72	1.000
GnRH								
No (19)	0.05	±	0.04	0.05	±	0.04	72	1.000
Not really (1)	0.00	±	0.18	0.00	±	0.18	72	1.000
A little bit (2)	0.00	±	0.13	0.00	±	0.13	72	1.000
Yes (3)	0.00	±	0.10	0.00	±	0.10	72	1.000

Table 5.8. Differences in pre/post-study peak fertility open responses.

P-values are two-tailed at a 0.05 significance level and were adjusted for multiple comparisons (Bonferroni) (mixed model analysis) (n=25 subjects with repeated measures). (df = degrees of freedom, Num = numerator, Den = denominator, F = F-statistic, *p* = p-value, EMM = estimated marginal means, SE = standard error)

Type III Tests

	df			
Fixed Effects	Num	Den	F	*p*
Intercept	1	21	72.758	<0.001
Pregnancy	4	1939	171.751	<0.001
Survey	1	1939	0.968	0.325
New Info	3	21	1.158	0.349
Pregnancy * Survey	4	1939	1.034	0.389
Pregnancy * Survey * New Info	27	1939	4.695	<0.001

Pairwise Tests

	Pre-study	Post-study	df	*p*
Pregnancy				
Menses	0.010 ± 0.050	0.000 ± 0.050	110	0.820
After menses	0.190 ± 0.050	0.290 ± 0.050	110	0.095
Mid-cycle	0.920 ± 0.050	0.960 ± 0.050	110	0.495
Toward beginning of next cycle	0.190 ± 0.050	0.250 ± 0.050	110	0.324
All points equal	0.070 ± 0.050	0.010 ± 0.050	110	0.363
Pregnancy * Survey * New Info				
Menses				
No (19)	0.050 ± 0.030	0.000 ± 0.030	110	0.173
Not really (1)	0.000 ± 0.150	0.000 ± 0.150	110	1.000
A little bit (2)	0.000 ± 0.110	0.000 ± 0.110	110	1.000
Yes (3)	0.000 ± 0.090	0.000 ± 0.090	110	1.000
After menses				
No (19)	0.260 ± 0.030	0.320 ± 0.030	110	0.173
Not really (1)	0.000 ± 0.150	0.000 ± 0.150	110	1.000
A little bit (2)	0.500 ± 0.110	0.500 ± 0.110	110	1.000
Yes (3)	0.000 ± 0.090	0.330 ± 0.090	110	0.001
Mid-cycle				
No (19)	0.680 ± 0.030	0.840 ± 0.030	110	<0.001
Not really (1)	1.000 ± 0.150	1.000 ± 0.150	110	1.000
A little bit (2)	1.000 ± 0.110	1.000 ± 0.110	110	1.000
Yes (3)	1.000 ± 0.090	1.000 ± 0.090	110	1.000
Toward beginning of next cycle				
No (19)	0.260 ± 0.030	0.160 ± 0.030	110	0.006
Not really (1)	0.000 ± 0.150	0.000 ± 0.150	110	1.000
A little bit (2)	0.500 ± 0.110	0.500 ± 0.110	110	1.000
Yes (3)	0.000 ± 0.090	0.330 ± 0.090	110	0.001
All points equal				
No (19)	0.260 ± 0.030	0.050 ± 0.030	110	<0.001
Not really (1)	0.000 ± 0.150	0.000 ± 0.150	110	1.000
A little bit (2)	0.000 ± 0.110	0.000 ± 0.110	110	1.000
Yes (3)	0.000 ± 0.090	0.000 ± 0.090	110	1.000

5.4.4 Prediction 1: Fertility and Sexuality

The analysis of Sexual Desire revealed Happiness as the only significant predictor of Desire (Table 5.9, Figure 5.5), with each level of increased Happiness being associated with increased odds of feeling increased Desire by 1.68 (0.52 ± 0.20, $p = 0.01$). Visual inspection of the data suggests a possible bimodal effect with respect to Happiness such that relatively higher Happiness is associated with both low Desire and high Desire (Figure 5.5a). Pursuant to the hypothesis, Probability of Conception was not significant ($p = 0.967$, Figure 5.5b).

Similarly, the analysis on hypothetical Sexual Response indicated that Desire was the only significant predictor of Response (Table 5.10, Figure 5.6). Unsurprisingly, those who indicated a willingness to Acquiesce to Sex had significantly greater Desire than those who preferred to Avoid Sex, with each level of Desire being associated with an increase in the odds of Acquiescing to Sex by 47.94 (3.87 ± 1.80, $p = 0.032$). This was not found in those who indicated an interest in Seeking Sex, possibly due to the scarcity of this response overall (6.4% of responses compared to 40.6% and 38.6% for Acquiesce and Avoid, respectively). Again, there was no relationship with Conception Probability ($p = 0.807$).

5.4.5 Prediction 2: Fertility and Belief

Participants were generally unable to accurately identify their fertility (Table 5.12, Figure 5.7). They believed they were fertile ("claimed fertile window") far more than they were – an average of 64% of the time compared to 21% of the time ($p < 0.001$), and thus had many "false belief" days. However, they were often able to capture much of the fertile window within their claimed window, though with a high degree of variation (captured 64 ± 43% of the fertile window, $p < 0.001$).

The results of the model on Fertile Belief identified three significant predictors: Sexual Desire, the Probability of Conception, and the interaction between Happiness and Probability (Table 5.13, Figure 5.8). As Sexual Desire increased, so did the likelihood of women indicating that they believed they were fertile (2.09 ± 0.93, $p = 0.025$; Figure 5.8a). Further, Conception Probability was a significant predictor (29.4 ± 10.8, $p = 0.007$); as discussed, while participants were not generally able to accurately pinpoint their fertile window, they often included fertile days within their claimed fertile window. The distribution of "yes" beliefs was bimodal, with a high proportion of "yes" responses on both days with the highest conception probability and on the days with zero conception probability (Figure 5.8b). Finally, the interaction of Happiness and Probability was significant (-3.46 ± 1.34, $p = 0.011$); at higher Conception Probability, higher levels of Happiness were associated with a lower likelihood of indicating a Belief that they were fertile (Figure 5.8b).

Table 5.9. Generalized linear mixed model results for Sexual Desire.

P-values are two-tailed at a 0.05 significance level and were adjusted for multiple comparisons (Bonferroni) (n=25 subjects with repeated measures). (df1 = variation between groups, df2 = variation within groups, F = F-statistic, *p* = p-value, EMM = estimated marginal means, SE = standard error)

Type III Tests	df1	df2	F	p
Corrected Model	6	231	9.27	<0.001
Belief	1	231	1.22	0.270
Happiness	1	231	15.84	<0.001
Probability	1	231	0.39	0.532
Belief * Happiness	1	231	0.18	0.673
Belief * Probability	1	231	2.06	0.152
Happiness * Probability	1	231	0.12	0.730

Estimates of Fixed Effects	Coeff	±	SE	*p*
Intercept: Desire(1)	3.20	±	1.39	0.023
Intercept: Desire(2)	4.53	±	1.41	0.001
Intercept: Desire(3)	6.45	±	1.44	<0.001
Intercept: Desire(4)	9.58	±	1.51	<0.001
Intercept: Desire(5)	12.24	±	1.67	<0.001
Belief(Yes)	1.48	±	1.34	0.270
Happiness	0.52	±	0.20	0.010
Probability	0.22	±	5.25	0.967
Happiness * Belief(Yes)	0.09	±	0.20	0.673
Probability * Belief(Yes)	5.14	±	3.58	0.152

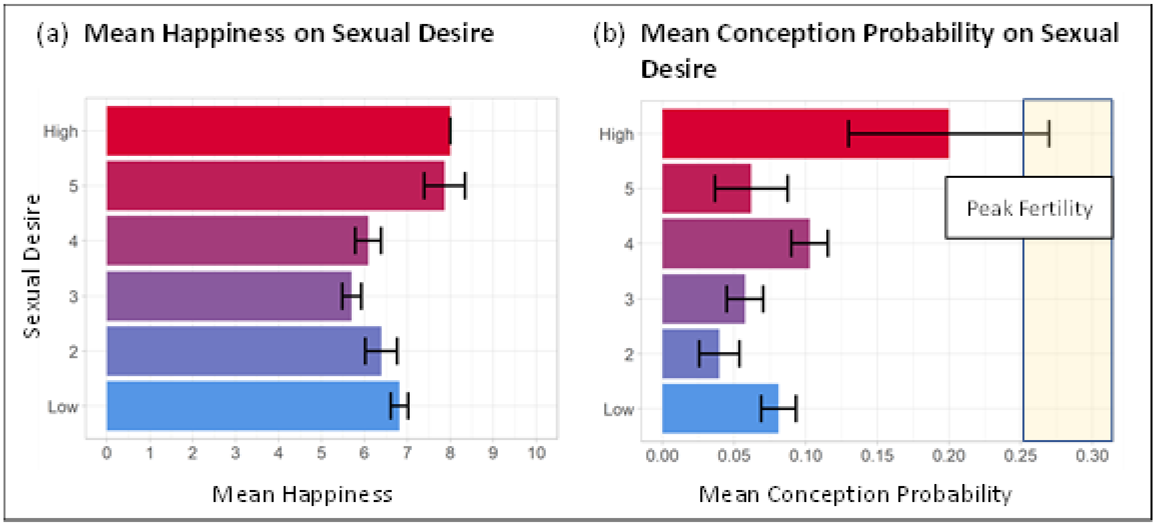


Figure 5.4. The relationships between Sexual Desire and (a) Happiness and (b) Conception Probability at each level of sexual desire.

Black bars denote standard errors.

(a) Higher Happiness was associated with increased Desire, though to only a marginal effect (0.26 ± 0.09, $p < 0.001$).

(b) There was no effect of Conception Probability on Desire ($p = 0.305$).

Table 5.10. Generalized linear mixed model results for Sexual Response.

P-values are two-tailed at a 0.05 significance level and were adjusted for multiple comparisons (Bonferroni). Sexual Desire was the only significant predictor of Sexual Response. (n=25 subjects with repeated measures, response of "Avoid" used as reference) (df1 = variation between groups, df2 = variation within groups, F = F-statistic, *p* = p-value, Coeff =coefficient, SE = standard error)

Type III Tests

	df1	df2	F	*p*
Corrected Model	20	219	2.38	0.001
Belief	2	219	1.13	0.324
Desire	2	219	3.45	0.033
Happiness	2	219	1.18	0.308
Probability	2	219	0.21	0.807
Belief * Desire	2	219	0.55	0.576
Belief * Happiness	2	219	0.60	0.548
Belief * Probability	2	219	0.17	0.845
Desire * Happiness	2	219	0.94	0.391
Desire * Probability	2	219	0.65	0.524
Happiness * Probability	2	219	1.09	0.339

Estimates of Fixed Effects

		Coeff	±	SE	*p*
Seek	Intercept	-40.34	±	28.74	0.162
	Belief(Yes)	-9.32	±	15.47	0.548
	Desire	9.39	±	7.24	0.196
	Happiness	3.41	±	2.97	0.253
	Probability	-39.25	±	69.23	0.571
	Desire * Belief(Yes)	2.74	±	3.66	0.455
	Happiness * Belief(Yes)	-0.16	±	1.28	0.902
	Probability * Belief(Yes)	2.23	±	29.22	0.939
	Desire * Happiness	-0.76	±	0.73	0.297
	Desire * Probability	8.83	±	13.36	0.509
	Happiness * Probability	1.13	±	5.06	0.824
Acquiesce	Intercept	-9.41	±	5.51	0.089
	Belief(Yes)	-6.05	±	4.08	0.139
	Desire	3.87	±	1.80	0.032
	Happiness	0.70	±	0.79	0.377
	Probability	-22.33	±	40.09	0.578
	Desire * Belief(Yes)	0.73	±	0.85	0.394
	Happiness * Belief(Yes)	0.51	±	0.50	0.312
	Probability * Belief(Yes)	8.44	±	14.97	0.573
	Desire * Happiness	-0.28	±	0.24	0.245
	Desire * Probability	11.19	±	9.90	0.260
	Happiness * Probability	-3.54	±	3.04	0.246

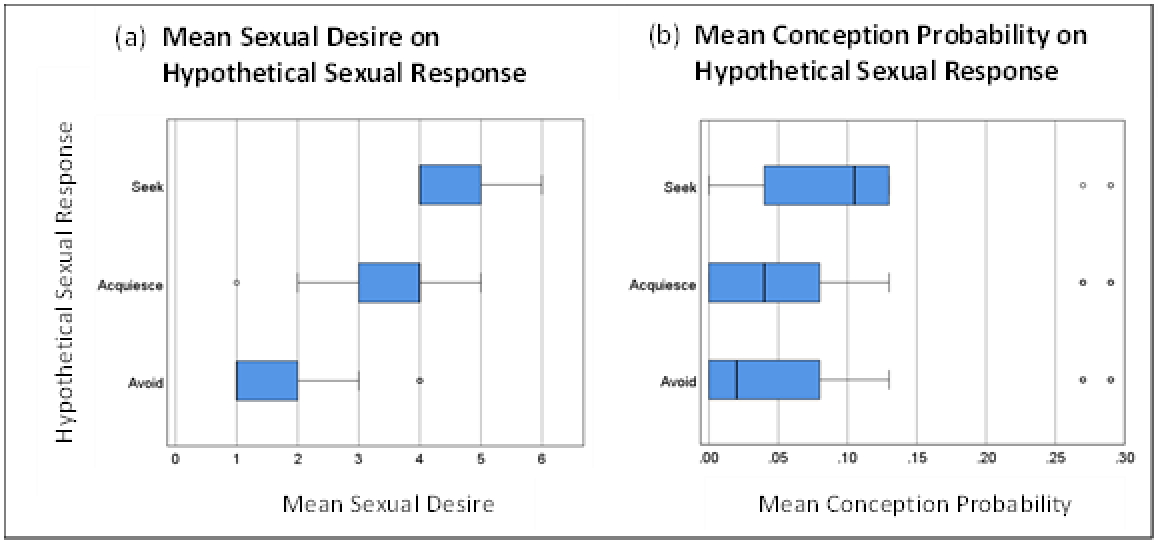


Figure 5.5. Boxplots illustrating the effects of Sexual Desire and Conception Probability on each of the three options for Sexual Response: Avoid Sex, Acquiesce to Sex, and Seek Sex.

(a) Desire was a significant predictor of Response ($p < 0.033$), and specifically with regards to being willing to acquiesce to sex (3.87 ± 1.80, $p = 0.032$).

(b) There was no significant relationship between Conception Probability and Response ($p = 0.807$)

Table 5.11. Participant belief accuracy.

Accuracy included measures with regards to both targeting the fertile window within their menstrual cycles and to capturing the actual fertile window within their claimed window. Participants were unable to target their fertile window, estimating that they were fertile approximately 17 days out of their cycle, an average of 64% of the time. This was significantly different from the amount of time they actually spent fertile, only approximately 21% of the time ($p < 0.001$). However, they often captured fertile days within this window with an average of 64% of the window (SD = standard deviation, p = p-value).

Participant Fertile Belief Accuracy

	Claimed	Actual	
	Mean ± SD (Median)	Mean ± SD (Median)	*p*
Within Menstrual Cycle			
Number of Days Fertile	16.64 ± 8.26 (18.5)	6	<0.001
As Proportion of Participant's Cycle	0.64 ± 0.31 (0.72)	0.21 ± 0.03 (0.21)	<0.001
Proportion of Actual Fertile Days Claimed	0.21 ± 0.15 (0.24)	1.00	<0.001
Within Fertile Window			
Number of Days Fertile	3.86 ± 2.57 (5.5)	6	<0.001
Proportion of Actual Fertile Days Claimed	0.64 ± 0.43 (0.92)	1.00	<0.001

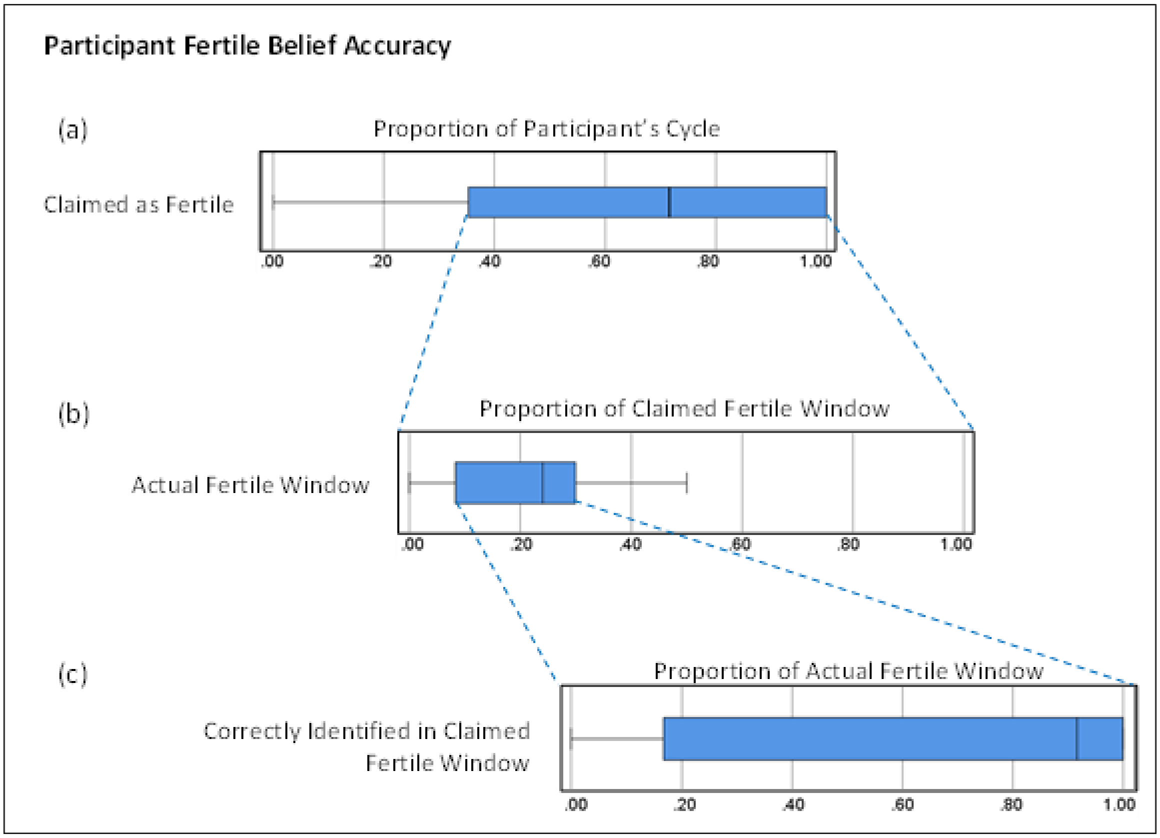


Figure 5.6. Boxplots of the relationships between the days that participants believed they were fertile and both their entire menstrual cycles and the actual fertile window.

(a) Most participants believed they were fertile for most of their cycles, with 75% of participants believing they were fertile for approximately 35% of their cycle.

(b) Approximately 25% of this claimed fertile window was a confirmed fertile day, with actual fertility occurring no more than half of this window.

(c) Participants varied a great deal in their ability to capture the actual fertile window within their claimed window, though most were able to capture most of the window within their claimed window.

Table 5.12. Generalized linear mixed model results for Fertile Belief.

Sexual Desire, Conception Probability, and the interaction of Happiness and Conception Probability all significantly predict Fertility Belief. P-values are two-tailed at a 0.05 significance level and were adjusted for multiple comparisons (Bonferroni) (n=25 subjects with repeated measures). (df = degrees of freedom, df1 = variation between groups, df2 = variation within groups, F = F-statistic, *p* = p-value, Coeff =coefficient, SE = standard error)

Type III Tests

	df1	df2	F	*p*
Corrected Model	6	235	4.15	0.001
Desire	1	235	5.10	0.025
Happiness	1	235	2.99	0.085
Probability	1	235	7.40	0.007
Desire * Probability	1	235	2.43	0.121
Happiness * Probability	1	235	6.62	0.011
Desire * Happiness	1	235	0.52	0.471

Estimates of Fixed Effects

	Coeff	±	SE	*p*
Intercept	-6.64	±	2.75	0.016
Desire	2.09	±	0.93	0.025
Happiness	0.68	±	0.39	0.085
Probability	29.40	±	10.80	0.007
Desire * Probability	-2.85	±	1.83	0.121
Happiness * Probability	-3.46	±	1.34	0.011
Desire * Happiness	-0.09	±	0.13	0.471

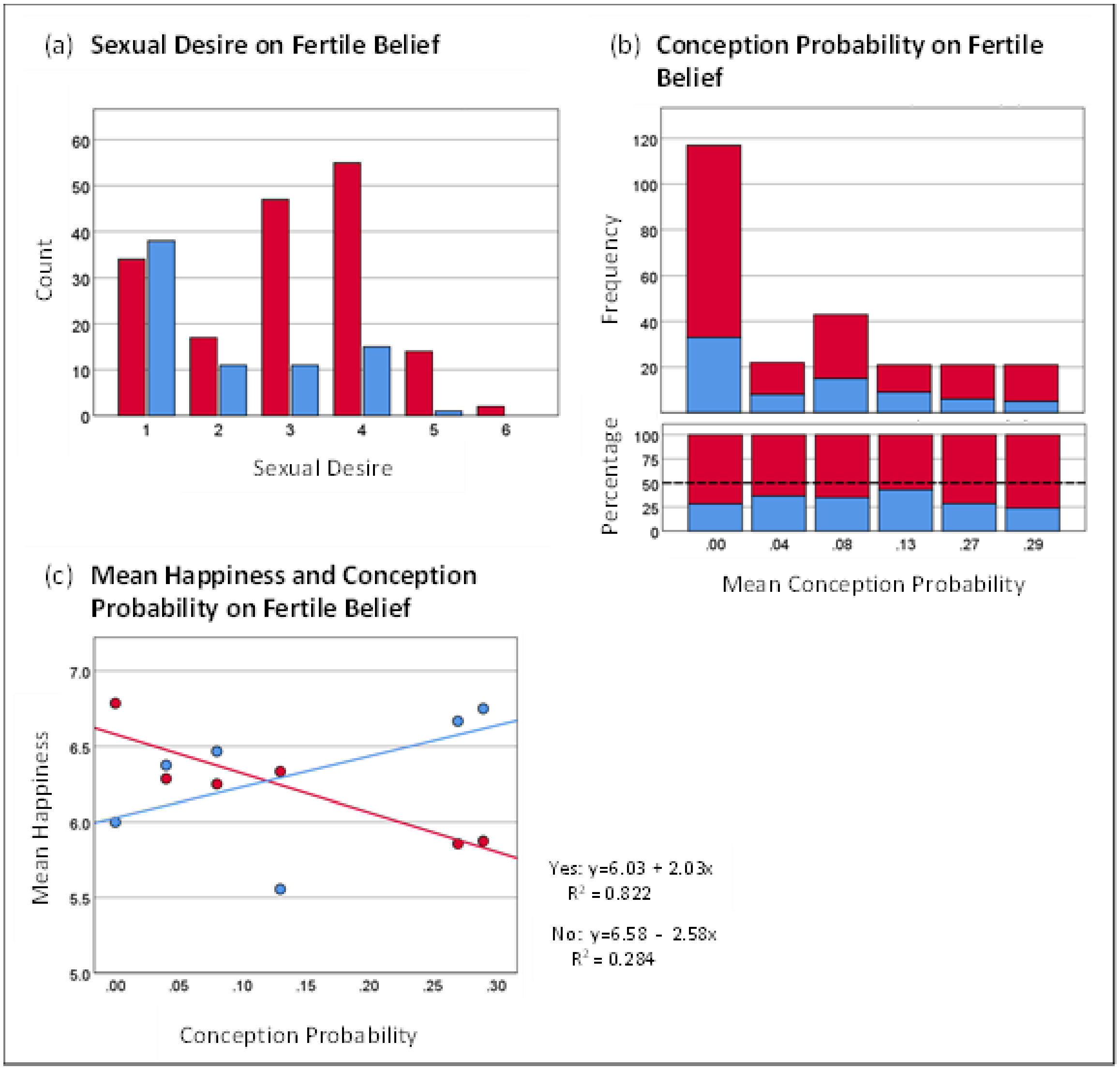


Figure 5.7. The relationship between Fertile Belief and Sexual Desire, Conception Probability, and the interaction between Happiness and Probability.

(a) Desire was positively and significantly associated with Fertile Belief (2.09 ± 0.93, p = 0.025).

(b) High conception probability was associated with participants believing they were fertile (29.4 ± 10.8, p = 0.007), though they also believed they were fertile more often than not, with more "Yes" responses being associated with both zero conception probability and the highest conception probabilities (0.27 and 0.29).

(c) At higher levels of Conception Probability, higher levels of Happiness were associated with a lower likelihood of indicating a Belief that they were fertile (-3.46 ± 1.34, p = 0.011).

5.4.6 Exploration of Methods of Determination

The informal exploration of the various methods of fertility determination revealed some potential avenues of future exploration. The results of each estimated method's accuracy in capturing the fertile window can be found in Table 5.14. There was no significant difference in their accuracy ($p = 0.968$); most methods captured an average of half of the actual fertile days and all had high degrees of variability.

Correlations between fertility and each of the response variables – Sexual Desire, Sexual Response, and Fertile Belief – can be found in Table 5.15. In general, the use of estimated methods resulted in correlations that indicated a significant relationship between fertility and the variables of interest more often than the hormonal methods did. The correlations were not particularly strong – most were between 0.1 and 0.2 – but the p-values were often highly significant.

Some notable trends emerged. Several methods seemed to result in significant findings more often than others, including the +Variable method, the Wilcox method, and both of the backwards counting methods. Further, highly significant correlations appeared more often when using the L8 and the "non-fertile" comparison window methods compared to the LM and the L3. Indeed, the only hormonal method that resulted in a positive association with any of the variables (Desire) occurred when using the NF8 method. Another notable trend relates to the pattern of significance between the three response variables. Significance, and high significance, occurred most often with Desire (89% at $p<0.05$, and 64% at $p<0.001$), followed by Response ($p<0.05$ – 78% , $p<0.001$ – 17%) and Belief ($p<0.05$ – 69%, $p<0.001$ – 50%); notably, p-values less than 0.001 occurred in only 17% of Response tests compared to 47% of Belief tests. Finally, the strengths of the significant correlations differ between the three variables: Response results tended to be weaker and Belief results stronger.

5.5 DISCUSSION

5.5.1 Preliminary Analysis: Within-Study Changes in Belief

We asked participants to complete surveys regarding their knowledge of the menstrual cycle, and their confidence in that knowledge, both before and after the study in order to determine if the study itself had an impact on participant beliefs. Little changed between the surveys. Before the study, participants reported high confidence in their knowledge of the menstrual cycle, and they reported, with reasonable accuracy given the information currently and widely available, the average cycle length, menses length, and date of ovulation for menstrual cycles. There was no significant difference in these answers between studies, nor were there any changes with regards to peak fertility or most of the involved hormones. It is possible that participant responses could have been influenced by the collection of urine for only 10 days. However, a visual inspection of the raw results for a pattern indicative of this reveals no trend that would indicate a shift that would occur in response to urine collection.

Table 5.13. Accuracy of fertility estimation methods.

No method was significantly more accurate than the others, as all had high degrees of variability. (+14 = 14 forward-counting method, +Var = variable forward-counting method, -13 = 13 backwards-counting method, -15 = 15 backwards-counting method, Jöchle = Jöchle actuarial method, Wilcox = Wilcox actuarial method, N = sample size, SD = standard deviation, df = degrees of freedom, F = F-statistic, *p* = p-value)

Accuracy

Method	N	Mean	SD
+14	22	51.6%	37.5%
+Var	22	53.4%	43.3%
-13	22	50.4%	39.9%
-15	22	60.2%	41.7%
Jöchle	22	51.8%	37.0%
Wilcox	22	50.8%	40.4%
Total	*132*	*53.0%*	*39.4%*

ANOVA Table

	Sum of Squares	df	Mean Square	F	*p*
Method					
Between Groups	30.833	11	2.803	0.950	0.496
Within Groups	354.167	120	2.951		
Total	385.000	131			

Table 5.14. The effects of various methods of phase of cycle classification on Sexual Desire, Sexual Response, and Fertile Belief.

Only one method of the hormonal comparisons (NF8) resulted in a significant relationship with any of the variables (Desire). In contrast, most of the estimated methods resulted in a significant relationship, especially with regards to Desire. Moreover, these relationships were often highly significant. Methods utilizing "non-fertile" and L8 comparisons and the +Var, -13, -15, and Wil fertility estimates tended to result in significant findings more than the other methods. (Horm = hormonal, +14 = 14 forward-counting method, +Var = variable forward-counting method, -13 = 13 backwards-counting method, -15 = 15 backwards-counting method, Joch = Jöchle actuarial method, Wil = Wilcox actuarial method, LM = luteal mid-point method, L3 = luteal plus 3 method, L8 = luteal plus 8 method, NF = non-fertile method, NF4 = non-fertile 4-day buffer method, NF8 = non-fertile 8-day buffer method)

Correlation Coefficients

Comparison Window Method				Horm	+14	+Var	-13	-15	Joch	Wil
Luteal		LM	Desire	0.08	0.10 *	0.19 ***	0.15 **	0.17 ***	0.08	0.15 **
			Response	0.07	0.07	0.13 **	0.13 **	0.14 **	0.04	0.12 *
			Belief	0.01	0.07	0.15 **	0.03	0.10 *	0.00	0.11 *
		L3	Desire	0.05	0.08	0.16 ***	0.15 **	0.14 **	0.04	0.12 *
			Response	0.04	0.08	0.11 *	0.13 **	0.11 *	0.03	0.10 *
			Belief	0.00	0.04	0.15 **	0.03	0.06	-0.10 *	0.08
		L8	Desire	0.07	0.14 **	0.22 ***	0.19 ***	0.18 ***	0.11 *	0.18 ***
			Response	0.08	0.08	0.12 *	0.16 **	0.16 ***	0.05	0.09
			Belief	0.07	0.16 ***	0.23 ***	0.15 **	0.16 ***	0.06	0.20 ***
Non-Fertile		NF	Desire	0.04	0.10 ***	0.13 ***	0.10 ***	0.11 ***	0.10 **	0.11 ***
			Response	0.04	0.07 *	0.07 *	0.08 **	0.09 **	0.06 *	0.07 *
			Belief	0.06	0.10 ***	0.17 ***	0.09 **	0.13 ***	0.04	0.12 ***
		NF4	Desire	0.07	0.13 ***	0.16 ***	0.12 ***	0.13 ***	0.12 ***	0.14 ***
			Response	0.07	0.09 **	0.10 **	0.10 **	0.11 ***	0.08 **	0.10 **
			Belief	0.06	0.13 ***	0.20 ***	0.11 ***	0.15 ***	0.05	0.16 ***
		NF8	Desire	0.10 *	0.16 ***	0.19 ***	0.15 ***	0.16 ***	0.14 ***	0.17 ***
			Response	0.09	0.12 ***	0.12 ***	0.12 ***	0.14 ***	0.09 *	0.12
			Belief	0.08	0.17 ***	0.24 ***	0.14 ***	0.18 ***	0.07	0.19 ***

p *<0.05, **<0.01, ***<0.001

Still, there were some differences in the surveys. The only overall across-the-study difference was a *decrease* in the number of participants who identified progesterone as being involved, an effect driven by 3 participants who indicated that they had sought new information during the study, to varying degrees ("not really" and "a little bit"). Further, participants who responded "yes" were more likely to believe peak fertility included after menses and the end of cycle. These shifts seem to indicate that those who sought more information during the study may have received poor information, as they were less likely to identify progesterone as an involved hormone and more likely to include non-middle-of-the-cycle phases in their assessment of peak fertility.

Further, differences in participant responses who did not seek more information potentially indicates an effect of the study on beliefs regarding the menstrual cycle. After the study, these participants were more likely to indicate peak fertility occurs mid-cycle and less likely to indicate both the end of cycle as well as the "all points equal" option. Thus, for these participants, participation in the study may have led to more accurate beliefs regarding peak fertility, a potential effect of the study design and the collection of urine for only 10 days post-menses. However, any effect of this was likely minimal for, as mentioned, the raw results showed no pattern suggestive of this. Further, any effect that this shift in beliefs may have had on the sexuality-related predictions would have been controlled for by including each day's fertile beliefs in the models. Finally, the results of Prediction 2 suggest that, even though participants may have become more likely to think that fertility was mid-cycle, they were still unable to predict when they themselves were fertile.

5.5.2 Prediction 1: Fertility and Sexuality

To test for an association between fertility and sexuality, I predicted that fertility would correspond with both sexual desire and sexual response, even after controlling for fertile belief and happiness. The results indicate no such relationship; instead, they indicate that happiness drives sexual desire, and sexual desire drives sexual response, independent of fertility.

While significant, the impact of happiness on sexual desire was small. This may have been due to the structure of the data; Figure 5.5a seems to indicate a bimodal effect, with sexual desire increasing in response to both high and low happiness. A bimodal result could reflect an authentic pattern, but it may also reflect a flaw in the study design; my scale for happiness was unintuitively reversed, with high happiness being "low" on the bar and vice versa. This could have resulted in a fairly high degree of error, though I hope that this would have diminished with usage. Still, the possibility must be considered.

The effect of sexual response was only found for those who indicated they might acquiesce to sex, as opposed to those who might seek it. This seems likely due to the relatively few responses that indicated an interest in seeking sex, as Figure 5.6a seems to suggest. A longer study with more participants might increase the ability to detect any effect.

5.5.3 Prediction 2: Fertility and Belief

I predicted that women would not be able to accurately report when they were fertile, and this prediction was supported. Participants showed no ability to target their fertile window, with most participants believing they could get pregnant throughout most of their cycles. This inevitably resulted in many of them being able to capture the fertile window within their believed window, but this was not consistent, and most of the participants did not capture all six days.

Still, conception probability was a significant predictor of fertile belief model. This seems an artifact of the prior knowledge that the participants have regarding their fertility, with most participants knowing that fertility is highest in the middle of the cycle. This would be expected to bias their beliefs and increase the likelihood of capturing the point of highest fertility in their claimed fertile window, even if they could not track it across the cycle accurately.

Importantly, while neither conception probability nor fertile belief influenced sexual desire, sexual desire did influence fertile belief. This has significant implications, as it reflects the results of early research into fertility-mediated sexuality. Those studies indicated that a woman's sexuality was not influenced by her fertility but was instead influenced by her *beliefs* about her fertility. An effect of participant beliefs is difficult to control for by simply blinding participants to either the nature of the study or to the phase of the menstrual cycle of interest, as is common in more recent studies. That is because this does not control for the beliefs that participants already have about their cycles and that they carry with them each day. Even if a researcher were to design a study that perfectly blinds the participant to the true nature of the investigation, it would not remove the beliefs that already exist. Thus, researchers should control for beliefs directly by explicitly asking participants about their beliefs and incorporating those beliefs in their analyses and conclusions.

Finally, this analysis identified a significant, negative interaction between happiness and conception probability as a predictor of fertile belief. This finding suggests either that increased happiness *decreased* a woman's likelihood of believing she was fertile, or that increased happiness was the *result* of a woman falsely believing she was not fertile. This finding has unclear implications, and may represent a purely chance finding. However, given the aforementioned relationships between happiness and sexual desire, and between sexual desire and fertile belief, this may also reflect an underlying pattern involving these factors that intersects with fertility. Specifically, it may be that happiness increases desire which in turn increase belief throughout the cycle *except* for when a woman is fertile; at that point, one or both of these relationships reverse, resulting in an inverted relationship at peak fertility. If this is the case, this may be evidence of a mechanism that aids in the maintenance of self-concealed ovulation in humans. This mechanism primarily acts, not to conceal fertility from others, but to conceal fertility from the individual who gains fitness benefits by mating outside of fertility. Indeed, if a woman could come to accurately associate increased sexual desire with fertility, then a range of possible behaviors might emerge, including avoiding sex at peak fertility as a contraceptive measure. However, this explanation is merely hypothetical, and a great deal of exploration is needed on this before any conclusions can be drawn.

5.5.4 Exploration of Methods of Determination

My final analyses involved exploring the effect that using estimated methods of fertility determination and different types of comparison windows would have on the results. My intention with these analyses was to identify potential avenues of exploration for future studies and not to conduct rigorous statistical analysis.

While none of the methods of fertility determination were statistically more accurate than another, when used to test for a relationship between sexuality and fertility, some methods seemed to result in significant findings, and often highly significant findings, more often than others (fertility: +Variable, -13, -15, and Wilcox; comparison: L8, and all of the non-fertile methods). This seems to suggest that there may be something unique about these methods that might be driving this association, and given the relationship between sexual desire and fertile belief identified above, it may be that the women themselves are more likely to estimate their own fertile using these methods. That these associations do not always correspond with admitted fertile belief does not necessarily contradict this possibility, as it is a human inclination to be blind to our subconscious beliefs and biases.

It is notable that the use of comparison methods that form the comparison window from the days of the cycle least likely to be associated with fertility – primarily the "non-fertile" methods that specifically exclude the days that surround the estimated fertile window – seem to be more likely to result in highly significant findings. There may be several reasons for this, including the fact that non-fertile methods also include premenstrual and menstrual days which may act to artificially amplify differences between symptoms on fertile and non-fertile days. It may also be that *non-fertile belief* is more important to an identified relationship between fertility and sexuality than either *fertility* or *fertility belief*. Indeed, only one analysis used hormonally-confirmed fertility found a significant relationship (with sexual desire) was the method that created the largest "buffer" around the fertile days as possible, thereby ensuring that only the "least likely to be fertile" days were included in the comparison window (NF8). It is also possible that, at least with regards to the non-fertile methods, the structure of the data might be influencing the result, as they compare a 6-day window of fertility against a window approximately 2-3 its size. However, that the L8 method was also associated with a high likelihood of significant findings make this possibility less likely, or at least less influential.

It is clear that more work is needed to devise reliable and accurate methods of menstrual cycle-related analyses that are reflective of the underlying biology, robust to errors, and considerate of participant beliefs. This work needs to proceed in at least two directions. The first direction is an independent investigation into menstrual cycle-related beliefs as a whole, including the specific beliefs that women might have and their likelihood of manifesting consciously or subconsciously. The second direction is the incorporation of broader "menstrual cycle knowledge and belief assessments" into menstrual cycle-related research as opposed to the inclusion of a simple question on "fertile belief." Doing this might allow for the identification of a more complex belief structure that might be informing reported results. For example, asking participants to estimate ovulation given different cycle lengths or to predict their expected symptoms at different stages of the cycle might allow for not only an identification of when they believe they are fertile, but how they are estimating that belief and what they believe would happen when they are fertile. These data could then be incorporated into their reported menstrual-cycle related shifts to determine the degree to which any shifts are associated with their beliefs.

5.5.5 General Conclusions

The results of this study suggest that the previously-reported relationship between sexuality and fertility may not be due to the physiology of the menstrual cycle but instead be due to the preexisting beliefs of the research participants. Women do not leave their beliefs at the door of a research lab, and these beliefs – influenced by culture, socioeconomic status, education, and access to medical care – act to shape each woman's decisions and behaviors, not the least of which includes decisions about her health and sexual behavior. Thus, research exploring menstrual cycle-related shifts in attitudes and behaviors need to incorporate the beliefs of the participants, or it will be inadequate to detect any actual effect of fertility.

Further, this area of research is predicated upon assumptions about the menstrual cycle that may not be valid. It assumes that, even though signs of fertility are concealed, fertility-mediated peaks in sexual behavior is likely adaptive. However, concealed ovulation is a primate-specific adaptation that allows for extended sexual receptivity, and it can thus be safely assumed that sexual behavior outside of fertility carries fitness benefits. While the specific benefits have been debated for at least the past 40 years (e.g., infanticide prevention, Hrdy 1979; incentivizes male-investment, Symons 1979; allows for extra-pair copulation, Benshoof and Thornhill 1979; see also Sillén-Tullberg and Møller 1993), and there is no doubt that it serves a crucial social function in primates (Wallen and Zehr 2004), it is entirely possible that the fitness benefits of non-fertile sexual behavior have reduced or erased fertility-associated peaks in sexual behavior in humans.

Indeed, it may even be that humans demonstrate *progesterone*-associated peaks in sexual behavior. It has been proposed that extended sexual receptivity in humans plays a crucial role in pregnancy maintenance by allowing the mother to use paternal semen as an antigen for immunoregulation (Robillard et al. 2008). The importance of adequate maternal-fetal immunoregulation is manifest in the evolution of the menstrual cycle itself, which seems to have emerged in specific mammalian lineages as an adaptive response to the demands of increased fetal cognitive growth and the degree of associated maternal-fetal immunoregulation (Emera et al. 2012, Brosens et al. 2014, Macklon and Brosens 2014, Alvergne and Tabor 2018 [review], Thomas 2019). These demands – and the degree of fetal-uterine implantation – are higher in humans than any other species, and regular exposure to paternal semen seems to be a crucial component in the mother's ability to maintain pregnancy (Robertson and Sharkey 2001, Robertson et al. 2003, Dekker and Robillard 2005, Robertson et al. 2013, Martinez-Varea et al. 2014). Poor immunoregulation is proposed to be the primary cause of preeclampsia, one of the leading causes of maternal deaths globally (Khan et al. 2006, Abalos et al. 2013). Indeed, a mother's exposure to paternal semen is a strong predictor of the likelihood of developing preeclampsia (Smith et al. 1997, Kho et al. 2009, Saftlas et al. 2013, Triche et al. 2014).

It is therefore possible that the shifts in sexual behavior associated with increased estrogen might not only disappear in species with concealed ovulation but might also become affiliated with progesterone if sexual behavior during pregnancy – when progesterone is the dominant hormone – becomes adaptive. Also, given that progesterone is dominant during the luteal phase, we might find shifts in sexual behavior during that phase as a byproduct of the adaptive benefits of these behaviors during pregnancy. Exploring this possibility might be a fruitful avenue of research.

In conclusion, it is clear that an expanded view of human sexual behavior that incorporates a wider understanding of human reproductive ecology is needed. This view should incorporate our knowledge of obstetric medicine, primate evolution, and human behavior, and would provide a more comprehensive and nuanced understanding of human reproductive behavior.

CHAPTER 6. CONCLUSION

Humans have been no exception to the evolutionary forces that have shaped all life on earth. The ability for symbolic cognition that emerged within the last 100,000 years cannot erase the millions that have influenced reproductive dynamics. Thus we find that the history of human evolution has left its imprints on modern human mating behavior, with the effects of parental care and inter- and intrasexual competition appearing in our mating behavior in ways that are consistent across time and culture.

Efforts to understand human behavior decoupled from the forces of evolution will only delay our ability to implement procedures, practices, and interventions that can improve our lives. Our evolved cognitive abilities that have been integral to human evolution and that allow for the complexities of human society can be used to shape that society. Identifying the biosocial developmental factors that influence the emergence of harmful behaviors and their adaptive significance for those individuals is a crucial step to prevention and mediation. Each of the scientific disciplines that have formed out of a need to understand the human condition holds keys to understanding our behavior, and it is only when we integrate the findings from each field within an evolutionary context that we gain the most accurate understanding of who we are and who we can become.

As we proceed with this work, we must do so with humble caution and challenge our assumptions at each step. Many of the hypotheses and avenues of investigation that have dominated research in human reproductive behavior have relied on unfounded assumptions – for example, that a nuclear family is representative of human society, that female ornamentation must be for the male gaze, or that male attraction to the female body means the female body evolved for that attraction. These assumptions are understandable given the lived experiences of the researchers – usually Western white males – but they must be discarded when unsupported by evidence. I hope that the conclusions drawn from this work will be used as a foundation to begin new investigations into aspects of the human condition previously unexplored.

This work – to both integrate a foundation of evolutionary biology into research and to challenge our biases and preconceptions – must not remain within the scientific community. It must extend into the public domain. The commonly-held beliefs that "biological" means "inevitable" and that "evolved" means "sanctioned" are fallacies that will impede this work, for even those who recognize the speciousness of these conclusions will resist their integration so long as they fear how some use it to further their own agendas. Scientists must engage in science communication and public policy work and use their expertise to address these misconceptions. Otherwise, we will continue to face resistance to funding for research, education, and public health, and our efforts to prevent harmful behavior will continue to be impeded.

APPENDICES

APPENDIX A: CHAPTER 3.1. DERIVATION, ALGEBRAIC RELATIONSHIPS, AND PROOFS

A.1. Female Mate Choice

We assume that all females have identical characteristics but may choose between two main categories of males. These are type 1, generally devoting a substantial amount of time t_1 to reproductive success ($0 < t_1 \leq t_f$, where t_f is the reproductive time spent by a fertilized female) and resulting in reproductive payoff for the pair of r_1 when the female is successfully fertilized; and type 2, generally devoting less time t_2 to reproductive success than type 1 ($0 < t_2 \leq t_1$) and typically resulting in lower reproductive payoff r_2 for the pair following successful fertilization ($r_2 \leq r_1$).

Females can devote time t_d to evaluating a male drawn randomly from the male pool; she successfully identifies his type with probability $d(t_d)$. This discrimination is conducted with diminishing returns following the exponential function $d(t_d) = 1 - e^{Dt_d}$, with D the exponential rate constant in units of 1/time. Let m_i be the chance that the female pairs with a male of type i encountered in the male pool. Here, pairing implies mating and a commitment of time t_i to support reproduction. We set $m_i = dc_i + (1\text{-}d)c_0$, where c_i is the chance that type i is chosen for pairing if successfully categorized by the female, and c_0 is the chance an individual of an undiscriminated type is chosen for pairing.

Let b_i be the chance that the pair involving a type i male breaks up after reproduction; then $1 - b_i$ is the probability of pair fidelity, the chance that the pairing is maintained through the next reproductive cycle. Then the expected number of reproductive cycles before break-up is $\sum_{j=0}^{\infty}(1 - b_i)^j = 1/b_i$, and the number of reproductive cycles beyond the first in a sequence is $1/b_i - 1 = (1\text{-}b_i)/b_i$. Let t_n be the time following reproduction that a female is temporarily infertile regardless of receptivity to mating (e.g. the time not in estrus for mammals). Let γ_i be the chance of fertilization and subsequent reproduction of a female pairing with a type i male. Then a male that pairs only once (or for the last time) with a female expects to invest time $\gamma_i t_i$ in reproduction (i.e. time t_i if the mating results in fertilization but zero time otherwise), and a male remaining with a female for additional reproductive cycles invests $\gamma_i t_f + t_n$ time in each cycle before the last (i.e. the same time as the female). This means that a male evaluated by a female leaves the male pool for expected time $T_i = t_d + m_i\gamma_i t_i + m_i(\gamma_i t_f + t_n)(1 - b_i)/b_i$. Males remain unselected in the male pool for time τ.

Let f_i be the fraction of all males *in the population* that are type i, and let p_i be the fraction of males *in the male pool* that are type i. Then with types 1 and 2 present, it follows that

$$p_1 = \frac{f_1\tau_{12}/(\tau_{12}+T_1)}{f_1\tau_{12}/(\tau_{12}+T_1)+f_2\tau_{12}/(\tau_{12}+T_2)} = \frac{f_1(\tau_{12}+T_2)}{f_1(\tau_{12}+T_2)+f_2(\tau_{12}+T_1)}, \text{ and } p_2 = 1\text{-}p_1.$$

There are n_m males and n_f females in the population and thus a population sex ratio $\sigma = n_m/n_f$. Let σ_0 be the sex ratio at maturation, and let λ_f and λ_i be the reproductively active lifetime of an individual female or type-i male. Then

$$\sigma = \sigma_0 \frac{\sum_{j=1}^{k} \lambda_j f_j}{\lambda_f}$$

with k male types in the population. With males types 1 and 2 in the population, the number of males in the pool is then

$$P = \frac{n_m f_1 \tau_{12}}{\tau_{12}+T_1} + \frac{n_m f_2 \tau_{12}}{\tau_{12}+T_2}.$$

Let ε be the expected time between visits to the male pool by a particular female. Then some female is expected to arrive at the pool after every interval of ε/n_f. A male in the pool has a probability $1/P$ of being selected when a female arrives. This means the expected number of arrivals until he is picked is $\sum_{j=0}^{\infty}(1-1/P)^j = P$. The expected total time the male waits to be picked in a pool containing male types 1 and 2 is then $\tau_{12} = P\varepsilon/n_f$. Thus

$$\tau_{12} = \left(\frac{f_1\tau_{12}}{\tau_{12}+T_1} + \frac{f_2\tau_{12}}{\tau_{12}+T_2}\right)\varepsilon\sigma.$$

Rearranging then yields

$$\varepsilon = \frac{(\tau_{12}+T_1)(\tau_{12}+T_2)}{\sigma(f_1T_2+f_2T_1+\tau_{12})}.$$

The time a female commits to each pairing with a type i male is

$$\theta_i = \left[\gamma_i t_f + t_n\right]/b_i.$$

We assume that the female always commits at least one reproductive cycle to a type 1 or type 2 male she pairs with even without successful fertilization, and thus $\theta_i \geq t_n$. With only a single male type i in the population, this implies that each male expects to wait in the male pool for time

$$\tau_i = \sigma\theta_i - T_i.$$

This is the expected number of female reproductive cycles per male, less the time he expects to spend out of the male pool during that interval.

Now another way to express the interval between visits to the male pool by a female is

$$\varepsilon = p_1 m_1 \theta_1 + p_2 m_2 \theta_2 + t_d = \frac{f_1(T_2+\tau_{12})(m_1\theta_1+t_d)+f_2(T_1+\tau_{12})(m_2\theta_2+t_d)}{f_1T_2+f_2T_1+\tau_{12}}.$$

Equating the two expressions for ε and rearranging then yields

$$\tau_{12}^2 + [T_1 + T_2 - \sigma(f_1m_1\theta_1 + f_2m_2\theta_2 + t_d)]\tau_{12} + \left[T_1T_2 - \sigma\left(f_1T_2(m_1\theta_1 + t_d) + f_2T_1(m_2\theta_2 + t_d)\right)\right] = 0,$$

solved for τ_{12} via the quadratic formula. (There is a single solution that yields a biologically relevant non-negative result.)

The output from a successful reproductive pairing with a type *i* male is r_i. Female fitness F_f is the expected rate of female reproduction R_f multiplied by her expected reproductive lifetime λ_f. R_f is the reproductive success from a visit to the male pool by a female, divided by the expected time commitment associated with this visit. Thus

$$F_f = R_f\lambda_f = \frac{\lambda_f(p_1m_1\gamma_1r_1/b_1+p_2m_2\gamma_2r_2/b_2)}{p_1m_1\theta_1+p_2m_2\theta_2+t_d}.$$

She chooses $d(t_d)$, c_0, c_1, and c_2 to maximize her fitness. With $r_1 > r_2$, $c_1 = 1$ and $c_2 = 0$. The probability c_0 of mating with an undiscriminated male must equal 1 as d -> 0; we therefore generally set $c_0 = 1$, though we can let $c_0 = (1-d)^\omega$, where $\omega > 0$, when c_0 decreases with increasing d. (This generally has little effect on the results unless $\omega >> 1$.) For the two male types, expected reproductive success of an individual is

$$F_1 = R_1\lambda_1 = \frac{\lambda_1m_1\gamma_1r_1/b_1}{\tau_{12}+T_1}, \text{ and } F_2 = R_2\lambda_2 = \frac{\lambda_2m_2\gamma_2r_2/b_2}{\tau_{12}+T_2}.$$

Suppose $F_1 > F_2$. Then f_1 will increase until $F_1 = F_2$ or until $f_1 = 1$. An analogous outcome results from $F_2 > F_1$. This logic holds whether types 1 and 2 are probabilistic strategies by single individuals *or* they represent pure strategies of competing individuals. (Technically, this corresponds to the distinction between an evolutionarily stable mixed strategy and an evolutionarily stable state of the male population.)

Putting the fitness terms together, we have that male fitness F_m is

$$F_m = f_1F_1 + f_2F_2.$$

The joint solution for t_d and f_1 (and thus f_2) is evolutionarily stable in the absence of mutant alternative male strategies. Of course $F_f = F_m$, which provides a check on the results.

A.2. Male Coercion

Consider a mutant male (type 3) that mates with any female encountered in the male pool, bypassing the evaluation process. This coercive male has the probability γ_3 of fertilizing and producing offspring with the female, despite a very low or zero time commitment t_3, resulting in a generally low reproductive output ($r_3 \leq r_2$). Because a type 3 male is assumed to mate only once (or in one brief sequence) with the female, she expends the additional non-reproductive time t_n in association with this mating only if fertilized. As a rare mutant, we assume the coercer has to wait time τ_i to encounter a female like the other males, where *i* designates the stable outcome in the absence of the mutant. The fitness of mutant type 3 is then $F_3 = R_3\lambda_3 = \lambda_3\gamma_3r_3/\tau_i$.

In the remainder of this section, we simplify by setting $\sigma_0 = 1$ and $\lambda_f = \lambda_1 = \lambda_2 = \lambda_3$ (and thus the sex ratio $\sigma = 1$), the chance of undiscriminated mating $c_0 = 1$, and the pairing fidelity parameters $b_1 = b_2 = 1$, though $\sigma \neq 1$, $c_0 = c_0(d)$, and the $b_i < 1$ could readily be accommodated. It follows, solving the quadratic equation for τ_i, that the coercer can invade a population of pure type 1 when

$$\frac{\lambda_3\gamma_3 r_3}{\tau_1} > \frac{\lambda_1\gamma_1 r_1}{\tau_1+T_1}, \text{ where } \tau_1 = \gamma_1(t_f - t_1) + t_n, \text{ and thus } \frac{\lambda_3\gamma_3 r_3}{\lambda_1\gamma_1 r_1} > \frac{\gamma_1(t_f-t_1)+t_n}{\gamma_1 t_f+t_n}.$$

The coercer can invade a population of pure type 2 when

$$\frac{\lambda_3\gamma_3 r_3}{\tau_2} > \frac{\lambda_2\gamma_2 r_2}{\tau_2+T_2}, \text{ where } \tau_2 = \gamma_2(t_f - t_2) + t_n, \text{ and thus } \frac{\lambda_3\gamma_3 r_3}{\lambda_2\gamma_2 r_2} > \frac{\gamma_2(t_f-t_2)+t_n}{\gamma_2 t_f+t_n}.$$

(Note: in these cases with a single type of male at the ESS, d and t_d are zero, because discrimination is useless.) And the coercer can invade a stable mixture of types 1 and 2 when

$$\frac{\lambda_3\gamma_3 r_3}{\tau_{12}} > \frac{\lambda_1\gamma_1 r_1}{\tau_{12}+\gamma_1 t_1+t_d},$$

where τ_{12}, the waiting time with a stable mixture of types 1 and 2, is defined as above (here with $b_1 = b_2 = 1$). This inequality expresses the condition for invasibility of the stable mixture; for this mixture, $F_1 = F_2$, and thus the inequality implies higher fitness for the coercer than for types 1 and 2. Once the coercer invades, it may eliminate its competitors, establishing a waiting time of $\tau_3 = \gamma_3(t_f + t_n)$, because each female either returns to the male pool after time $t_f + t_n$ if fertilized or immediately otherwise. Alternatively, the competitor(s) may be able to invade a pure type 3 population. Coercers are invasible by type 1 males when

$$\frac{\lambda_3\gamma_3 r_3}{\tau_3} < \frac{\lambda_1\gamma_1 r_1}{\tau_3+T_1}$$

and by type 2 males when

$$\frac{\lambda_3\gamma_3 r_3}{\tau_3} < \frac{\lambda_2\gamma_2 r_2}{\tau_3+T_2}.$$

Putting these results together, mutual invasibility implies coexistence of types 1 and 3 when

$$1 + \frac{\gamma_1 t_1}{\gamma_3(t_f+t_n)} < \frac{\lambda_1\gamma_1 r_1}{\lambda_3\gamma_3 r_3} < 1 + \frac{\gamma_1 t_1}{\gamma_1(t_f-t_1)+t_n}$$

and coexistence of types 2 and 3 when

$$1 + \frac{\gamma_2 t_2}{\gamma_3(t_f+t_n)} < \frac{\lambda_2\gamma_2 r_2}{\lambda_3\gamma_3 r_3} < 1 + \frac{\gamma_2 t_2}{\gamma_2(t_f-t_2)+t_n}.$$

A.3. Female Resistance and Policing

Female resistance to coercion is assumed to be expressed as reduced magnitudes of the fertilization probability γ3 and of reproductive success given fertilization r3. The γ3 coefficient may be low in part because female resistance reduces the duration or frequency of mating per coercive event. In some species, post-copulatory mechanisms may further reduce the chance of coercive fertilization. The r3 coefficient may be diminished by the lack of time or other resource commitment by the male to coercive reproduction or by damage to the female during coercion.

In some species, coercion may be restricted through social policing. In an unpoliced population with only coercive males, each male expects to obtain

$$n = \frac{\lambda_3}{\tau_3 + T_3}$$

matings in his reproductive lifetime. Now let x be the probability that a coercer is apprehended and prevented from further reproduction after any particular coercive mating. Then his expected number of coercive matings with policing is

$$C = \sum_{i=1}^{n}(1-x)^{i-1} = \sum_{i=0}^{\infty}(1-x)^{i} - \sum_{i=n}^{\infty}(1-x)^{i} = \frac{1}{x} - (1-x)^{n}\sum_{i=0}^{\infty}(1-x)^{i} = \frac{1-(1-x)^{n}}{x},$$

where $x > 0$. (As x approaches 0, the limit is found from L'Hopital's Rule:

$$\lim_{x\to 0}\frac{1-(1-x)^{n}}{x} = n.)$$

Then type 3 can be invaded by type i when

$$C\gamma_3 r_3 < \frac{\lambda_i \gamma_i r_i}{\tau_3 + T_i}.$$

Now let

$$n = \frac{\lambda_3}{\tau_i + T_3}.$$

Now type 3 can invade stable type i when

$$C\gamma_3 r_3 > \frac{\lambda_i \gamma_i r_i}{\tau_i + T_i}.$$

Because C is less than n in each case, both conditions are less favorable for type 3.

The proportion p_C of n expected to be accomplished despite policing is

$$p_C = \frac{1-(1-x)^{n}}{xn}.$$

We address an example of policing and its implications below.

A.4. Extra-Pair Paternity

To this point, the description of the model has implied serial monogamy. But despite social pairing, there may be extra-pair mating and reproduction between types. Since pairing with type 2 and with type 3 males is typically brief, we restrict these cuckoldry effects to type 1 by types 2 and 3 and type 2 by type 3. Shifting paternity between types does not affect overall reproductive success (i.e., $F_f = F_m$) but does alter the balance of fitnesses among male types and thus their frequencies and chance of persisting.

We include these effects in the model by transforming the fitness magnitudes for males of each type at follows:

$$F_1' = F_1(1 - k_{12}f_2 - k_{13}f_3),$$

$$F_2' = F_2(1 - k_{23}f_3) + k_{12}f_1F_1, \text{ and}$$

$$F_3' = F_3 + k_{13}f_1F_1 + k_{23}f_2F_2.$$

The coefficients k_{ij} express the magnitude of the fitness increment lost by a type i male from reproduction by his mate with a type j male, per unit frequency of type j. The fitness of type 1 males is thus reduced by each of the two extra-pair coefficients for types 2 and 3 multiplied by the corresponding frequencies of the other types. The fitness of type 2 males is reduced by the type 3 coefficient multiplied by the frequency of type 3—and augmented by the type 1 coefficient multiplied by the frequency of type 1 and its fitness. The type 3 fitness is similarly augmented by the fitness increments from types 1 and 2. Note that these fitness redistributions leave total fitness unchanged, since

$$F_f = F_m = f_1F_1' + f_2F_2' + f_3F_3' = f_1F_1 + f_2F_2 + f_3F_3.$$

By influencing male fitness magnitudes, this extra-pair reproduction alters some of the τ values and invasion criteria (see Online Resource 2), shifting the frequencies of male types in the population.

A.5. Fitness Relationships

In each case, F_{xy} is the fitness of male type x in a population of type y; F_{xyz} is the fitness of male type x in a stable combination of types y and z. Females do not discriminate between types except as indicated. The f_i* represent evolutionarily stable frequencies of the male types in mixtures; these magnitudes are given below when discrimination is absent. In a stable mixture of types 1 and 2 when females discriminate, f_1* and f_2* must be determined numerically.

$$F_{11} = \lambda_1\gamma_1(r_1/b_1)/(\tau_1 + T_1)$$

$$F_{12} = \lambda_1(1 - k_{12})\gamma_1(r_1/b_1)/(\tau_2 + T_1)$$

$$F_{13} = \lambda_1(1 - k_{13})\gamma_1(r_1/b_1)/(\tau_3 + T_1)$$

$$F_{21} = \lambda_2\gamma_2(r_2/b_2)/(\tau_1 + T_2) + k_{12}F_{11}$$

$$F_{22} = \lambda_2\gamma_2(r_2/b_2)/(\tau_2 + T_2)$$

$$F_{23} = \lambda_2(1 - k_{23})\gamma_2(r_2/b_2)/(\tau_3 + T_2)$$

$$F_{31} = \lambda_3\gamma_3 r_3/(\tau_1 + T_3) + k_{13}F_{11}$$

$$F_{32} = \lambda_3\gamma_3 r_3/(\tau_2 + T_3) + k_{23}F_{22}$$

$$F_{33} = \lambda_3\gamma_3 r_3/(\tau_3 + T_3)$$

$$F_{112} = \lambda_1(1 - k_{12}f_2^*)\gamma_1(r_1/b_1)/(\tau_{12} + T_1)$$

$$F_{113} = \lambda_1(1 - k_{13}f_3^*)\gamma_1(r_1/b_1)/(\tau_{13} + T_1)$$

$$F_{123} = \lambda_1(1 - k_{12}f_2^* - k_{13}f_3^*)\gamma_1(r_1/b_1)/(\tau_{23} + T_1)$$

$$F_{212} = F_{112}$$

$$F_{213} = \lambda_2(1 - k_{23}f_3^*)\gamma_2(r_2/b_2)/(\tau_{13} + T_2) + F_{113}k_{12}f_1^*$$

$$F_{223} = \lambda_2(1 - k_{23}f_3^*)\gamma_2(r_2/b_2)/(\tau_{23} + T_2)$$

$$F_{312} = \lambda_3\gamma_3 r_3/(\tau_{12} + T_3) + F_{112}(k_{12}f_1^* + k_{23}f_2^*)$$

$$F_{313} = F_{113}$$

$$F_{323} = F_{223}$$

A.6. Times males are out of the male pool per cycle

$$T_1 = t_d + m_1\gamma_1 t_1 + m_1(\gamma_1 t_f + t_n)(1 - b_1)/b_1$$

$$T_2 = t_d + m_2\gamma_2 t_2 + m_2(\gamma_2 t_f + t_n)(1 - b_2)/b_2$$

$$T_3 = \gamma_3 t_3$$

When females discriminate between male types 1 and 2, $m_1 = dc_1 + (1 - d)c_0$ and $m_2 = dc_2 + (1 - d)c_0$; otherwise, $m_1 = m_2 = 1$ and $t_d = d(t_d) = 0$.

A.7. Time between mating with a particular male type and the female's return to the male pool

$$\theta_1 = (\gamma_1 t_f + t_n)/b_1$$

$$\theta_2 = (\gamma_2 t_f + t_n)/b_2$$

$$\theta_3 = \gamma_3(t_f + t_n)$$

A.8. Waiting times for males in the male pool (without discrimination)

$$\tau_1 = \sigma\theta_1 - T_1$$

$$\tau_2 = \sigma\theta_2 - T_2$$

$$\tau_3 = \sigma\theta_3 - T_3$$

where $\sigma = \sigma_0\ (\lambda_i / \lambda_f)$

$$\tau_{12} = \frac{T_1\gamma_2\lambda_2 r_2/b_2 - T_2\gamma_1(1-k_{12})\lambda_1 r_1/b_1}{\gamma_1(1-k_{12})\lambda_1 r_1/b_1 - \gamma_2\lambda_2 r_2/b_2}$$

$$\tau_{13} = \frac{T_1\gamma_3\lambda_3 r_3 - T_3\gamma_1(1-k_{13})\lambda_1 r_1/b_1}{\gamma_1(1-k_{13})\lambda_1 r_1/b_1 - \gamma_3\lambda_3 r_3}$$

$$\tau_{23} = \frac{T_2\gamma_3\lambda_3 r_3 - T_3\gamma_2(1-k_{23})\lambda_2 r_2/b_2}{\lambda_2\gamma_2(1-k_{23}) r_2/b_2 - \gamma_3\lambda_3 r_3}$$

A.9. Frequencies of male types in stable mixtures (without discrimination)

Note: Only the 1-2 mixture may involve discrimination; in that case, f_1 (where $f_2 = 1\text{-}f_1$) and t_d are optimized numerically. In the absence of discrimination, the τ_{ij} value can be directly calculated (above); this is substituted into the quadratic equation for τ in the text and solved for f_i. Because the sex ratio also depends on the frequencies, the result is a quadratic equation in f_i of the form

$$af_i^2 + bf_i + c = 0,$$

where

$$a = \left(\tau_{ij}(\theta_i - \theta_j) + \theta_i T_j - \theta_j T_i\right)(\sigma_0/\lambda_f)(\lambda_i - \lambda_j),$$

$$b = \left(\tau_{ij}(\theta_i - \theta_j) + \theta_i T_j - \theta_j T_i\right)(\sigma_0/\lambda_f)\lambda_j + \theta_j(\tau_{ij} + T_i)(\sigma_0/\lambda_f)(\lambda_i - \lambda_j), \text{ and}$$

$$c = -\tau_{ij}^2 - (T_i + T_j)\tau_{ij} - T_i T_j + \theta_j(\tau_{ij} + T_i)(\sigma_0/\lambda_f)\lambda_j.$$

This is solved by the quadratic formula for the biologically relevant positive term. Then $f_j = 1\text{-}f_i$.

A.10. Proof that a stable mix of all three male types is impossible

For clarity, we consider the case with all k's = 0, $\sigma_0 = 1$; all λ's equal.

A stable mix of all three male types requires that each type could invade a stable mix of the other two. So we need $F_{312} > F_{112}$, $F_{123} > F_{223}$, and $F_{213} > F_{113}$. From the last two of those relationships, we have that

$$\gamma_1(r_1/b_1)(\tau_{23}+T_2) > \gamma_2(r_2/b_2)(\tau_{23}+T_1),$$

and

$$\gamma_2(r_2/b_2)(\tau_{13}+T_1) > \gamma_1(r_1/b_1)(\tau_{13}+T_2).$$

Now substituting for τ_{23} and τ_{13} and simplifying, the two inequalities respectively yield

$$\gamma_1(r_1/b_1)T_2 > \gamma_2(r_2/b_2)T_1,$$

and

$$\gamma_2(r_2/b_2)T_1 > \gamma_1(r_1/b_1)T_2,$$

a direct contradiction. Thus the three criteria cannot be simultaneously satisfied, and a stable mix of all three male types is impossible. Note that this contradiction implies that the successful invasion of a stable mix of types 2 and 3 by type 1 and the successful invasion of a stable mix of types 1 and 3 by type 2 are jointly impossible. Neither of these stable mixes involves female discrimination, and so the altered susceptibility to invasion when females discriminate is irrelevant to this main conclusion.

A.11. Proof that a repeating sequence of the three male types is impossible

As in the previous proof, we consider the case with all k's = 0, $\sigma_0 = 1$; all λ's equal.

A repeating sequence might go from dominance by type 1 to dominance by type 2 to type 3 to type 1 and so on (here called sequential replacement), or it might go from type 3 to type 2 to type 1 to type 3 and so on (here called counter-sequential replacement). We show the proof that sequential replacement is impossible; the other proof proceeds in an analogous manner and thus will not be included here.

Type 1 is unidirectionally replaced by type 2 if $F_{21} > F_{11}$ and $F_{22} > F_{12}$; type 2 is then replaced in like manner by type 3 if $F_{32} > F_{22}$ and $F_{33} > F_{23}$; and type 3 is replaced by type 1 if $F_{13} > F_{33}$ and $F_{11} > F_{31}$.

Rearranging inequality $F_{11} > F_{31}$ yields

$$\frac{\tau_1}{\tau_1+T_1} > \frac{\lambda_3\gamma_3 r_3}{\lambda_1\gamma_1 r_1/b_1}.$$

Now we rearrange relationships $F_{33} > F_{23}$ and $F_{21} > F_{11}$ so that the $\lambda\gamma r/b$ terms, one divided by the other, are on the greater-than side of the inequality in each case. In multiplying the greater-than sides together and then the less-than sides together, the inequality must still hold, yielding

$$\frac{\lambda_3\gamma_3 r_3}{\lambda_1\gamma_1 r_1/b_1} > \frac{\tau_3(\tau_1+T_2)}{(\tau_3+T_2)(\tau_1+T_1)}.$$

It follows that

$$\frac{\tau_1}{\tau_1+T_1} > \frac{\tau_3(\tau_1+T_2)}{(\tau_3+T_2)(\tau_1+T_1)}.$$

Cross-multiplying and simplifying then results in $\tau_1 > \tau_3$. $F_{13} > F_{33}$ implies that

$$\frac{\tau_3}{\tau_3+T_1} > \frac{\lambda_3\gamma_3 r_3}{\lambda_1\gamma_1 r_1/b_1}.$$

Now again using the result derived from $F_{33} > F_{23}$ and $F_{21} > F_{11}$, we have

$$\frac{\tau_3}{\tau_3+T_1} > \frac{\tau_3(\tau_1+T_2)}{(\tau_3+T_2)(\tau_1+T_1)}.$$

In this case, rearrangement yields

$$\tau_3(T_1 - T_2) > \tau_1(T_1 - T_2).$$

We are only interested in cases with $T_1 \geq T_2$, since $\gamma_1 > \gamma_2$, $t_1 > t_2$, and $b_1 \leq b_2$; and with discrimination, $m_1 > m_2$. This means that either $\tau_3 > \tau_1$ or $\tau_3 = \tau_1$ (based on $\lim_{T_1 \to T_2}\left(\frac{\tau_3}{\tau_1}\right) = 1$), which directly contradicts the result above. We conclude from this (and the analogous counter-sequential result not shown) that a repeating sequence of the three male types is impossible.

APPENDIX B: CHAPTER 3.2. BRIEF EXPLANATION OF THE MATLAB® COMPUTER PROGRAM DatingGame USED TO OBTAIN THE MAIN RESULTS

After the descriptive heading in the program listing is a list of parameters that can be modified to produce different runs. Each run generates four figures in the format of text Figures 2, 4, and 5. The correspondence between the parameters in text Table 1 and those in the code is obvious with a few exceptions: D in the text is del in the code; λ parameters in the text are lam parameters in the code; γ parameters in the text are gam parameters in the code; ω in the text is om in the code; σ in the supplement derivation is sigp in the code; and half and mult in the code are parameters that apply when the $d(t_d)$ function is sigmoid rather than hyperbolic, a case not addressed either in the manuscript or the supplement.

Just below the parameter list in the code are three lines marked ***modify***. The four output graphs are plotted against an abscissa that runs from xmin to xmax and has a default magnitude of xdef. Below the vectors initialized with zeros is a line marked *****parameter being varied on x axis*****. This indicates that in the default run this parameter is r_2. In the line immediately after, the magnitude of r_3 is linked to that of r_2 by the multiplier R23. This can be commented out when r_3 is to remain fixed. When the run is based on varying r_3 alone, both previous lines would be commented out and the comment symbol % would be removed from r3 = x(i);. Obviously r_1 could be varied in this way instead, or some other parameter of interest. Details of the graphics formatting can be altered in the final lines of code. The precision of the hill-climbing algorithms to find fitnesses and t_d is fixed in the code at 0.00001 (1e-5 in MATLAB), which seems to provide plenty of precision, but this could easily be adjusted.

Any problems implementing this program should be referred to the authors.

APPENDIX C: CHAPTER 3.3. MATLAB® DatingGame CODE

```
%DatingGame --a game between choosy females and three types of males.
%Females invest time attempting to discriminate between male types 1 & 2,
%then mate or not based on this "dating" process. This version finds the
%frequency-dependent solutions and plots the results across a range of the
%magnitude of a particular parameter. It also finds ESS outcomes across the
%parameter range with the coercer (male type 3) included on equal terms
%with the other two types. In this version type 3 may or may not invest
%time pairing like the other two types do. *Note*: types 2 & 3 must differ
%in more than just coercion per se for results to be obtained. We include
%partial access (cuckoldry) to partners of types 1 and 2 by type 3 and
%partners of type 1 by 2.

r1   = 1.0;  %1.0; repro payoff for mating of female & type 1 male, fitness
r2   = 0.6;  %0.6; repro payoff for mating of female & type 2 male, fitness
R32  = 0.8;  %0.8; r3/r2, to account for any repro've cost of coercion
r3   = R32*r2; %R32*r2; repro payoff for type 3 male, fitness
tf   = 12;   %12;  time female invests in a reproductive event, time
t1   = 12;   %12;  time type 1 male invests in a reproductive event, time
t2   = 1;    %1;   time type 2 male is in a reproductive event, time
t3   = 0;    %0; time type 3 male is in a reproductive event, time
tn   = 1;    %1;   time female is not in estrus per cycle, time
b1   = 0.5;  %0.5; male 1 prob of break-up after a reproductive event
b2   = 1;    %1;   male 2 prob of break-up after a reproductive event
del  = 3;    %3;   exponential discrimination parameter, 1/time
half = 3;    %3;   sigmoid discrimination time at half maximal, time
mult = 1.5;  %1.5; sigmoid discrimination exponent multiplier, 1/time
sigp = 1;    %1;   primary sex ratio: # males / # females at fertilization
lamf = 1;    %1;   expected reproductive lifetime of male type 1, time
lam1 = 1;    %1;   expected reproductive lifetime of male type 2, time
lam2 = 1;    %1;   expected reproductive lifetime of females, time
lam3 = 1;    %1;   expected reproductive lifetime of male type 3, time
gam1 = 1;    %1;   chance a reproductive liaison yields offspring, type 1
gam2 = 0.4;  %0.4; chance a reproductive liaison yields offspring, type 2
gam3 = 0.1;  %0.1; chance a forced mating yields offspring, type 3
Dfn  = 0;    %0;   discrimination function: 0 = hyperbolic, 1 = sigmoid
c1   = 1;    %1;   1=choose male type 1; 0=avoid type 1
c2   = 0;    %0;   1=choose male type 2; 0=avoid type 2
c0  =  1;    %1;   1=take unidentified males; 0=avoid unidentified males
om   = 0;    %0;   exponent of c0=(1-d)^om
k12  = 0;    %0; frac of type 1 offspring fathered by 2 per unit freq
k13  = 0;    %0; frac of type 1 offspring fathered by 3 per unit freq
k23  = 0;    %0; frac of type 2 offspring fathered by 3 per unit freq

%Variables and code for production runs
res = 500;   %Sets resolution of the graphs
xx = 1:res+1;%Vector of run numbers
xmax = 1.0;  %Largest magnitude of the parameter of interest  %***modify***
xmin = 0.0;  %Smallest magnitude of the parameter of interest %***modify***
xdef = 0.6;  %Default value of the parameter being varied     %***modify***
xinc = (xmax - xmin)/res; %Increment size for each calculation
x = (xx - 1) * xinc + xmin; %x-vector for graphing
f1   = zeros(1,res+1);  %Fraction of males in population that are type 1
f2   = zeros(1,res+1);  %Fraction of males in population that are type 2
f3   = zeros(1,res+1);  %Fraction of males in population that are type 3
f12  = zeros(1,res+1);  %Unstable male 1-2 combination
```

```
f13  = zeros(1,res+1);  %Unstable male 1-3 combination
f23  = zeros(1,res+1);  %Unstable male 2-3 combination
f123 = zeros(1,res+1);  %Unstable male 1-2-3 combination
M1   = zeros(1,res+1);  %Fraction of all mated males that are type 1
M2   = zeros(1,res+1);  %Fraction of all mated males that are type 2
M3   = zeros(1,res+1);  %Fraction of all mated males that are type 3
d    = zeros(1,res+1);  %Fraction of dates for which types are discerned
Ff   = zeros(1,res+1);  %Fitness of females
F1   = zeros(1,res+1);  %Fitness of type 1 males
F2   = zeros(1,res+1);  %Fitness of type 2 males
F3   = zeros(1,res+1);  %Fitness of type 3 males
p1   = zeros(1,res+1);  %Frequency of type 1 males in the dating pool
p2   = zeros(1,res+1);  %Frequency of type 2 males in the dating pool
p3   = zeros(1,res+1);  %Frequency of type 3 males in the dating pool
tau  = zeros(1,res+1);  %Time a male spends in the dating pool
td   = zeros(1,res+1);  %Time spent attempting to recognize a male's type
                        %xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx
ESSold = [4];           %Set ESSold to a unique value
for i = 1:res+1         %for loop for storing data
    FLAG = 1;           %Signals absence of one-type or two-type ESS
    FLAG123 = 0;        %Signals no unstable mix of all 3 types
    r2 = x(i);          %******parameter being varied on x axis***********
    r3 = R32*r2;
    %r3 = x(i);
    T1 = gam1*t1 + (gam1*tf + tn)*(1 - b1)/b1; %Time male 1 out of pool
    T2 = gam2*t2 + (gam2*tf + tn)*(1 - b2)/b2; %Time male 2 out of pool
    T3 = gam3*t3;                              %Time male 3 out of pool
    the1 = (gam1*tf + tn)/b1; %Time until fem visits pool after type 1 mate
    the2 = (gam2*tf + tn)/b2; %Time until fem visits pool after type 2 mate
    the3 = gam3*(tf + tn);     %Time until fem visits pool after type 3 mate
    tau1 = sigp*(lam1/lamf)*the1 - T1;      %Wait time for pure male 1
    if tau1 < 0
        tau1 = 0;
    end
    tau2 = sigp*(lam2/lamf)*the2 - T2;      %Wait time for pure male 2
    if tau2 < 0
        tau2 = 0;
    end
    tau3 = sigp*(lam3/lamf)*the3 - T3;      %Wait time for pure male 3
    if tau3 < 0
        tau3 = 0;
    end
                                       %Wait times for mixes of male types:
    tau12 = (T1*gam2*lam2*r2/b2 - T2*gam1*lam1*r1*(1-k12)/b1)/...
            (gam1*lam1*r1*(1-k12)/b1 - gam2*lam2*r2/b2);
    tau13 = (T1*gam3*lam3*r3 - T3*gam1*lam2*r1*(1-k13)/b1)/...
            (gam1*lam1*r1*(1-k13)/b1 - lam3*gam3*r3);
    tau23 = (T2*gam3*lam3*r3 - T3*gam2*lam3*r2*(1-k23)/b2)/...
            (gam2*lam2*r2*(1-k23)/b2 - lam3*gam3*r3);
    F11 = lam1*(gam1*r1/b1)/(tau1 + T1);  %Fxy=fit of type x in pure type y
    F12 = lam1*(1-k12)*(gam1*r1/b1)/(tau2 + T1);
    F13 = lam1*(1-k13)*(gam1*r1/b1)/(tau3 + T1);
    F21 = lam2*(gam2*r2/b2)/(tau1 + T2) + k12*F11;
    F22 = lam2*(gam2*r2/b2)/(tau2 + T2);
    F23 = lam2*(1-k23)*(gam2*r2/b2)/(tau3 + T2);
    F31 = lam3*(gam3*r3)/(tau1 + T3) + k13*F11;
    F32 = lam3*(gam3*r3)/(tau2 + T3) + k23*F22;
    F33 = lam3*(gam3*r3)/(tau3 + T3);
```

```
F112y = lam1*(gam1*r1/b1)/(tau12 + T1); %Fxyz=fit: type x in y-z mix
F113y = lam1*(gam1*r1/b1)/(tau13 + T1);
F123y = lam1*(gam1*r1/b1)/(tau23 + T1);
F212y = lam2*(gam2*r2/b2)/(tau12 + T2);
F213y = lam2*(gam2*r2/b2)/(tau13 + T2);
F223y = lam2*(gam2*r2/b2)/(tau23 + T2);
F312y = lam3*(gam3*r3)/(tau12 + T3);
F313y = lam3*(gam3*r3)/(tau13 + T3);
F323y = lam3*(gam3*r3)/(tau23 + T3);

ESS = [];                  %Start with no ESS
f1(i) = 0; f2(i) = 0; f3(i) = 0;
F1(i) = 0; F2(i) = 0; F3(i) = 0; Ff(i) = 0;
p1(i) = 0; p2(i) = 0; p3(i) = 0;
M1(i) = 0; M2(i) = 0; M3(i) = 0;
d(i) = 0; td(i) = 0; tau(i) = 0;
if (F11 > F21)&&(F11 > F31) %Condition for pure type 1 ESS
    ESS = [ESS 1];          %Concatenate ESS id#
    FLAG = 0;               %No unstable 3-type mix is possible
    f1(i) = 1; f2(i) = 0; f3(i) = 0; %Frequencies of male types
    tau(i) = tau1;                   %Set waiting time
    F1(i) = F11; F2(i) = F21; F3(i) = F31; %Male fitnesses
    p1(i) = 1; p2(i) = 0; p3(i) = 0; %Fractions of male types in pool
    M1(i) = 1; M2(i) = 0; M3(i) = 0; %Fractions of male types mated
    d(i) = 0; td(i) = 0;    %No discrimination
end
if (F22 > F12)&&(F22 > F32) %Condition for pure type 2 ESS
    ESS = [ESS 2];          %Above comments apply
    FLAG = 0;
    f1(i) = 0; f2(i) = 1; f3(i) = 0;
    tau(i) = tau2;
    F1(i) = F12; F2(i) = F22; F3(i) = F32;
    p1(i) = 0; p2(i) = 1; p3(i) = 0;
    M1(i) = 0; M2(i) = 1; M3(i) = 0;
    d(i) = 0; td(i) = 0;
end
if (F33 > F13)&&(F33 > F23) %Condition for pure type 3 ESS
    ESS = [ESS 3];          %Above comment apply
    FLAG = 0;
    f1(i) = 0; f2(i) = 0; f3(i) = 1;
    tau(i) = tau3;
    F1(i) = F13; F2(i) = F23; F3(i) = F33;
    p1(i) = 0; p2(i) = 0; p3(i) = 1;
    M1(i) = 0; M2(i) = 0; M3(i) = 1;
    d(i) = 0; td(i) = 0;
end
if (F12 > F22)&&(F21 > F11)   %Possible 1-2 mix ESS
    ff1 = 0.5; ff1st = 0.051; %Freq of type 1 males & step size for f1
    FF1 = 1.0; FF2 = 0.5;     %Starting fitnesses of types 1+2
    flag = 1;                 %0 ends the loop when f1=0 or 1 & F1<>F2
    while (abs(FF1 - FF2) > 1e-5)&&flag %Keep adjusting toward FF1=FF2
        ff1 = ff1 + ff1st;    %Take a step with f1(i)
        if ff1 < 0            %Restrict f1(i) between 0 and 1
            ff1 = 0;
        elseif ff1 > 1
            ff1 = 1;
        end
        ff2 = 1-ff1;          %Find f2(i) from f1(i)
```

```
        if (abs(ff1st) < 1e-5)&&((ff1 <= 0)||(ff1 >= 1))
            flag = 0;  %Stop the loop with f1 = 0 or 1 & fitnesses ~=
        end            %Now do a hill climb based on td to maximize Ff
        td(i) = 0; tdst = 0.11/del; Ffold = 0; %Initialize
        while (abs(tdst) > 1e-5/del)  %While step size is large enough
            td(i) = td(i) + tdst; %Take a step with td(i)
            if td(i) < 0          %Restrict td(i) to non-zero values
                td(i) = 0;
            end
            dd = 1 - exp(-del*td(i));   %Discrimination fraction
            c0 = (1 - dd)^om;           %c0 can depend on d(i)
            m1 = dd*c1 + (1 - dd)*c0;   %Mate prob for encountered 1
            m2 = dd*c2 + (1 - dd)*c0;   %Mate prob for encountered 2
                                        %Time spent with a female
            T1 = td(i) + m1*gam1*t1 + m1*(gam1*tf + tn)*(1-b1)/b1;
            T2 = td(i) + m2*gam2*t2 + m2*(gam2*tf + tn)*(1-b2)/b2;
            the1 = (gam1*tf + tn)/b1;   %Time female spends with mate 1
            the2 = (gam2*tf + tn)/b2;   %Time female spends wiht mate 2
            sig = sigp*(ff1*lam1 + ff2*lam2)/lamf; %Sex ratio
            %bb and cc are terms in the quadratic equation for tau12
            bb = T1+T2-sig*(ff1*m1*the1 + ff2*m2*the2 + td(i));
            cc = T1*T2 - sig*(ff1*T2*(m1*the1 + td(i)) ...
                 + ff2*T1*(m2*the2 + td(i)));
            ttau = (-bb + sqrt(bb*bb - 4*cc))/2;  %tau12 quadratic
            pp1 = ff1*(ttau+T2)/(ff1*(ttau+T2) + ...
                    ff2*(ttau+T1));     %Type 1 male freq in mate pool
            pp2 = 1 - pp1;              %Type 2 male freq in mate pool
            pp3 = 0;                    %Type 3 male freq in mate pool
            Ff(i) = lamf*(pp1*m1*gam1*r1/b1+pp2*m2*gam2...%Female fit
                   *r2/b2)/(pp1*m1*the1 + pp2*m2*the2 + td(i));
            F1y   = lam1*(m1*gam1*r1/b1)/(ttau + T1); %Baseline F1
            F2y   = lam2*(m2*gam2*r2/b2)/(ttau + T2); %Baseline F2
            FF1 = (1-k12*ff2)*F1y;      %Type 1 male fitness
            FF2 = ff1*k12*F1y + F2y;    %Type 2 male fitness
            if (Ff(i) < Ffold)||((td(i) <= 0)&&(tdst < 0))
                tdst = -tdst/2.1; %Reverse direction and shrink step
            end
            Ffold = Ff(i);  %Store Ff as Ffold for next loop comparison
        end
        if FF1 > FF2        %Reverse direction and shrink step size?
            if ((ff1st < 0)&&(ff1 < 1))||((ff1st > 0)&&(ff1 >= 1))
                ff1st = - ff1st/2.1;
            end
        elseif FF2 > FF1    %Reverse direction and shrink step size?
            if ((ff1st > 0)&&(ff1 > 0))||((ff1st < 0)&&(ff1 <= 0))
                ff1st = -ff1st/2.1;
            end
        end
    end
    ttd = td(i); td(i) = 0; %Prevents td(i) carry-over to other cases
    FF3 = lam3*gam3*r3/(ttau+T3)+k13*ff1*F1y+k23*ff2*F2y; %Coercer fit
    if (FF1 > FF3)          %Coercer cannot invade
        if flag             %Signals 0<f1<1
            ESS = [ESS 12]; %Stores ESS result
            FLAG = 0;       %No unstable 3-type mix is possible
            d(i) = dd; td(i) = ttd; tau(i) = ttau;  %Set d, td, tau
            p1(i) = pp1; p2(i) = pp2; p3(i) = pp3;  %fractions in pool
            M1(i) = p1(i)*m1/(p1(i)*m1 + p2(i)*m2); %type 1 mate frac
```

```
            M2(i) = 1 - M1(i);                      %type 2 mate frac
            M3(i) = 0;                              %type 3 mate frac
            f3(i) = 0;                 %No type 3 males in this case
            f1(i) = ff1; f2(i) = ff2;  %Set fractions of types 1 & 2
            F1(i) = FF1; F2(i) = FF2; F3(i) = FF3;  %Set fitnesses
        else                           %f1(i)>1 or f1(i)<0
            if ff1 >= 1           %Type 1 tends to frequency 1
                ESS = [ESS 1201]; %Unstable 1-2 mix dominated by type 1
                f12(i) = 0.9;     %Store graph indicator of 1201
            else                  %f(i) <= 0, Type 2 -> frequency 1
                ESS = [ESS 1202]; %Unstable 1-2 mix dominated by type 2
                f12(i) = 0.1;     %Store graph indicator of 1202
            end
            d(i) = 0; td(i) = 0; tau(i) = 0; %Set all values to zero
            f1(i) = 0; f2(i) = 0; f3(i) = 0;
            F1(i) = 0; F2(i) = 0; F3(i) = 0;
            p1(i) = 0; p2(i) = 0; p3(i) = 0;
            M1(i) = 0; M2(i) = 0; M3(i) = 0;
        end
    elseif FLAG %Restore the null results and T1 and T2 + non-discr 1-2
        FLAG = 0; FLAG123 = 1;    %123 is a potential outcome
    end
end                               %ends the if for the 12 mixture case
T1 = gam1*t1 + (gam1*tf + tn)*(1 - b1)/b1; %Set T1 & T2 to no-discrim
T2 = gam2*t2 + (gam2*tf + tn)*(1 - b2)/b2;
if (F13 > F33)&&(F31 > F11)       %Condition for 1-3 mix ESS
    aa = (sigp/lamf)*(lam1-lam3)*(tau13*(the1-the3)+T3*the1-T1*the3);
    bb = (sigp/lamf)*lam3*(tau13*(the1-the3)+the1*T3-the3*T1);
    cc = lam3*the3*(sigp/lamf)*(tau13+T1)-tau13^2-(T1+T3)*tau13-T1*T3;
    if abs(aa) < 1e-6             %aa, bb, & cc are quadratic terms
        f1y = -cc/bb;             %Solves the linear equation
    else
        f1y = (-bb + sqrt(bb^2 - 4*aa*cc))/(2*aa); %Solve the quadratic
    end
    if f1y >= 1               %Type 1 only, correct fits for extra-pair
        F113 = F113y;
        F213 = F213y + k12*F113y;
    elseif f1y <= 0           %Type 3 only, correct fits for extra-pair
        F113 = F113y*(1-k13);
        F213 = F213y*(1-k23);
    else                      %Types 1 & 3 both present -> corrections
        F113 = F113y*(1-k13*(1-f1y));
        F213 = F213y*(1-k23*(1-f1y)) + f1y*k12*F113y;
    end
    if F113 > F213            %Type 2 cannot invade
        if (f1y >= 1)||(f1y <= 0) %Outcome unstable
            if f1y >= 1
                ESS = [ESS 1301]; %Unstable 1-3 mix dominated by type 1
                f13(i) = 0.9;     %Store graph indicator of 1301
            else                  %f1(i) <= 0
                ESS = [ESS 1303]; %Unstable 1-3 mix dominated by type 3
                f13(i) = 0.1;     %Store graph indicator of 1303
            end
            tau(i) = 0;           %Set variables to zero
            f1(i) = 0; f2(i) = 0; f3(i) = 0;
            p1(i) = 0; p2(i) = 0; p3(i) = 0;
            M1(i) = 0; M2(i) = 0; M3(i) = 0;
            F1(i) = 0; F2(i) = 0; F3(i) = 0;
```

```
            d(i) = 0; td(i) = 0;
        else                        %Outcome stable
            ESS = [ESS 13];         %Stable 1-3 mix
            FLAG = 0;               %No unstable 3-type mix is possible
            f1(i) = f1y;            %Variables determined as above
            f3(i) = 1 - f1(i);
            f2(i) = 0;
            tau(i) = tau13;
            F1(i) = F113; F2(i) = F213; F3(i) = F113;
            p1(i) = f1(i)*(tau(i)+T3)/(f1(i)*(tau(i)+T3) + f3(i) ...
                    *(tau(i)+T1));
            p3(i) = 1 - p1(i);
            p2(i) = 0;
            M1(i) = p1(i); M2(i) = p2(i); M3(i) = p3(i);
            d(i) = 0; td(i) = 0;
            f123(i) = 0;       %Removing the 12300 signal if present
        end
    elseif FLAG                 %F113 < F213 and type 2 can invade
        FLAG = 0; FLAG123 = 1; %123 is a potential outcome
    end
end
if (F23 > F33)&&(F32 > F22)    %Condition for 2-3 mix ESS
    aa = (sigp/lamf)*(lam2-lam3)*(tau23*(the2-the3)+T3*the2-T2*the3);
    bb = (sigp/lamf)*lam3*(tau23*(the2-the3)+the2*T3-the3*T2);
    cc = lam3*the3*(sigp/lamf)*(tau23+T2)-tau23^2-(T2+T3)*tau23-T2*T3;
    f2y = (-bb + sqrt(bb^2 - 4*aa*cc))/(2*aa); %Quadratic for f2
    if abs(aa) < 1e-6
        f2y = -cc/bb;
    else
        f2y = (-bb + sqrt(bb^2 - 4*aa*cc))/(2*aa); %Solve the quadr
    end
    if f2y >= 1
        F323 = F323y + k23*F223y;
        F123 = F123y*(1-k12);
    elseif f2y <= 0
        F323 = F323y;
        F123 = F123y*(1-k13);
    else
        F323 = F323y + k23*f2y*F223y;
        F123 = F123y*(1-k12*f2y-k13*(1-f2y));
    end
    if F323 > F123                 %Type 1 cannot invade
        if (f2y >= 1)||(f2y <= 0) %If f2 is out of range (unstable mix)
            if f2y >= 1
                ESS = [ESS 2302]; %Unstable 2-3 mix dominated by 2
                f23(i) = 0.9;     %Store graph indicator of 2302
            else %f2(i) <= 0
                ESS = [ESS 2303]; %Unstable 2-3 mix dominated by 3
                f23(i) = 0.1;     %Store graph indicator of 2303
            end
            tau(i) = 0;
            f1(i) = 0; f2(i) = 0; f3(i) = 0;
            p1(i) = 0; p2(i) = 0; p3(i) = 0;
            M1(i) = 0; M2(i) = 0; M3(i) = 0;
            F1(i) = 0; F2(i) = 0; F3(i) = 0;
            d(i) = 0; td(i) = 0;
        else
            ESS = [ESS 23];       %Stable 2-3 mix
```

```
                FLAG = 0;             %No unstable 3-type mix is possible
                f2(i) = f2y;
                f3(i) = 1 - f2(i);
                f1(i) = 0;
                tau(i) = tau23;
                F1(i) = F123; F2(i) = F223; F3(i) = F323;
                p2(i) = f2(i)*(tau(i)+T3)/(f2(i)*(tau(i)+T3) + f3(i) ...
                        *(tau(i)+T2));
                p3(i) = 1 - p2(i);
                p1(i) = 0;
                M1(i) = p1(i); M2(i) = p2(i); M3(i) = p3(i);
                d(i) = 0; td(i) = 0;
            end
        elseif FLAG                   %F323 < F123 and type 1 can invade
            FLAG = 0; FLAG123 = 1;    %123 is a potential outcome
        end
    end
    if FLAG123&&(numel(ESS) == 0)         %123 outcome applies if no ESS's
        ESS = [123];
        f123(i) = 0.3333; tau(i) = 0;     %Set variables to zero
        f1(i) = 0; f2(i) = 0; f3(i) = 0;
        F1(i) = 0; F2(i) = 0; F3(i) = 0;
        p1(i) = 0; p2(i) = 0; p3(i) = 0;
        M1(i) = 0; M2(i) = 0; M3(i) = 0;
        d(i) = 0; td(i) = 0;
    end
    if (ESS ~= ESSold)  %Send each new ESS to screen with boundary x value
        disp(x(i))
        disp(ESS)
    elseif (numel(ESS) ~= numel(ESSold)) %Check for double ESS
        disp(x(i))
        disp(ESS)
    end
    ESSold = ESS;       %Update ESSold so new ESS's can be recognized
end
disp(1)
                        %Four output figures
figure                  %Figure 1 Frequencies of Male Types
hold on
plot([xdef xdef],[0 1],'k--')
plot(x,f1,'b')
plot(x,f2,'r')
plot(x,f3,'g')
plot(x,f12,'Color',[1,0.5,1]) %Unstable 1-2 mix is purple
plot(x,f13,'Color',[1,0.5,0]) %Unstable 1-3 mix is orange
plot(x,f23,'c')               %Unstable 2-3 mix is cyan
plot(x,f123,'k')              %Unstable 1-2-3 mix is black
xlabel('Reproductive success of type 2 males, r2')
%xlabel('Reproductive success of type 3 males, r3')
ylabel('Frequencies: f1=blue, f2=red, f3=green')
axis([0 xmax 0 1])
hold off

figure                  %Figure 2 Tau and td
hold on
AX=plotyy(x,tau,x,td,'plot');
plot([xdef xdef],[0 8],'k--')
axis([0 xmax 0 8])
```

```
set(get(AX(1),'Ylabel'),'String','Time in male pool (tau, blue)')
set(get(AX(2),'Ylabel'),'String','Discrimination time (td, carmine)')
set(AX(1),'Ylim',[0 8])
set(AX(2),'Ylim',[0 0.2])
set(AX(1),'YTick',[0:1:8])
set(AX(2),'YTick',[0:0.02:0.2])
xlabel('Reproductive success of type 2 males, r2')
%xlabel('Reproductive success of type 3 males, r3')
hold off

figure                 %Figure 3 Fitnesses
hold on
%plot(x,Ff,'k')
plot(x,F1,'b')
plot(x,F2,'r')
plot(x,F3,'g')
plot([xdef xdef],[0 0.2],'k--')
axis([0 xmax 0 0.2])
xlabel('Reproductive success of type 2 males, r2')
%xlabel('Reproductive success of type 3 males, r3')
ylabel('Fitnesses: males 1=blue 2=red 3=green; females=top male')
hold off

figure                %Figure 4 Pool proportions and d
hold on
plot(x,p1,'c')
plot(x,p2,'Color',[1,0.5,0])
plot(x,M1,'b')
plot(x,M2,'r')
plot(x,M3,'g')
plot(x,d,'k')
plot([xdef xdef],[0 1],'k--')
axis([0 xmax 0 1])
xlabel('Reproductive success of type 2 males, r2')
%xlabel('Reproductive success of type 3 males, r3')
ylabel('M1=blue, p1=cyan; M2=red, p2=orange; M3=green; d=black')
hold off
```

APPENDIX D: CHAPTER 3.4. FINDING PARAMETER MAGNITUDES FOR THE SIX FOCAL SYSTEMS

D.1. Japanese Water Striders

Most male water striders engage exclusively in forced copulation, but Japanese water striders are an exception. Type 1 males are those that defend territories, call for mates, and guard their females while they lay eggs. Type 2 males are non-territorial males that only call for mates. Type 3 males are non-territorial males that engage in forced copulations. Flexibility in mating behavior is not correlated to male morphology, and the strategies chosen vary throughout the season (late March to early June), with type 1 strategies emerging mid-season (Hayashi 1985). We estimate $r_1 = r_2 = 1$ and $r_3 = 0.95$ to account for the usurpation of female choice and effects of mating with a non-chosen male.

The time females spend in reproduction is estimated from the average copulation time plus oviposition time ($t_f = 0.00045$). Type 1 males guard mates for as long as females oviposit ($t_1 = t_f$), and type 2 males do not guard at all ($t_2 = 0.0001$). Type 3 males guard only sometimes and are known to leave before the female has finished ($t_3 = 0.00022$). The mating season lasts approximately 2 months ($t_n = 10$), and there is no pairing fidelity ($b_i = 1$) (Hayashi 1985). There is no information on the sex ratios of Japanese water striders, so we estimate equal λ_i values; but since water striders are known to have fluctuating sex ratios throughout the breeding season (Vepsalainen and Savolainen 1995), we explore the effect of this.

There is no information on chances of fertilization for each type of mating strategy; however, water striders are believed to have sperm competition favoring the most recent sperm (displacing up to 65% of the previous male's sperm) (Rubenstein 1989). Since type 2 males mate first without an accompanying oviposition, we estimate a 30% chance of reproduction ($\gamma_2 = 0.3$). Type 1 males mate-guard while the females oviposit, so we estimate a 90% chance of fertilization ($\gamma_1 = 0.9$). As type 3 males mate when a female is unguarded, potentially displacing a previous male's sperm, we estimate a 60% chance of fertilizing ($\gamma_3 = 0.6$) (Hayashi 1985). We explore a range of magnitudes for these parameters as well.

Since there is no extra-pair copulation, the magnitudes of k_{12}, k_{13}, and k_{23} were set to zero. The discrimination coefficient D was estimated from assuming that the females are able to distinguish between type 1 and 2 males accurately approximately half the time in approximately 10 minutes ($D = 4300$).

D.2. Scorpionflies

There are three mating strategies for male scorpionflies. Type 1 males guard an arthropod as a nuptial gift that the female consumes while mating. Type 2 males produce and offers a salivary mass; this strategy is linked to inability to find or defend an arthropod. Type 3 males engage in forced copulations with females without offering any nuptial gifts, either because they could not gain access to an arthropod and could not produce a salivary mass or because they have higher reproductive success via coercion (Thornhill 1980a,b, 1981, 1982).

The r-values were chosen based on the number of eggs laid for each type of reproductive event. Females lay the most eggs with an arthropod nuptial gift; when given a salivary mass, they produce approximately two-thirds of the arthropod amount; in forced copulations, they produce approximately one-sixth of the arthropod amount (Thornhill 1982) ($r_1 = 1$, $r_2 = 0.67$, $r_3 = 0.17$). The amount of time a female spends reproductive depends on the type of mating she received; she lays eggs much faster after a forced copulation than she does a consensual copulation (Thornhill 1982); we estimated by using the average of these ($t_f = 0.052$), though we explore this as well. Females are sexually receptive for all but the time that they are inseminated (Thornhill 1982), which is included in t_f, so we set $t_n = 0$ to represent extended receptivity. Since egg batches seem to be fertilized by a single male, we set $k_{12} = k_{13} = k_{23} = 0$.

Males do not differ in copulation time (Thornhill 1982), but males defending arthropods or salivary masses spend additional time guarding the nuptial gift. We estimate the time for arthropod-guarding to be approximately 30 minutes t and for salivary-guarding to be approximately 1 hr ($t_1 = 0.0036$, $t_2 = 0.0048$, $t_3 = 0.0024$). There is no pairing fidelity ($b_i = 1$). The reproductive sex ratio is 1:1 (Thornhill 1980b), but type 2 males and type 3 males are expected to have shorter reproductive lifespans than females or type 1 males (Thornhill 1980a, 1981) ($\lambda_f = \lambda_1 = 1$, $\lambda_2 = 0.8$, $\lambda_3 = 0.5$). However, since type 1 males tend to find their insects in spider webs, and since spiders are the primary predators of scorpionflies (Thornhill 1980b), it is possible that type 1 and 2 males have the highest mortality rates, followed by type 3 ($\lambda_f = \lambda_3 = 1$, $\lambda_1 = 0.5$, $\lambda_2 = 0.8$).We explore this as well.

Fertilization rates for type 1 and 2 males are approximately equal ($\gamma_1 = \gamma_2 = 1$) (Thornhill 1981, 1982); when forced copulations are successful, they have an insemination rate of approximately 50% (Thornhill 1980b, 1982). However, since forced copulation is achieved in only about 22% of attempts, the insemination rate becomes 11% ($\gamma_3 = 0.11$) (Thornhill 1980b). We explore both of these rates. For our default, we varied r_2, with r_3 being one-fourth of r_2.

Since there is no extra-pair copulation, the magnitudes of k_{12}, k_{13}, and k_{23} were set to zero. The discrimination coefficient D was estimated from the time females spend between mating events, estimated at one day (Thornhill 1974) ($D = 21$).

D.3. Guppies

Guppies have two different male mating strategies: those that display and are chosen by females to mate and those that engage in sneak copulations when females are unreceptive. Both are short-term matings, and we have designated them type 2 and type 3, respectively. Male reproductive behavior differs dramatically based on the level of predation they experience, so we did separate runs for low-predation environments and high-predation environments (Liley 1966).

The reproductive success per reproductive cycle for type 2 and 3 males (r_2 and r_3) were set at 1, as there is no known influence on offspring success based on reproductive strategy; however, we vary the r-values to explore this. Females devote basically their entire lives to reproduction—they are either fertile and mating, pregnant, or giving birth. Their time commitment per birth event has been estimated as 24 hours ($t_f = 0.033$) (B.D. Neff, personal communication). Because females are only sexually receptive during the first 3-5 days after giving birth (once per month) (Liley 1966; Magurran and Nowak 1991), we estimate the time that a female is not sexually receptive to be the other 26 days of the month ($t_n = 0.87$). Type 2 males spend approximately 5 seconds for each S-display (Luyten and Liley 1985) ($t_2 = 0.0000014$/month), and type 3 males considerably less (estimated at half of t_2).

There is no pair fidelity in guppies ($b_i = 1$). The sex ratios vary depending on the population: in low-predator populations, females outnumber males almost four to one (Rodd and Reznick 1997) ($\lambda_1 = \lambda_2 = \lambda_3 = 0.28\lambda_f$); in high predator, it is almost two to one (Rodd and Reznick 1997) ($\lambda_1 = \lambda_2 = \lambda_3 = 0.53\lambda_f$). Time spent reproductive is approximately the same, except for the effects of predation on males, which influenced the sex ratios.

Little is known about the chance of conceiving an offspring per reproductive event, but we estimated this based on the odds of each type of sexual event releasing sperm (Baerends et al. 1955; Liley 1966;), the amount of sperm that each type successfully delivers (Pilastro et al. 2002), the estimated number of events a female encounters each month (Magurran and Seghers 1994), which varies based on predator status (Endler 1987), and on the number of males in each population, which also varies based on predator status (Rodd and Reznick 1997). Estimates for low predator populations are 0.0082 for S-display and 0.0013 for sneak attempts. For high predator populations, they are 0.014 and 0.0011, respectively.

Since there is no extra-pair copulation, the magnitudes of k_{12}, k_{13}, and k_{23} were set to zero. The discrimination coefficient D was estimated from assuming that the male evaluation process lasts approximately 10 minutes of observing the sigmoid display (Liley 1966; Magurran and Nowak 1991) ($D = 4300$).

D.4. Mallard Ducks

Mallard reproduction consists of long-term pairs that mate primarily consensually with each other; in addition to this type 1 strategy, however, males often switch strategies and sexually coerce females mated to other males. We are primarily interested in sexual coercion outside of mated pairs, though our fertilization calculation of type 1 males includes the negative influence of this secondary strategy.

Offspring viability is significantly lower when females are coerced to mate with their non-primary partner (Bluhm and Gowaty 2004) ($r_1 = 1$, $r_3 = 0.739$). Females spend approximately 9 months in reproduction, from courtship to offspring maturing to flight ($t_f = 9$); type 1 males invest the same amount of time up until hatching ($t_1 = 7$) (Drilling et al. 2002). Type 3 males invest very little in reproduction ($t_3 = 0.0002$). The probability of breakup in type 1 relationships is very low ($b_1 = 0.019$), while coercion results in immediate breakup ($b = 1$). The primary sex ratio is presumed to be 1 (Giudice 2003, but see Denk 2005).

Reproductive lifetimes are similar for adult males and females, and we set $\lambda_f = \lambda_1 = \lambda_2 = \lambda_3 = 1$. Hunting may help maintain the equal sex ratio in some populations; severely restricted hunting may result in a male-biased sex ratio (Giudice 2003).

The empirically-established chance of a type 1 mating fertilizing an egg $\gamma_1 = 0.59$, and for type 3 $\gamma_3 = 0.37$ (Cunningham 2003). The rate of extra-pair paternity in mallards is approximately 14% (Denk 2005), and since all EPCs are coerced in mallards, this becomes the fraction of potential type 1 offspring instead fathered by type 3 males ($k_{13} = 0.14$; $k_{12} = k_{23} = 0$).

As pairs usually take approximately one month to form at the beginning of courtship in the fall (Drilling et al. 2002), we estimated the time for a female to distinguish types 1 and 3 males with a probability of 50% to be about 1 week ($D = 3$).

D.5. Chimpanzees

Chimpanzee males have three different mating strategies. Type 1 males are chosen by females as consorts, spending an extended period of time mating exclusively with each other while she is in estrus and providing her with resources. Type 2 males are opportunistic males that copulate with females in estrus within the group. Type 3 males are possessive opportunistic males that aggressively defend estrus females from other males in order to mate exclusively with them (Tutin 1979). We set $r_1 = 1$ and $r_2 = r_3 = 0.9$, as there was little evidence for differences in reproductive success for types 2 and 3.

The birth interval, composed of mating, pregnancy, and rearing, is 70 months ($t_f = 70$). Type 1 males engage in approximately 10-day consorts with females ($t_1 = 0.3$). Type 2 males are opportunistic and invest very little time in reproduction ($t_2 = 0.001$, approximately 1 hour). Type 3 males prevent the female from mating with other males while she is fertile, approximately 2-3 days ($t_3 = 0.075$) (Tutin 1979), and females spend approximately 26 days out of their 36-day cycle not in estrus ($t_n = 0.72$) (Graham 1979). There is no pairing fidelity (the $b_i = 1$), and the sex ratios are approximately equal. Females tend to be reproductive for slightly less time than the males ($\lambda_f = 0.95$ and $\lambda_1 = \lambda_2 = \lambda_3 = 1$) (Tutin 1979).

Approximately half of all consorts result in pregnancy ($\gamma_1 = 0.5$) (Tutin 1979). In opportunistic mating, a female mates with approximately 12 males (Tutin 1979), so we estimate the chances of one of those males fertilizing an egg to be 1/12 ($\gamma_2 = 0.042$). Since type 3 males spend approximately one quarter of the time that type 1 males spend per reproductive event (Tutin 1979), we estimate their chances of fertilization to be approximately one quarter that of type 1 ($\gamma_3 = 0.13$).

Since there is no extra-pair copulation, the magnitudes of k_{12}, k_{13}, and k_{23} were set to zero. As chimpanzee females regularly mate with males from outside of the group (Tutin 1979), it is reasonable to assume a female should be able to discern between the type 1 and 2 males with a probability of 50% in approximately 1 week ($D = 3$).

D.6. Humans

In humans, type 1 males contribute time (and other resources) to child rearing; type 2 do not contribute appreciably in this way; and type 3 males coerce females when they encounter them. For default values, we set $r_1 = 1$. In unigenerational families, raising a child without paternal support can have serious negative effects of offspring success ($r_2 = 0.9$); however, humans evolved in extended family kin groups with extensive grandparent support, and children in these multigenerational families with only one mother have shown to have success at least equal to those from families with only one parent (DaLeire and Kalil 2002). We therefore consider $r_2 = 1$ as well. We set $r_3 = 0.90r_2$ to incorporate the physical, emotional, psychological, and social effects on children conceived from rape (see van Ee and Kleber 2013 for review). The time the female spends in reproduction is estimated based on time to conceive. This includes the typical within-pair time to conception (approximately10-12 months for 95% of couples; Potter and Parker 1964), the duration of pregnancy, and the duration of lactation (which varies culturally but averages around 1-1.5 years; Jones 1986; Jakobsen et al. 1996), resulting in an interbirth interval of approximately 3 years ($t_f = t_1 = 36$).

We assume that type 2 males engaging in short-term reproductive strategies spend approximately 1 month in each relationship ($t_2 = 1$), with type 3 males spending approximately 2 weeks in a relationship to take into account varying coercive strategies (date rape, kidnapping, stalking, etc.) ($t_3 = 0.5$). We suggest that type 1 males have a 94% chance of remaining in a long-term relationship after conceiving a child ($b_1 = 0.06$—based on data from Kawamura 2009), whereas all other types breakup immediately after the reproductive event ($b_2 = b_3 = 1$). Women have a reproductive lifetime approximately 75% that of men (Carlier and Steeno 1984; Paulson et al. 2001; te Velde and Pearson 2002; Vincent et al. 2002; Anderson et al. 2003) ($\lambda_f = 0.75$). But type 1 males have high pair fidelity and generally tend to match the reproductive lifetime of their mates. So we set $\lambda_1 = \lambda_f = 0.75$ but explore variation in operational sex ratio.

Males who engage in a short-term reproductive strategy are prone to risky and criminal behavior and may thus depart early from the population either by decreased lifespan or incarceration (Lalumière and Quinsey 1996; Gladden et al. 2008; Jonason et al. 2009). We therefore estimate the reproductive lifetime of type 2 males to be slightly less than the physiological relative maximum of 1 ($\lambda_2 = 0.95$), with an even lower reproductive lifetime of type 3 males ($\lambda_3 = 0.9$).

We estimated $\gamma_1 = 0.95$, as 95% of couples conceive within 10-12 months (Potter and Parker 1964). We estimated the odds of conceiving for other males based on female fertility at different points in their cycle. Women have no chance of conceiving outside an approximate 6-day window leading up to ovulation, with probability of conception during that 6-day window varying from 0.1 to 0.33 (Wilcox et al. 1995). Type 2 fertilization rates depend on the type of relationship. For the default, we address the effect of a "new, short-lived relationship" (six episodes of intercourse over two weeks, including the week of high fertility, $\gamma_2 = 0.44$). We also consider a "one-night stand" outside the week of menstruation ($\gamma_2 = 0.061$) and a "weekend fling" scenario (intercourse three times during the week of high fertility, $\gamma_2 = 0.516$). For type 3 males, evidence suggests that the per-incident pregnancy rate is approximately 0.08, which is higher than the random chance of fertilization, suggesting that type 3 males may be able to selectively choose women in the fertile phase of their cycle by detecting subtle cues of fertility and fecundity (Gottschall and Gottschall 2003) ($\gamma_3 = 0.08$).

We estimated k_{12} from the proportion of human births resulting from extra-pair paternity (Larmuseau et al. 2016). The magnitudes of k_{13} and k_{23} were set to 0.2 and 0.3, respectively, as rough guesses. We assume that if coercers were to become abundant in the population, a substantial proportion of births would result from coercion, despite protection that might be afforded by pairing with a type 1 or type 2 male. The level of protection would presumably be less with a type 2 male than with type 1. That these numbers are only guesses becomes important in the context of our results showing that if k_{13} is a substantial over-estimate, then the expected outcome for humans becomes a stable mix of types 1 and 2. Improved estimates of these extra-pair paternity parameters is a high priority for future work with this model and more sophisticated successors.

The discrimination coefficient D was estimated from assuming that an evaluation process lasting about one week should enable the female to distinguish types 1 and 2 males with a probability of 50% ($D = 3$). The out-of-estrus interval t_n was set at 0.8 of a month (time unit), corresponding to the infertile proportion of the monthly cycle.

APPENDIX E: CHAPTER 4.1. SURVEY

E.1. Informed Consent

Consent to Participate in a Research Study KEY INFORMATION FOR

Survey on Personality, Biology and Reproductive Behavior:

You are being invited to take part in a research study about reproductive behavior.

WHAT IS THE PURPOSE, PROCEDURES, AND DURATION OF THIS STUDY?

By doing this study, we hope to learn about the relationship between biology and personality on reproductive behavior. Your participation in this research will last about 20 minutes today and another 20 minutes in two weeks.

WHAT ARE REASONS YOU MIGHT CHOOSE TO VOLUNTEER FOR THIS STUDY?

If you volunteer for this study, you might receive one of three $50 gift cards. Your odds of winning will be 1 in 500 or better. For a complete description of benefits, refer to the Detailed Consent.

WHAT ARE REASONS YOU MIGHT CHOOSE NOT TO VOLUNTEER FOR THIS STUDY?

You might not want to participate if you do not want to spend approximately 20 minutes completing the survey, or do not want to do the survey again in 2 weeks. For a complete description of risks, refer to the Detailed Consent/Appendix.

DO YOU HAVE TO TAKE PART IN THE STUDY?

If you decide to take part in the study, it should be because you really want to volunteer. You will not lose any services, benefits, or rights you would normally have if you choose not to volunteer.

WHAT IF YOU HAVE QUESTIONS, SUGGESTIONS OR CONCERNS?

The person in charge of this study is Kaylynne Glover of the University of Kentucky, Department of Biology. If you have questions, suggestions, or concerns regarding this study or you want to withdraw from the study his/her contact information is kmglover.research@gmail.com.

If you have any questions, suggestions or concerns about your rights as a volunteer in this research, contact staff in the University of Kentucky (UK) Office of Research Integrity (ORI) between the business hours of 8am and 5pm EST, Monday-Friday at 859-257-9428 or toll free at 1-866-400-9428.

DETAILED CONSENT:

ARE THERE REASONS WHY YOU WOULD NOT QUALIFY FOR THIS STUDY?

You should not participate in this study if you are transgender, not heterosexual, or not a female. You also should not participate if you are using hormonal contraceptives, if you are not between the ages of 18 and 25, or if you are not enrolled in the University of Kentucky.

WHERE IS THE STUDY GOING TO TAKE PLACE AND HOW LONG WILL IT LAST?

The research procedures will be conducted at online and should take approximately 20 minutes.

WHAT WILL YOU BE ASKED TO DO?

We will ask you to complete a survey asking you questions on your menstrual cycle, on your opinion on images of men, and some basic demographic information. We will contact you approximately two weeks later to have you do the survey again.

WHAT ARE THE POSSIBLE RISKS AND DISCOMFORTS?

To the best of our knowledge, the things you will be doing have no more risk of harm than you would experience in everyday life. You may also experience a previously unknown risk or side effect.

WILL YOU BENEFIT FROM TAKING PART IN THIS STUDY?

There is no guarantee that you will get any benefit from taking part in this study. Your willingness to take part, however, may, in the future, help society as a whole better understand this research topic.

WHAT WILL IT COST YOU TO PARTICIPATE?

There are no costs associated with taking part in the study except the time it takes to complete it.

WHO WILL SEE THE INFORMATION THAT YOU GIVE?

We will make every effort to keep confidential all research records that identify you to the extent allowed by law.

Your information will be combined with information from other people taking part in the study. When we write about the study to share it with other researchers, we will write about the combined information we have gathered. You will not be personally identified in these written materials. We may publish the results of this study; however, we will keep your name and other identifying information private. We will make every effort to prevent anyone who is not on the research team from knowing that you gave us information, or what that information is.

Your name and personally-identifying information will be coded, and the code will be maintained in a password-protected file kept separate from all other researchers and research files. All digital files will be stored on hard drives (not cloud storage) that will be password protected (either on a laptop or a desktop), and all paper files will be kept in a locked office (in paper form). Only the PIs will have access to the digital data.

We will keep private all research records that identify you to the extent allowed by law. However, there are some circumstances in which we may have to show your information to other people. For example, the law may require us to show your information to a court.

Also, we may be required to show information which identifies you to people who need to be sure we have done the research correctly; these would be people from such organizations as the University of Kentucky.

We will make every effort to safeguard your data, but, the security of data obtained through commercial survey companies cannot be guaranteed. It is also possible the data collected for research purposes may be used for marketing or reporting purposes by the company, depending on the company's Terms of Service and Privacy policies.

CAN YOU CHOOSE TO WITHDRAW FROM THE STUDY EARLY?

You can choose to leave the study at any time. You will not be treated differently if you decide to stop taking part in the study.

If you choose to leave the study early, data collected until that point will remain in the study database and may not be removed.

The investigators conducting the study may need to remove you from the study. This may occur for a number of reasons. You may be removed from the study if you are not able to follow the directions, they find that your participation in the study is more risk than benefit to you, or the agency paying for the study chooses to stop the study early for a number of scientific reasons.

WILL YOU RECEIVE ANY REWARDS FOR TAKING PART IN THIS STUDY?

You may receive a monetary reward for taking part in this study. If you complete the survey, you will be offered the chance to win one of three $50 gift cards, and your odds of winning will be 1 in 500 or better.

WHAT IF NEW INFORMATION IS LEARNED DURING THE STUDY THAT MIGHT AFFECT YOUR DECISION TO PARTICIPATE?

You will be informed if the investigators learn new information that could change your mind about staying in the study. You may be asked to sign a new informed consent form if the information is provided to you after you have joined the study.

WILL YOU BE GIVEN INDIVIDUAL RESULTS FROM THE RESEARCH TESTS/SURVEYS?

This survey is not designed to provide clinical information, and any results will not be provided to you.

WHAT ELSE DO YOU NEED TO KNOW?

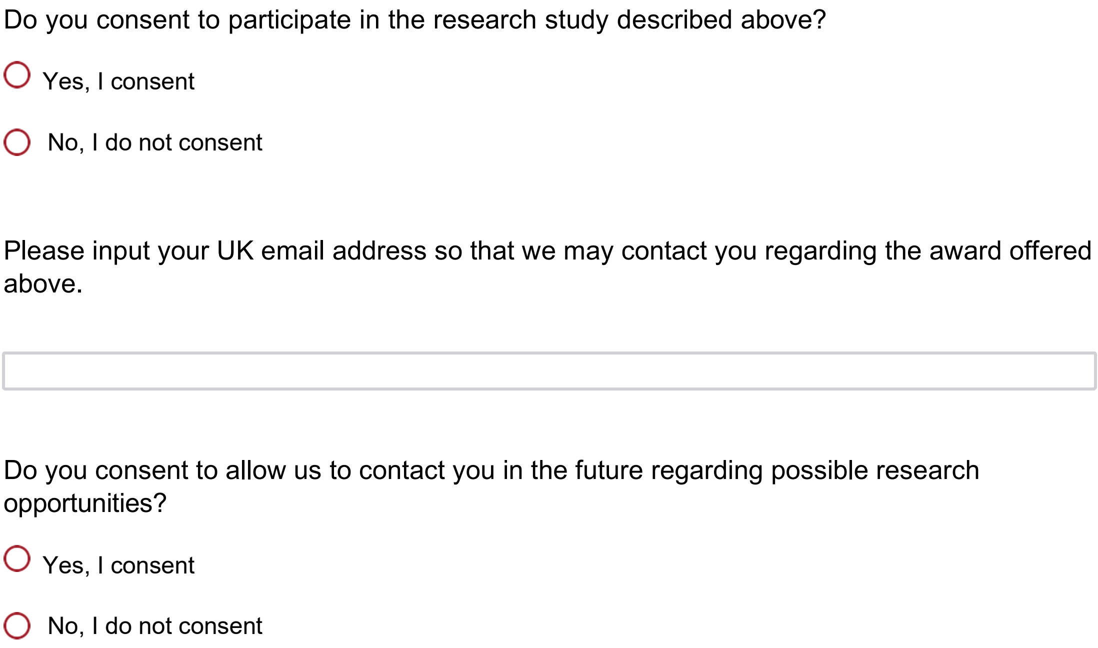
If you volunteer to take part in this study, you will be one of about 1500 people to do so. The research is being conducted by a graduate student, and she is being guided in this research by Dr. Phil Crowley, a professor in the biology department. There may be other people on the research team assisting at different times during the study.

The Howard Hughes Medical Institute is providing financial support and/or material for this study.

FUTURE USE OF YOUR INFORMATION:

Identifiable information such as your name, clinical record number, or date of birth may be removed from the data collected in this study. After removal of the identifiable information, the data may be used for future research or shared with other researchers without your additional informed consent.

In addition to the main study, you are being asked to allow us to contact you in the future for related studies. This is unrelated to your participation in this study and will not affect your eligibility for this study. You have the ability to indicate your preference below.



Do you consent to participate in the research study described above?

○ Yes, I consent

○ No, I do not consent

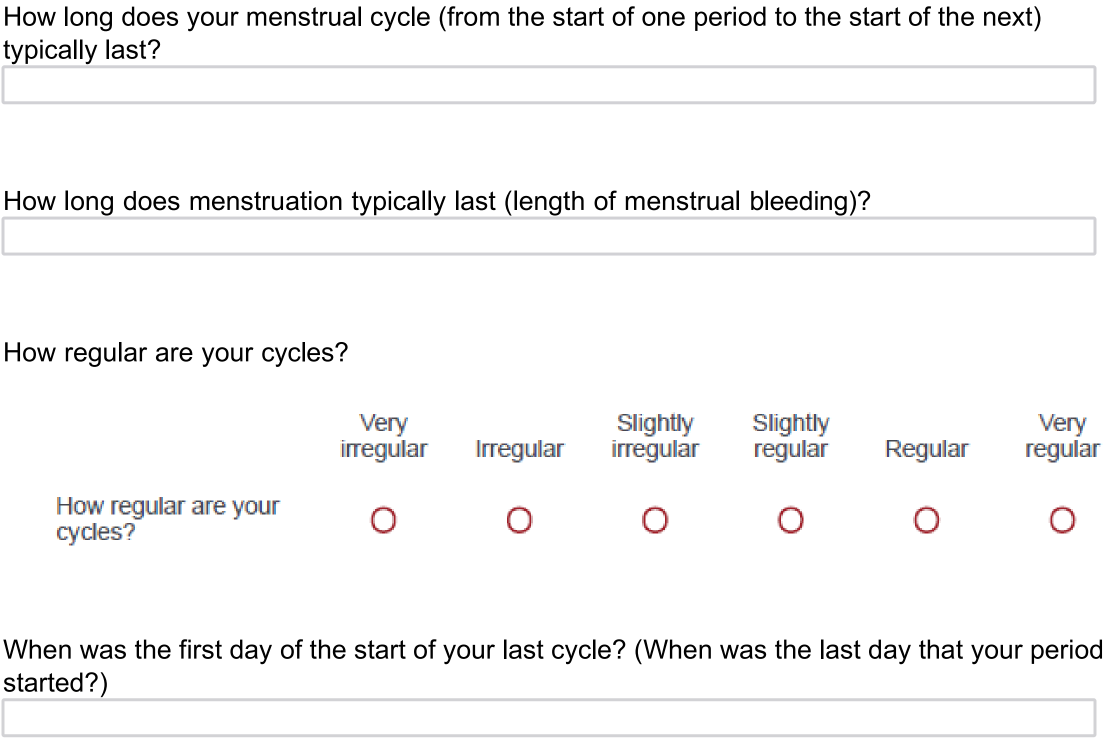
Please input your UK email address so that we may contact you regarding the award offered above.

Do you consent to allow us to contact you in the future regarding possible research opportunities?

○ Yes, I consent

○ No, I do not consent

E.2. Fertility Questions



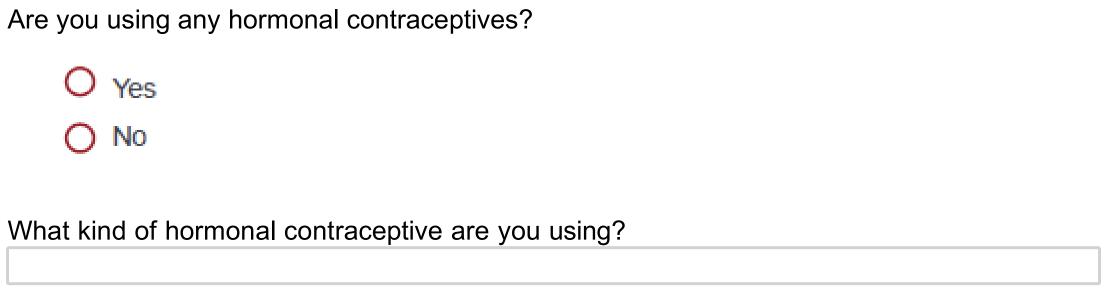
How long does your menstrual cycle (from the start of one period to the start of the next) typically last?

How long does menstruation typically last (length of menstrual bleeding)?

How regular are your cycles?

	Very irregular	Irregular	Slightly irregular	Slightly regular	Regular	Very regular
How regular are your cycles?	○	○	○	○	○	○

When was the first day of the start of your last cycle? (When was the last day that your period started?)



Are you using any hormonal contraceptives?

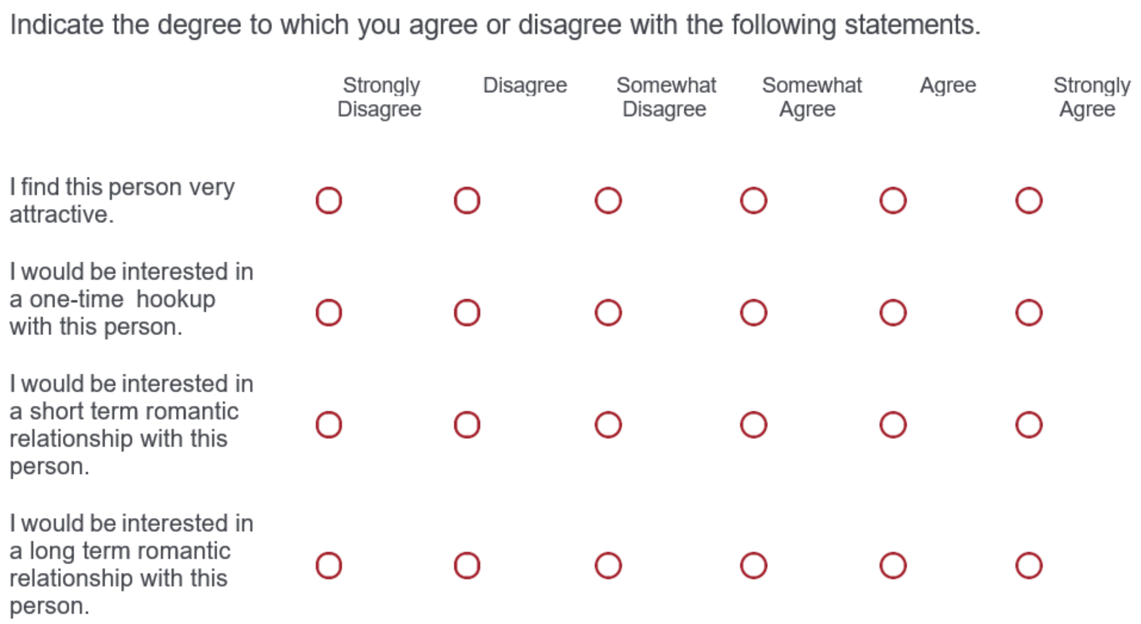
○ Yes

○ No

What kind of hormonal contraceptive are you using?

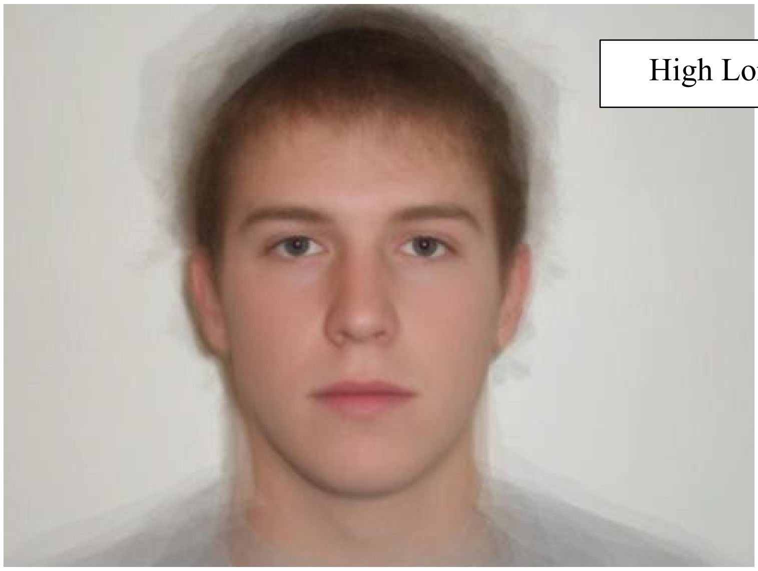
E.3. Faces and Questions

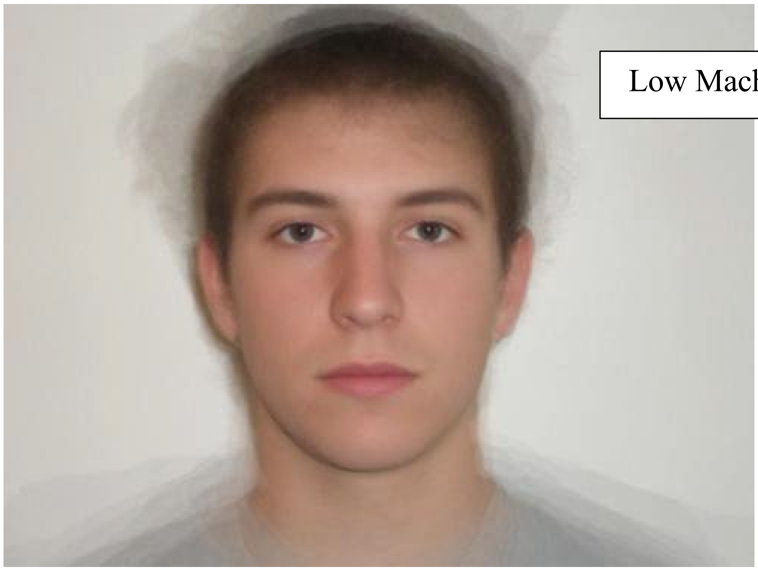
The participants were asked to answer the following questions for each of the subsequently following images, which were presented individually. The images are labeled with their associated trait; these labels were not presented to participants.



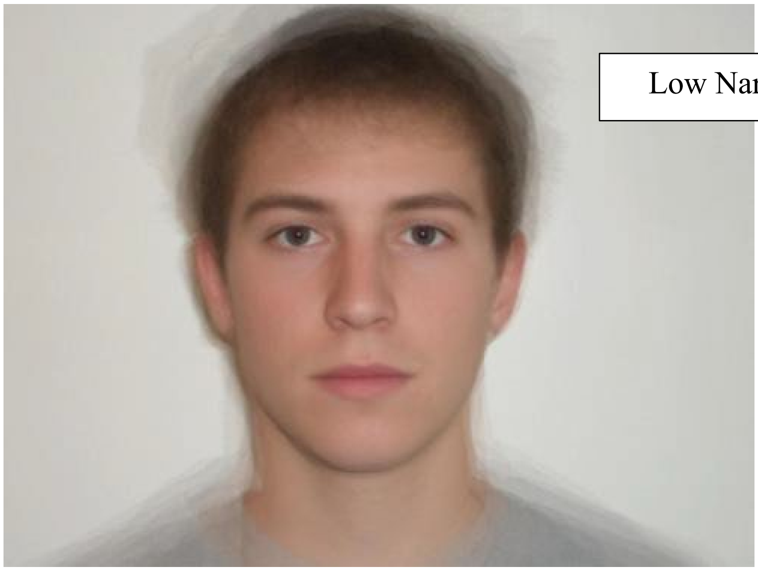
Indicate the degree to which you agree or disagree with the following statements.

	Strongly Disagree	Disagree	Somewhat Disagree	Somewhat Agree	Agree	Strongly Agree
I find this person very attractive.	○	○	○	○	○	○
I would be interested in a one-time hookup with this person.	○	○	○	○	○	○
I would be interested in a short term romantic relationship with this person.	○	○	○	○	○	○
I would be interested in a long term romantic relationship with this person.	○	○	○	○	○	○

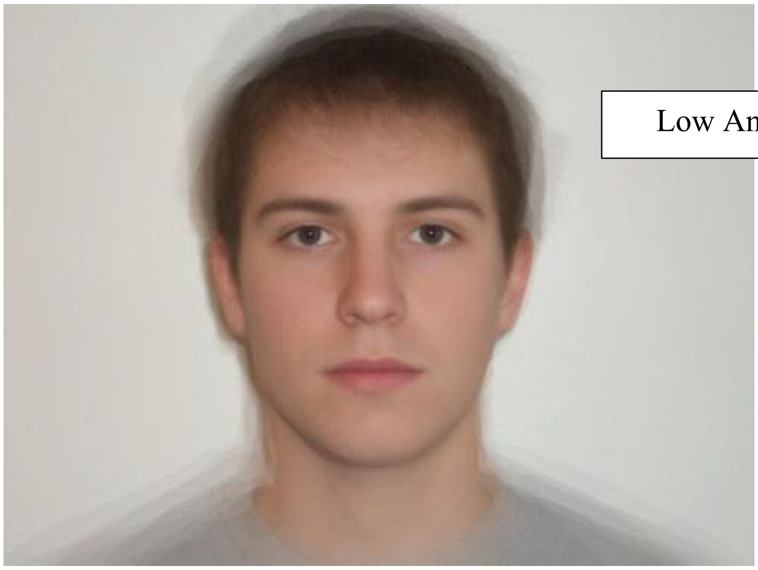

High Long-term


Low Machiavellian

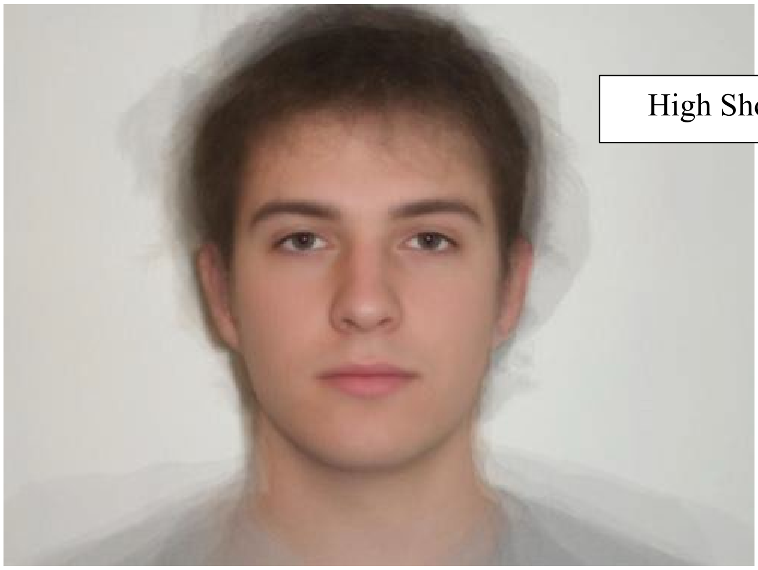

High Psychopathy



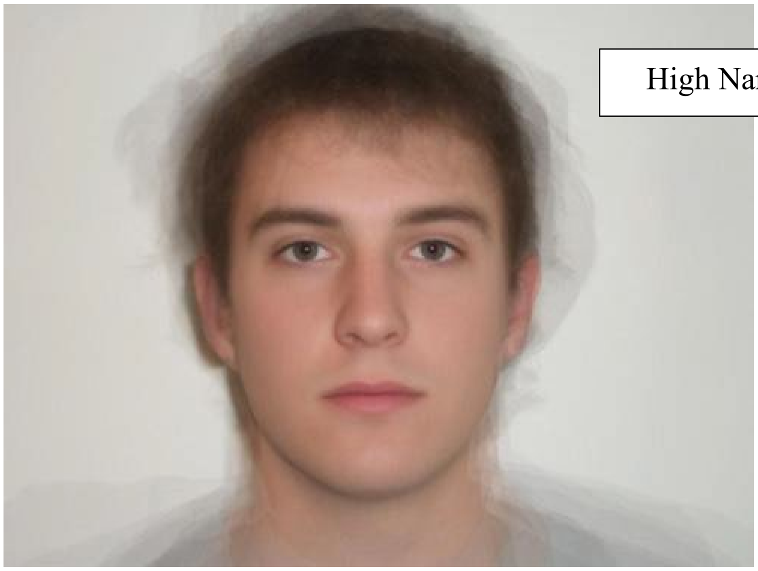
Low Narcissism



Low Antisocial

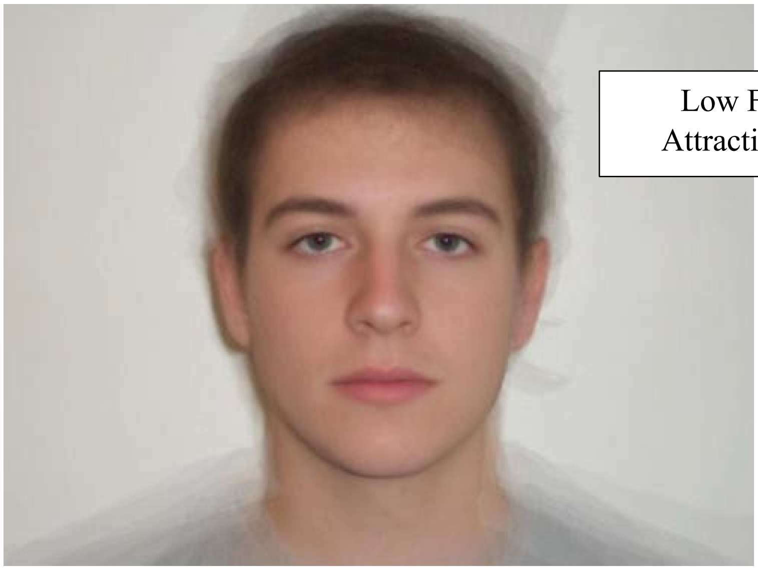


High Short-term



High Narcissism

High Machiavellianism



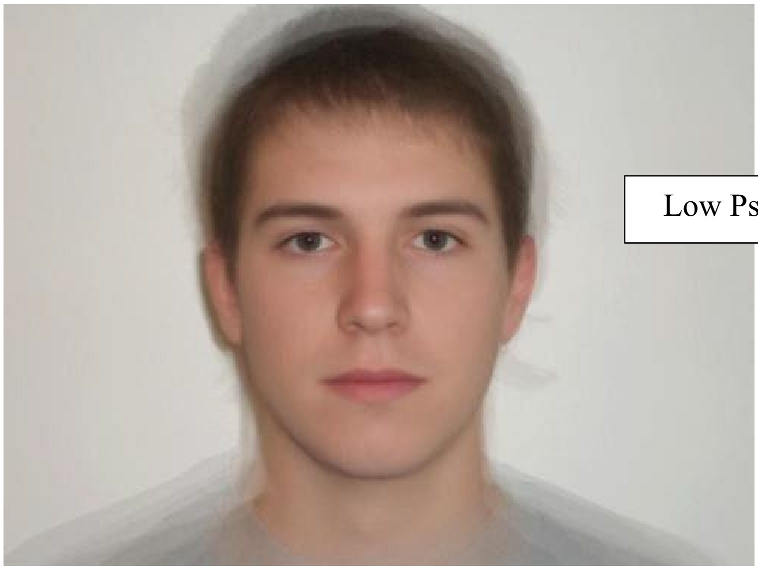
Low Facial Attractiveness


High Facial Attractiveness


High Antisociality


Low Short-term

Low Long-term



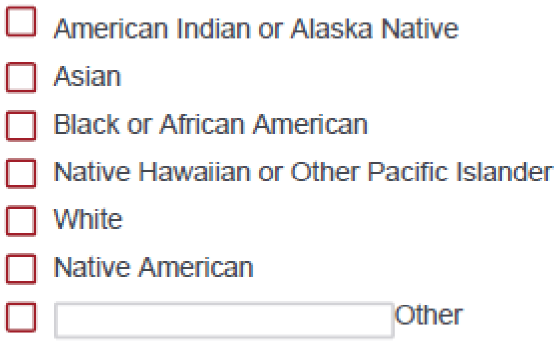
Low Psychopathy

E.4. Demographic Questions

What is your age?

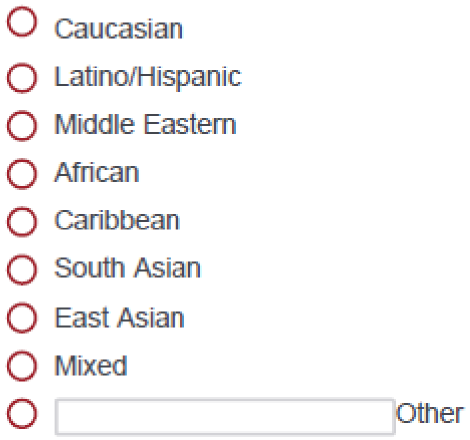
- ○ 18
- ○ 19
- ○ 20
- ○ 21
- ○ 22
- ○ 23
- ○ 24
- ○ 25

Please indicate your racial identity. You may select more than one option.



- ☐ American Indian or Alaska Native
- ☐ Asian
- ☐ Black or African American
- ☐ Native Hawaiian or Other Pacific Islander
- ☐ White
- ☐ Native American
- ☐ Other

Please indicate your ethnicity (i.e. peoples' ethnicity describes their feeling of belonging and attachment to a distinct group of a larger population that shares their ancestry, color, language or religion). You may select more than one option.



- ○ Caucasian
- ○ Latino/Hispanic
- ○ Middle Eastern
- ○ African
- ○ Caribbean
- ○ South Asian
- ○ East Asian
- ○ Mixed
- ○ Other

Are you now or were you in the past ever legally married to a partner?

- ○ Yes: Currently Married
- ○ Yes: Divorced / Separated
- ○ Yes: Widowed
- ○ No

Which option best describes your current relationship status?

- ○ Single: Looking
- ○ Single: Not Looking
- ○ Dating: One or more casual partners
- ○ Committed: Closed Relationship / Monogamous
- ○ Committed: Open or Poly Relationship
- ○ Other

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APPENDIX F: CHAPTER 4.2. SPSS SYNTAX

F.1. Model Factors (Table 3.5)

Context of Rating (Context)	
Attractiveness	AttRate
Hookup Interest Potential	HookRate
Long-term Interest Potential	LongRate
Short-term Interest Potential	ShortRate

Image Types (ImageType)		**Axis**	**Level**
High Facial Attractiveness	HFA	FA	High
Low Facial Attractiveness	LFA	FA	Low
High Long-term Potential	HLT	LT	High
Low Long-term Potential	LLT	LT	Low
High Short-term Potential	HST	ST	High
Low Short-term Potential	LST	ST	Low
High Antisocial	HAS	AS	High
Low Antisocial	LAS	AS	Low
High Machiavellianism	HMA	MA	High
Low Machiavellianism	LMA	MA	Low
High Narcissism	HNA	NA	High
Low Narcissism	LNA	NA	Low
High Psychopathy	HPS	PS	High
Low Psychopathy	LPS	PS	Low

Menstrual Cycle Phase (Phase)	**Fertile Status (FertStat)**	**Luteal Status (LutStat)**
Other	Not Fertile	Not Luteal
Menstrual	Not Fertile	Not Luteal
Fertile	Fertile	Not Luteal
Luteal	Not Fertile	Luteal

Relationship Status (RelShip)	**Looking Status**
Single: Not Looking	Not Looking
Single: Looking	Look
Dating: One or more casual partners	Look
Committed: Open or Poly Relationship	Look
Committed: Closed Relationship / Monogamous	Not Looking
Other	Look

F.2. Syntax for Analyses

```
* Encoding: UTF-8.
*H1a.
DATASET ACTIVATE DataSet1.
USE ALL.
compute filt_2 = 0.
if(Context# <= 2 & Axis#=1) filt_2 = 1.
variable labels filt_2 'Filter AttRate and HookRate for FA'.
```

```
filter by filt_2.
crosstabs Context by Axis.
EXECUTE.
DATASET ACTIVATE DataSet1.
MIXED Rating BY Context Level AssignedID
    /CRITERIA=DFMETHOD(SATTERTHWAITE) CIN(95) MXITER(50) MXSTEP(10) SCORING(1)
    SINGULAR(0.000000000001) HCONVERGE(0, ABSOLUTE) LCONVERGE(0, ABSOLUTE)
                PCONVERGE(0.000001, ABSOLUTE)
  /FIXED=Context Level Context*Level | SSTYPE(3)
  /METHOD=REML
  /PRINT=LMATRIX SOLUTION HISTORY(1)
  /RANDOM=AssignedID | COVTYPE(VC)
  /EMMEANS=TABLES(OVERALL)
  /EMMEANS=TABLES(Context) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(Level) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(Context*Level) COMPARE(Context) ADJ(LSD)
  /EMMEANS=TABLES(Context*Level) COMPARE(Level) ADJ(LSD)

*H1b.
DATASET ACTIVATE DataSet1.
USE ALL.
compute filt_2 = 0.
if(Context#=3 & Axis#=2) filt_2 = 1.
variable labels filt_2 'Filter LongRate for LT'.
filter by filt_2.
crosstabs Context by Axis.
EXECUTE.
MIXED Rating BY Level AssignedID
    /CRITERIA=DFMETHOD(SATTERTHWAITE) CIN(95) MXITER(50) MXSTEP(10) SCORING(1)
    SINGULAR(0.000000000001) HCONVERGE(0, ABSOLUTE) LCONVERGE(0, ABSOLUTE)
                PCONVERGE(0.000001, ABSOLUTE)
  /FIXED= Level | SSTYPE(3)
  /METHOD=REML
  /PRINT=CPS CORB COVB DESCRIPTIVES G  LMATRIX R SOLUTION TESTCOV HISTORY(1)
  /RANDOM=AssignedID | COVTYPE(VC)
  /EMMEANS=TABLES(OVERALL)
  /EMMEANS=TABLES(Level) COMPARE ADJ(LSD).

 * H1c.
DATASET ACTIVATE DataSet1.
USE ALL.
compute filt_2 = 0.
if(Context#=4 & Axis#=3) filt_2 = 1.
variable labels filt_2 'Filter ShortRate for ST'.
filter by filt_2.
crosstabs Context by Axis.
EXECUTE.
MIXED Rating BY Level AssignedID
    /CRITERIA=DFMETHOD(SATTERTHWAITE) CIN(95) MXITER(50) MXSTEP(10) SCORING(1)
    SINGULAR(0.000000000001) HCONVERGE(0, ABSOLUTE) LCONVERGE(0, ABSOLUTE)
                PCONVERGE(0.000001, ABSOLUTE)
  /FIXED= Level | SSTYPE(3)
  /METHOD=REML
```

```
 /PRINT=LMATRIX SOLUTION HISTORY(1)
 /RANDOM=AssignedID | COVTYPE(VC)
 /EMMEANS=TABLES(OVERALL)
 /EMMEANS=TABLES(Level) COMPARE ADJ(LSD)

 * H1d.
DATASET ACTIVATE DataSet1.
USE ALL.
compute filt_2 = 0.
if(Axis#>=4) filt_2 = 1.
variable labels filt_2 'Filter AllRate for SCP'.
filter by filt_2.
frequencies Axis.
EXECUTE.
MIXED Rating BY Context Axis Level AssignedID
   /CRITERIA=DFMETHOD(SATTERTHWAITE) CIN(95) MXITER(50) MXSTEP(10) SCORING(1)
   SINGULAR(0.000000000001) HCONVERGE(0, ABSOLUTE) LCONVERGE(0, ABSOLUTE)
         PCONVERGE(0.000001, ABSOLUTE)
 /Fixed = Context Axis Level Context*Axis Context*Level Axis*Level Context*Axis*Level
| SSTYPE(3)
 /METHOD=REML
 /PRINT=LMATRIX SOLUTION HISTORY(1)
 /RANDOM=AssignedID | COVTYPE(VC)
 /EMMEANS=TABLES(OVERALL)
 /EMMEANS=TABLES(Context) COMPARE ADJ(LSD)
 /EMMEANS=TABLES(Axis) COMPARE ADJ(LSD)
 /EMMEANS=TABLES(Level) COMPARE ADJ(LSD)
 /EMMEANS=TABLES(Context*Axis) COMPARE(Context) ADJ(LSD)
 /EMMEANS=TABLES(Context*Axis) COMPARE(Axis) ADJ(LSD)
 /EMMEANS=TABLES(Context*Level) COMPARE(Level) ADJ(LSD)
 /EMMEANS=TABLES(Context*Level) COMPARE(Context) ADJ(LSD)
 /EMMEANS=TABLES(Axis*Level) COMPARE(Axis) ADJ(LSD)
 /EMMEANS=TABLES(Axis*Level) COMPARE(Level) ADJ(LSD)
 /EMMEANS=TABLES(Context*Axis*Level) COMPARE(Level) ADJ(LSD)
 /EMMEANS=TABLES(Context*Axis*Level) COMPARE(Axis) ADJ(LSD)
 /EMMEANS=TABLES(Context*Axis*Level) COMPARE(Context) ADJ(LSD)
 /EMMEANS=TABLES(Axis*Level*Context) COMPARE(Level) ADJ(LSD)
 /EMMEANS=TABLES(Axis*Level*Context) COMPARE(Axis) ADJ(LSD)
 /EMMEANS=TABLES(Axis*Level*Context) COMPARE(Context) ADJ(LSD)
 /EMMEANS=TABLES(Level*Context*Axis) COMPARE(Level) ADJ(LSD)
 /EMMEANS=TABLES(Level*Context*Axis) COMPARE(Axis) ADJ(LSD)
 /EMMEANS=TABLES(Level*Context*Axis) COMPARE(Context) ADJ(LSD)

 * H2.
DATASET ACTIVATE DataSet1.
USE ALL.
compute filt_2 = 0.
if(Axis#=2 & Context#=1 OR Axis#=2 & Context#=3) filt_2 = 1.
variable labels filt_2 'Filter AttRate & LongRate for LT'.
filter by filt_2.
crosstabs Context by Axis.
EXECUTE.
MIXED Rating BY Context Level AssignedID
```

```
    /CRITERIA=DFMETHOD(SATTERTHWAITE) CIN(95) MXITER(50) MXSTEP(10) SCORING(1)
    SINGULAR(0.000000000001) HCONVERGE(0, ABSOLUTE) LCONVERGE(0, ABSOLUTE)
            PCONVERGE(0.000001, ABSOLUTE)
 /Fixed = Context Level Context*Level  | SSTYPE(3)
  /METHOD=REML
  /PRINT=LMATRIX SOLUTION HISTORY(1)
  /RANDOM=AssignedID | COVTYPE(VC)
  /EMMEANS=TABLES(OVERALL)
  /EMMEANS=TABLES(Context) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(Level) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(Context*Level) COMPARE(Level) ADJ(LSD)
  /EMMEANS=TABLES(Context*Level) COMPARE(Context) ADJ(LSD)

 * H3.
DATASET ACTIVATE DataSet1.
USE ALL.
EXECUTE.
crosstabs Context by LookStat.
MIXED Rating BY Context LookStat AssignedID
    /CRITERIA=DFMETHOD(SATTERTHWAITE) CIN(95) MXITER(50) MXSTEP(10) SCORING(1)
    SINGULAR(0.000000000001) HCONVERGE(0, ABSOLUTE) LCONVERGE(0, ABSOLUTE)
            PCONVERGE(0.000001, ABSOLUTE)
  /Fixed = Context LookStat Context*LookStat | SSTYPE(3)
  /METHOD=REML
  /PRINT=LMATRIX SOLUTION HISTORY(1)
  /RANDOM=AssignedID | COVTYPE(VC)
  /EMMEANS=TABLES(OVERALL)
  /EMMEANS=TABLES(Context) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(LookStat) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(Context*LookStat) COMPARE(LookStat) ADJ(LSD)
  /EMMEANS=TABLES(Context*LookStat) COMPARE(Context) ADJ(LSD)

 * H4a.
DATASET ACTIVATE DataSet1.
USE ALL.
compute filt_2 = 0.
if(Context#=1 & Image#=3 OR Context#=1 & Image#=5) filt_2 = 1.
variable labels filt_2 'Filter AttRate for HLT and HST'.
filter by filt_2.
crosstabs Context by Axis.
EXECUTE.
MIXED Rating BY Image LutStat AssignedID
    /CRITERIA=DFMETHOD(SATTERTHWAITE) CIN(95) MXITER(50) MXSTEP(10) SCORING(1)
    SINGULAR(0.000000000001) HCONVERGE(0, ABSOLUTE) LCONVERGE(0, ABSOLUTE)
            PCONVERGE(0.000001, ABSOLUTE)
/Fixed = Image LutStat Image*LutStat | SSTYPE(3)
  /METHOD=REML
  /PRINT=LMATRIX SOLUTION HISTORY(1)
  /RANDOM=AssignedID | COVTYPE(VC)
  /EMMEANS=TABLES(OVERALL)
  /EMMEANS=TABLES(Image) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(LutStat) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(Image*LutStat) COMPARE(Image) ADJ(LSD)
```

```
   /EMMEANS=TABLES(Image*LutStat) COMPARE(LutStat) ADJ(LSD)

 * H4b.
DATASET ACTIVATE DataSet1.
USE ALL.
compute filt_2 = 0.
if(Context#=1 & Level#=2 & Axis#=4 OR Context#=1 & Level#=2 & Axis#=5 OR Context#=1 & Level#=2 &
            Axis#=6 OR Context#=1 & Level#=2 & Axis#=7
) filt_2 = 1.
variable labels filt_2 'Filter AttRate for SCP'.
filter by filt_2.
crosstabs Context by Axis.
EXECUTE.
MIXED Rating BY Axis FertStat AssignedID
   /CRITERIA=DFMETHOD(SATTERTHWAITE) CIN(95) MXITER(50) MXSTEP(10) SCORING(1)
   SINGULAR(0.000000000001) HCONVERGE(0, ABSOLUTE) LCONVERGE(0, ABSOLUTE)
            PCONVERGE(0.000001, ABSOLUTE)
  /Fixed = Axis FertStat Axis*FertStat | SSTYPE(3)
  /METHOD=REML
  /PRINT=LMATRIX SOLUTION HISTORY(1)
  /RANDOM=AssignedID | COVTYPE(VC)
  /EMMEANS=TABLES(OVERALL)
  /EMMEANS=TABLES(Axis) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(FertStat) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(FertStat*Axis) COMPARE(FertStat) ADJ(LSD)
  /EMMEANS=TABLES(FertStat*Axis) COMPARE(Axis) ADJ(LSD).

 * H5.
DATASET ACTIVATE DataSet1.
USE ALL.
compute filt_2 = 0.
if(Context#=1 & Image#=5) filt_2 = 1.
variable labels filt_2 'Filter AttRate for HST'.
filter by filt_2.
crosstabs Context by Image.
EXECUTE.
MIXED Rating BY LookStat FertStat AssignedID
   /CRITERIA=DFMETHOD(SATTERTHWAITE) CIN(95) MXITER(50) MXSTEP(10) SCORING(1)
   SINGULAR(0.000000000001) HCONVERGE(0, ABSOLUTE) LCONVERGE(0, ABSOLUTE)
            PCONVERGE(0.000001, ABSOLUTE)
  /Fixed = LookStat FertStat LookStat*FertStat | SSTYPE(3)
  /METHOD=REML
  /PRINT=LMATRIX SOLUTION HISTORY(1)
  /RANDOM=AssignedID | COVTYPE(VC)
  /EMMEANS=TABLES(OVERALL)
  /EMMEANS=TABLES(LookStat) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(FertStat) COMPARE ADJ(LSD)
  /EMMEANS=TABLES(LookStat*FertStat) COMPARE(FertStat) ADJ(LSD)
  /EMMEANS=TABLES(LookStat*FertStat) COMPARE(LookStat) ADJ(LSD).
```

APPENDIX G: CHAPTER 5.1. SPSS SYNTAX FOR PRELIMINARY ANALYSES

G.1. Model terms and definitions.

Random Effects

- Participant ID (ID)
- Each cycle for which we have data (CycleID)

Fixed Effects

Preliminary Analyses

- Pre- or Post-Study Survey (Survey)
- Hormone Types (HormType) (open response)
  - Estrogen, Estradiol, Testosterone, Progesterone, FSH, LH, Prostaglandins, GnRH
- When Pregnancy Might Be Possible (Pregnancy) (options provided, more than one response allowed)
  - Menses, After Menses, Midcycle, Toward the beginning of the next cycle, All points are equal
- Did Participants Seek New Information (NewInfo) (open response)
  - No, Not really, A little bit, Yes

Prediction Analyses

- Rating of Sexual Desire (Desire) (scale 1-6)
- Indicated Sexual Response (Response)
  - Avoid, Acquiesce, Seek
- Rating of Happiness (Happiness) (scale 1-10)
- Cycle with Confirmed Fertility (LHState)
- Method of State Designation
  - Hormonal, Luteal Midpoint (H-LM)
  - Hormonal, Non-fertile, 4-day buffer (H-NF-4)
  - Estimated +14, Luteal Midpoint (+14-LM)
  - Estimated +14, Non-fertile, 4-day buffer (+14-NF-4)
- The estimated probability of conception each day for each cycle (Probability)

G.2. Analysis: Hormones in Cycle.

```
DATASET ACTIVATE DataSet3.
USE ALL.
MIXED HormResponse BY HormType NewInfo Survey ID
  /CRITERIA=DFMETHOD(SATTERTHWAITE) CIN(95) MXITER(100) MXSTEP(10) SCORING(1)
    SINGULAR(0.000000000001) HCONVERGE(0, ABSOLUTE) LCONVERGE(0, ABSOLUTE)
          PCONVERGE(0.000001, ABSOLUTE)
  /FIXED=HormType Survey NewInfo HormType*Survey HormType*NewInfo*Survey  | SSTYPE(3)
  /METHOD=REML
  /PRINT=CPS CORB COVB DESCRIPTIVES G  LMATRIX R SOLUTION TESTCOV HISTORY(1)
  /RANDOM=ID | COVTYPE(VC)
  /EMMEANS=TABLES(OVERALL)
  /EMMEANS=TABLES(Survey) COMPARE ADJ(BONFERRONI)
  /EMMEANS=TABLES(HormType) COMPARE ADJ(BONFERRONI)
  /EMMEANS=TABLES(HormType*Survey) COMPARE(Survey) ADJ(BONFERRONI)
  /EMMEANS=TABLES(HormType*NewInfo*Survey) COMPARE(Survey) ADJ(BONFERRONI)   .
```

G.3. Analysis: Peak Fertility.

```
DATASET ACTIVATE DataSet3.
USE ALL.
MIXED PregResponse BY Pregnancy Survey NewInfo ID
 /CRITERIA=DFMETHOD(SATTERTHWAITE) CIN(95) MXITER(100) MXSTEP(10) SCORING(1)
   SINGULAR(0.000000000001) HCONVERGE(0, ABSOLUTE) LCONVERGE(0, ABSOLUTE)
         PCONVERGE(0.000001, ABSOLUTE)
 /FIXED=Pregnancy Survey NewInfo Pregnancy*Survey Pregnancy*NewInfo*Survey | SSTYPE(3)
 /METHOD=REML
 /PRINT=CPS CORB COVB DESCRIPTIVES G  LMATRIX R SOLUTION TESTCOV HISTORY(1)
 /RANDOM=ID | COVTYPE(VC)
 /EMMEANS=TABLES(OVERALL)
 /EMMEANS=TABLES(Survey) COMPARE ADJ(BONFERRONI)
 /EMMEANS=TABLES(Pregnancy) COMPARE ADJ(BONFERRONI)
 /EMMEANS=TABLES(Pregnancy*Survey) COMPARE(Survey) ADJ(BONFERRONI)
 /EMMEANS=TABLES(Pregnancy*NewInfo*Survey) COMPARE(Survey) ADJ(BONFERRONI)   .
```

APPENDIX H: CHAPTER 5.2. SPSS SYNTAX FOR MODELS

H.1. Model terms and definitions.

Random Effects

- Participant ID (ID)
- Each cycle for which we have data (CycleID)

Fixed Effects

- Preliminary Analyses
  - Pre- or Post-Study Survey (Survey)
  - Hormone Types (HormType) (open response)
    - Estrogen, Estradiol, Testosterone, Progesterone, FSH, LH, Prostaglandins, GnRH
  - When Pregnancy Might Be Possible (Pregnancy) (options provided, more than one response allowed)
    - Menses, After Menses, Midcycle, Toward the beginning of the next cycle, All points are equal
  - Did Participants Seek New Information (NewInfo) (open response)
    - No, Not really, A little bit, Yes
- Prediction Analyses
  - Rating of Sexual Desire (Desire) (scale 1-6)
  - Indicated Sexual Response (Response)
    - Avoid, Acquiesce, Seek
  - Rating of Happiness (Happiness) (scale 1-10)
  - Cycle with Confirmed Fertility (LHState)
  - Method of State Designation
    - Hormonal, Luteal Midpoint (H-LM)
    - Hormonal, Non-fertile, 4-day buffer (H-NF-4)
    - Estimated +14, Luteal Midpoint (+14-LM)
    - Estimated +14, Non-fertile, 4-day buffer (+14-NF-4)
  - The estimated probability of conception each day for each cycle (Probability)

H.2. Analysis: Desire Models

```
OUTPUT NEW.
OUTPUT NAME H.Desire.
OUTPUT ACTIVATE H.Desire.


*DESIRE
*HProbability.
*Luteal.
*HLM, 2-way.
DATASET ACTIVATE DataSet1.
USE ALL.
COMPUTE filter_$=(Method="HLM" AND State<>0 AND LHState=1).
VARIABLE LABELS filter_$ 'Method="HLM" AND State<>0 AND LHState=1 (FILTER)'.
VALUE LABELS filter_$ 0 'Not Selected' 1 'Selected'.
FORMATS filter_$ (f1.0).
FILTER BY filter_$.
EXECUTE.
GENLINMIXED
  /DATA_STRUCTURE SUBJECTS=ID*CycleID
  /FIELDS TARGET=DesireOrdinal TRIALS=NONE OFFSET=NONE
  /TARGET_OPTIONS  DISTRIBUTION=MULTINOMIAL LINK=LOGIT
  /FIXED EFFECTS=Belief  Happiness Probability
  Belief* Happiness Belief* Probability Happiness * Probability USE_INTERCEPT=TRUE
  /RANDOM EFFECTS=ID*CycleID SUBJECTS=ID USE_INTERCEPT=FALSE
        COVARIANCE_TYPE=VARIANCE_COMPONENTS SOLUTION=FALSE
  /BUILD_OPTIONS TARGET_CATEGORY_ORDER=ASCENDING INPUTS_CATEGORY_ORDER=ASCENDING
        MAX_ITERATIONS=100
  CONFIDENCE_LEVEL=95 DF_METHOD=RESIDUAL COVB=MODEL PCONVERGE=0.000001(ABSOLUTE)
        SCORING=0 SINGULAR=0.000000000001 .
OUTPUT MODIFY
/SELECT OUTLINEHEADERS
/IF LABELS=[EXACT('Generalized Linear Mixed Models')]
/OBJECTPROPERTIES
OUTLINELABEL = "Des HLM 2-way".
*HLM, 3-way.
GENLINMIXED
  /DATA_STRUCTURE SUBJECTS=ID*CycleID
  /FIELDS TARGET=DesireOrdinal TRIALS=NONE OFFSET=NONE
  /TARGET_OPTIONS  DISTRIBUTION=MULTINOMIAL LINK=LOGIT
  /FIXED EFFECTS=Belief  Happiness Probability
  Belief* Happiness Belief* Probability Happiness * Probability
  Belief* Happiness * Probability USE_INTERCEPT=TRUE
  /RANDOM EFFECTS=ID*CycleID SUBJECTS=ID USE_INTERCEPT=FALSE
        COVARIANCE_TYPE=VARIANCE_COMPONENTS SOLUTION=FALSE
  /BUILD_OPTIONS TARGET_CATEGORY_ORDER=ASCENDING INPUTS_CATEGORY_ORDER=ASCENDING
        MAX_ITERATIONS=100
  CONFIDENCE_LEVEL=95 DF_METHOD=RESIDUAL COVB=MODEL PCONVERGE=0.000001(ABSOLUTE)
        SCORING=0 SINGULAR=0.000000000001 .
```

```
OUTPUT MODIFY
/SELECT OUTLINEHEADERS
/IF LABELS=[EXACT('Generalized Linear Mixed Models')]
/OBJECTPROPERTIES
OUTLINELABEL = "Des HLM 3-way".
```

H.3. Analysis: Response Models

```
OUTPUT NEW.
OUTPUT NAME H.Response.
OUTPUT ACTIVATE H.Response.

*RESPONSE
*HProbability.
*Luteal.

*HLM, 2-way.
DATASET ACTIVATE DataSet1.
USE ALL.
COMPUTE filter_$=(Method="HLM" AND State<>0 AND LHState=1).
VARIABLE LABELS filter_$ 'Method="HLM"  AND State<>0 AND LHState=1 (FILTER)'.
VALUE LABELS filter_$ 0 'Not Selected' 1 'Selected'.
FORMATS filter_$ (f1.0).
FILTER BY filter_$.
EXECUTE.
GENLINMIXED
 /DATA_STRUCTURE SUBJECTS=ID*CycleID
 /FIELDS TARGET=Response TRIALS=NONE OFFSET=NONE
 /TARGET_OPTIONS REFERENCE=1 DISTRIBUTION=MULTINOMIAL LINK=LOGIT
 /FIXED EFFECTS=Belief Desire Happiness Probability
 Belief*Desire Belief* Happiness Belief* Probability Desire * Happiness Desire * Probability Happiness *
        Probability USE_INTERCEPT=TRUE
 /RANDOM EFFECTS=ID*CycleID SUBJECTS=ID USE_INTERCEPT=FALSE
        COVARIANCE_TYPE=VARIANCE_COMPONENTS SOLUTION=FALSE
 /BUILD_OPTIONS TARGET_CATEGORY_ORDER=DESCENDING INPUTS_CATEGORY_ORDER=ASCENDING
        MAX_ITERATIONS=100
 CONFIDENCE_LEVEL=95 DF_METHOD=RESIDUAL COVB=MODEL PCONVERGE=0.000001(ABSOLUTE)
        SCORING=0 SINGULAR=0.000000000001 .
OUTPUT MODIFY
/SELECT OUTLINEHEADERS
/IF LABELS=[EXACT('Generalized Linear Mixed Models')]
/OBJECTPROPERTIES
OUTLINELABEL = "Res HLM 2-way".

*HLM, 3-way.
GENLINMIXED
 /DATA_STRUCTURE SUBJECTS=ID*CycleID
 /FIELDS TARGET=Response TRIALS=NONE OFFSET=NONE
 /TARGET_OPTIONS REFERENCE=1 DISTRIBUTION=MULTINOMIAL LINK=LOGIT
 /FIXED EFFECTS=Belief Desire Happiness Probability
```

```
  Belief*Desire Belief* Happiness Belief* Probability Desire * Happiness Desire * Probability Happiness *
        Probability
  Belief*Desire * Happiness  Belief*Desire * Probability  Desire * Happiness * Probability
        USE_INTERCEPT=TRUE
  /RANDOM EFFECTS=ID*CycleID SUBJECTS=ID USE_INTERCEPT=FALSE
        COVARIANCE_TYPE=VARIANCE_COMPONENTS SOLUTION=FALSE
  /BUILD_OPTIONS TARGET_CATEGORY_ORDER=DESCENDING INPUTS_CATEGORY_ORDER=ASCENDING
        MAX_ITERATIONS=100
  CONFIDENCE_LEVEL=95 DF_METHOD=RESIDUAL COVB=MODEL PCONVERGE=0.000001(ABSOLUTE)
        SCORING=0 SINGULAR=0.000000000001 .
OUTPUT MODIFY
/SELECT OUTLINEHEADERS
/IF LABELS=[EXACT('Generalized Linear Mixed Models')]
/OBJECTPROPERTIES
OUTLINELABEL = "Res HLM 3-way".

*HLM, 4-way.
GENLINMIXED
  /DATA_STRUCTURE SUBJECTS=ID*CycleID
  /FIELDS TARGET=Response TRIALS=NONE OFFSET=NONE
  /TARGET_OPTIONS REFERENCE=1 DISTRIBUTION=MULTINOMIAL LINK=LOGIT
  /FIXED EFFECTS=Belief Desire Happiness Probability
  Belief*Desire Belief* Happiness Belief* Probability Desire * Happiness Desire * Probability Happiness *
        Probability
  Belief*Desire * Happiness  Belief*Desire * Probability  Desire * Happiness * Probability
  Belief*Desire * Happiness * Probability USE_INTERCEPT=TRUE
  /RANDOM EFFECTS=ID*CycleID SUBJECTS=ID USE_INTERCEPT=FALSE
        COVARIANCE_TYPE=VARIANCE_COMPONENTS SOLUTION=FALSE
  /BUILD_OPTIONS TARGET_CATEGORY_ORDER=DESCENDING INPUTS_CATEGORY_ORDER=ASCENDING
        MAX_ITERATIONS=100
  CONFIDENCE_LEVEL=95 DF_METHOD=RESIDUAL COVB=MODEL PCONVERGE=0.000001(ABSOLUTE)
        SCORING=0 SINGULAR=0.000000000001 .
OUTPUT MODIFY
/SELECT OUTLINEHEADERS
/IF LABELS=[EXACT('Generalized Linear Mixed Models')]
/OBJECTPROPERTIES
OUTLINELABEL = "Res HLM 4-way".
```

H.4. Analysis: Belief Models

```
*Target(Response) Reference = 1, or "No".

OUTPUT NEW.
OUTPUT NAME H.Belief.
OUTPUT ACTIVATE H.Belief.

*BELIEF BeliefString="Yes" OR BeliefString="No" OR BeliefString="Yes " AND
*HProbability.
*Luteal.
OUTPUT NAME H.Belief.
```

```
*HLM, 2-way.
DATASET ACTIVATE DataSet1.
USE ALL.
COMPUTE filter_$=(Method="HLM" AND State<>0 AND LHState=1 AND Belief >= 0).
VARIABLE LABELS filter_$ 'Method="HLM" AND State<>0 AND LHState=1 AND Belief >= 0"  (FILTER)'.
VALUE LABELS filter_$ 0 'Not Selected' 1 'Selected'.
FORMATS filter_$ (f1.0).
FILTER BY filter_$.
EXECUTE.
GENLINMIXED
  /DATA_STRUCTURE SUBJECTS=ID*CycleID
  /FIELDS TARGET=Belief TRIALS=NONE OFFSET=NONE
  /TARGET_OPTIONS REFERENCE=1 DISTRIBUTION=BINOMIAL LINK=LOGIT
  /FIXED  EFFECTS= Desire Happiness Probability
  Desire * Probability    Happiness * Probability    Desire * Happiness  USE_INTERCEPT=TRUE
  /RANDOM EFFECTS=ID*CycleID SUBJECTS=ID USE_INTERCEPT=FALSE
            COVARIANCE_TYPE=VARIANCE_COMPONENTS SOLUTION=FALSE
  /BUILD_OPTIONS MAX_ITERATIONS=100
  CONFIDENCE_LEVEL=95 DF_METHOD=RESIDUAL COVB=MODEL PCONVERGE=0.000001(ABSOLUTE)
            SCORING=0 SINGULAR=0.000000000001 .
OUTPUT MODIFY
/SELECT OUTLINEHEADERS
/IF LABELS=[EXACT('Generalized Linear Mixed Models')]
/OBJECTPROPERTIES
OUTLINELABEL = "Bel HLM 2-way".

*HLM, 3-way.
GENLINMIXED
  /DATA_STRUCTURE SUBJECTS=ID*CycleID
  /FIELDS TARGET=Belief TRIALS=NONE OFFSET=NONE
  /TARGET_OPTIONS REFERENCE=1 DISTRIBUTION=BINOMIAL LINK=LOGIT
  /FIXED  EFFECTS= Desire Happiness Probability
  Desire * Probability    Happiness * Probability    Desire * Happiness
  Desire * Happiness * Probability   USE_INTERCEPT=TRUE
  /RANDOM EFFECTS=ID*CycleID SUBJECTS=ID USE_INTERCEPT=FALSE
            COVARIANCE_TYPE=VARIANCE_COMPONENTS SOLUTION=FALSE
  /BUILD_OPTIONS MAX_ITERATIONS=100
  CONFIDENCE_LEVEL=95 DF_METHOD=RESIDUAL COVB=MODEL PCONVERGE=0.000001(ABSOLUTE)
            SCORING=0 SINGULAR=0.000000000001 .
OUTPUT MODIFY
/SELECT OUTLINEHEADERS
/IF LABELS=[EXACT('Generalized Linear Mixed Models')]
/OBJECTPROPERTIES
OUTLINELABEL = "Bel HLM 3-way".
```

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