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The impact of fertility cues on intrasexual competition and threat perception

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Abstract

Humans are capable of detecting subtle fertility indicators that change across women’s menstrual cycle. One such indicator is the voice, which may change over the course of the menstrual cycle and provide fertility cues to listeners. Such cues provide an obvious advantage to men selecting mates, however research suggests that women can also detect these cues. Women may monitor the fertility of others to more effectively adjust their own mating strategies. By monitoring women’s skin conductance, cortisol, and testosterone responses to hearing high- and low-fertility female voices, the current study further investigated whether vocal cues of fertility may physiologically prime intrasexual competition. Researchers assessed attractiveness ratings of the voices recorded at high- and low- fertility to further support perceptual differences between voices of women at differing levels of fertility. These responses were examined as a function of the fertility status of the listener by conducting identical trials with women both when they were at high- and low-fertility. Although women did not exhibit a rise in cortisol, and skin conductance did not differ in response to voices of high- and low- fertility, women did find high-fertility voices more attractive, and their testosterone levels rose following exposure to stimuli. Our findings also suggest that women may be more attune to fertility cues when they are at high-fertility themselves. These reactions are discussed in light of how they may affect mating strategies and behavior following fertility cue exposure.
PHYSIOLOGICAL RESPONSES TO FERTILITY CUES

The Impact of Fertility Cues on Intrasexual Competition and Threat Perception

Across the different menstrual cycle phases, women exhibit a variety of physical, neural, and psychological changes. Sex hormone levels dramatically differ between menstrual cycle phases, and this largely affects the observed cyclical changes. Of particular interest are the physical differences between the high-fertility and low-fertility menstrual cycle phases. Many mammals have an estrous cycle, rather than a menstrual cycle. Generally, an estrous cycle contains an estrus phase preceding peak fertility during which mammals exhibit overt physical changes that inform male conspecifics of fertility and sexual receptivity. Humans have menstrual cycles, and most researchers posit the humans conceal overt signs of fertility (see Alexander & Noonan, 1979). However, observations of some cyclical changes suggest that women do not completely conceal their fertility, and that men and women alike may alter their mating strategies because of these changes. When interpreting changes that take place across the menstrual cycle, it is important to understand the typical hormonal characteristics of the human menstrual cycle.

The Menstrual Cycle

Although not all menstrual cycles are the same, they typically last 28 days. The follicular phase begins with menstruation and continues through approximately the fourteenth day of the cycle, the last 14 days of the cycle are referred to as the luteal phase, and ovulation typically takes place in the late-follicular phase around days 12-14. Estrogen levels are lowest during the menses and slowly rise throughout the mid-follicular phase. Levels spike to their highest during the late-follicular phase and during ovulation, only to markedly decrease after ovulation, increase slightly during the mid-luteal phase, and
progressively decrease back to very low levels during the late-luteal phase. Women exhibit negligible progesterone levels throughout the follicular phase. Progesterone levels rise soon after the onset of ovulation and reach their peak during the mid-luteal phase, then decrease in transition to the late-luteal phase. Ovulation, when present, begins in the late-follicular phase and is accompanied by a large increase in levels of luteinizing hormone (LH), as well as a small spike in follicle-stimulating hormone, both of which return to low levels after ovulation (for illustration, see Appendix A). Ova released during ovulation can survive for up to two days, and given that sperm can survive for up to five days in the female reproductive tract, females are at high-fertility between the five days prior to ovulation (during the late-follicular phase) and the second day after ovulating.

**Changes throughout the Menstrual Cycle**

Sex hormone receptors are present throughout many areas of the body as well as some structures of the brain. The neural structures that signal for the release of these hormones, as well as other parts of the brain, are in turn, affected by them as well. The hypothalamus releases gonadotropin-releasing hormone, which signals the anterior pituitary gland to release gonadotropins into the bloodstream. Gonadotropins signal for the gonads to produce androgens, estrogens, and progesterone. Sex steroid receptors are densely present throughout hypothalamic structures, limbic areas, and dopaminergic pathways (see Dreher et al. 2007; Österlund, Kuiper, Gustafsson, & Hurd, 1998; Österlund & Hurd, 2001; Pfaff & Keiner, 1973).

Changes in brain activity and patterns of activity occur throughout the different phases of the menstrual cycle, and may help explain behavioral differences between phases of the cycles. Resting brain wave patterns reflect increased creativity and divergent
thinking during high-fertility phases compared to low-fertility phases (Krug, Mölle, Fehm, and Born, 1999). Neural activation patterns (Andreano and Cahill, 2010; Protopoeescu et al., 2005) and hemispheric dominance lateralization (Hwang, Wu, Chen, Yeh and Hsih, 2008) suggest heightened appraisal of and response towards negative stimuli in women at high-fertility. However, high-fertility women also exhibit an increase in activation of cortical structures involved with positive appraisal, compared to the same women in their luteal phase (Rupp et al., 2009). Women report increased efficacy of and desire for dopamine agonists during the follicular phase compared to during the luteal phase (Evans, Haney & Foltin, 2001; Justice & de Wit, 1999; Sofuoglu, Dudis-Poulsen, Nelson, Hatsukami & Pentel, 1999). Considering the potential influence individual hormones, progesterone and estradiol may affect dopaminergic, reward-related brain regions in opposing fashions (Dreher et al., 2007). Research regarding functional neural changes may aid in explaining some of the differences in reaction to varying stimuli between cycle phases. However, considerably more research has focused on the behavioral and physical changes that take place across the menstrual cycle.

Female olfactory sensitivity and subjective perception of smell change throughout the menstrual cycle. Olfactory sensitivity is highest mid-cycle, within a day of the LH surge that signals for ovulation (Doty, Snyder, Huggins & Lowry, 1981). Specifically, sensitivity to androstenone (a steroid hormone associated with pheromone-like activity), is higher among naturally cycling women during the late-follicular phase than the early-follicular or late-luteal phases, and these women perceive the smell as more pleasant (Grammer, 1993). However, females taking hormonal contraceptives do not show a cyclical change in sensitivity to androstenone, which further supports the effect of sex
hormone levels on olfactory sensitivity (Grammer, 1993). Lundström, McClintock and Olsson (2006) compared sensitivity to the smell of androstadienone (a steroid similar to androstenone) and an environmental odorant (similar to the smell of rose) between fertile women and women on hormonal contraceptives. When naturally cycling females were at high-fertility, they exhibited an increase in sensitivity to androstadienone, but not an increase in sensitivity to the environmental odor. This finding did not generalize to women on hormonal contraceptives. These studies reflect a tendency for women to be most sensitive to hormones that may affect mate-seeking behavior during peak fertility.

Aside from olfactory sensitivity, female body odor also changes throughout the menstrual cycle and may serve as an indicator of fertility. Men judge the odor of women in their late-follicular phase to be least intense, most pleasant, and most attractive compared to the body odor of women in their menstrual or luteal phases (Havlíček, Dvořáková, Bartoš & Flegr, 2006). Even after researchers allow odors to dissipate for week at room temperature, men perceive the odor of women in their late-follicular phase to be more pleasant and sexy compared women in their luteal stage (Singh & Bronstad, 2001). Not only do men perceive the odors of high-fertility women as more attractive, they exhibit physiological responses to these odors. Men’s testosterone levels (Miller & Maner, 2010) and cortisol levels (Cerda-Molina, Hernández-López, de la O, Chavirez-Ramírez, & Mondragón-Ceballos, 2013) increase more dramatically after smelling shirts worn during ovulation than those worn by women in their late luteal phase. Whether or not directly perceived as a fertility cue, men detect this cyclical change in body odor, judge it as more attractive, and react to it at a physiological level.
Facial attractiveness ratings differ between cycle phases and may cue fertility, affecting mating strategies. Men and women alike perceive pictures of female faces taken at high-fertility as more attractive than pictures taken during their luteal phase (Roberts et al., 2001). Although there may be an increase in redness of the cheeks during the ovulatory period, researchers suggest that this difference in color is below the threshold of human detection and should not be responsible for higher ratings of attractiveness (Burriss et al. 2015). Instead of changes in hue, changes in face shape throughout the menstrual cycle may be responsible for differences in perception of attractiveness. Bobst and Lobmaier (2012) found that there are subtle face shape differences between ovulating women and women in the luteal phase and created prototypical pictures of women in each phase, while controlling for any difference in skin tone. They found that men rated ovulating prototypes as more attractive, caring, flirtatious, and more likely to respond as willing to go on dates with them, based solely on the change in shape. Puts et al. (2013) found that, among male and female observers, facial attractiveness ratings were negatively correlated with the progesterone levels of women pictured, implying that men and women alike may be attune to cyclical changes in facial characteristics.

Many cyclical changes alter the perception of female attractiveness and perhaps even cue fertility. Certain changes that are connected to increasing sexual attractiveness, such as decreased cyclical asymmetry (Manning, Scutt, Whitehouse, Leinster & Walton, 1996; Scutt & Manning, 1996) and waist-to-hip ratio (Kirchengast & Gartner, 2001) while women are at high-fertility, may fall below the threshold of the average observer’s detection. However, men and women may detect other changes associated with fertility such as facial, vocal, and body odor attractiveness more easily, whether or not they
consciously recognize them as fertility cues. Relative to the current investigation, changes in vocal acoustics relative to voice attractiveness are of particular interest.

**Acoustic Properties of the Voice**

Humans use their voices as a method to convey verbal communication. However, the voice itself has acoustic properties that convey information other than just the words produced. Although counterintuitive, acoustic properties of the voice are a form of nonverbal communication. Most can make inferences about the emotional state of another based on how they speak, or conclude that some utterances have an underlying connotation not explicitly stated, based on changes in vocal acoustics. There are many inferences humans make based on perception of changes in vocal acoustics, such as if the voice from a large or small, healthy or unhealthy, and even an attractive or unattractive individual.

The human voice varies in many acoustic properties, including but not limited to: fundamental frequency (F₀), intensity, frequency perturbation (jitter), amplitude perturbation (shimmer), timbre, and harmonics to noise ratio (HNR). Humans often refer to F₀ as the “pitch” of someone’s voice, and measure F₀ based on cycles per second in units of Hertz (Hz). Humans often refer to intensity as “loudness”, and measure intensity in units of decibels (dB). Jitter is a measure of the variability in F₀ in a vocal production, whereas shimmer is a measure of the variability in intensity in a vocal production. HNR quantifies how much sound the vibration of the vocal folds produce relative to how much sound there is outside of that, which is a product of the passage of air through the articulators or produced by the articulators. All of these properties of the voice are produced through vibrations of the vocal folds combined with the passage of air through
the resonances formed by the articulators of the vocal-tract airways (for review, see Ghazanfar & Rendell, 2008).

Given the interaction between these physical structures, the human voice varies such that we can distinguish between voices of the same “pitch” and “loudness.” The F₀ of the voice is its lowest frequency of high intensity, produced directly from the vibration of the vocal folds. Additional high intensity frequencies are produced due to alterations in the length, shape, and cross-sectional area of vocal tract airways, which serve as sound filters, and these frequencies are called formants (see Ghazanfar & Rendell, 2008). Formant dispersion (D₀) is the average distance between successive formants. Formant dispersion is a distinguishing feature between voices of the same F₀ and overall intensity, which contributes to differences in timbre. Based on F₀, most people can distinguish between the voices of a child, male adult, and female adult. An average adult male has a F₀ that is generally around half that of the adult female (Childers & Wu, 1991; Hollien, Dew & Philips, 1971). This difference is largely due to how much larger the increase in the size of male vocal folds is throughout puberty, as a result of the activational effects of heightened testosterone, compared to the average increase in pubescent females (Abitbol, Abitbol & Abitbol, 1999).

**Voice Attractiveness**

Much of the research regarding perceived voice attractiveness has focused on changes and alterations to vocal F₀. Males and females alike perceive voices from either sex with lower F₀ as belonging to people of higher dominance (Borkowska & Pawlowski, 2011) and rate female voices with higher F₀ as more attractive (Borkowska & Pawlowski, 2011; Feinberg et al., 2006; Puts Barndt, Welling, Dawood, & Burriss 2011 ). Conversely,
women rate male voices with lower F₀ as more attractive (Feinberg et al., 2006; Feinberg, Jones, Little, Burt & Perret, 2005). Taking fertility status and mating context into account, high-fertility women rate male voices of lower F₀ to be more attractive specifically in the context of a short-term sexual relationship, but not in the context of a long-term relationship, and F₀ influences the voice attractiveness rating of low-fertility women less in either context (Puts, 2005). Given that higher testosterone levels are associated with voices of lower F₀ (Dabbs & Mallinger, 1999), the tendency of women to find male voices with lower F₀ as more attractive may serve as a proximate mechanism driving attraction to males of higher genetic quality. Additionally, markers of high genetic quality may be particularly salient to women at high-fertility, because this is when mate selection has a larger potential to affect their future offspring.

Voices of differing timbre with shorter formant dispersion are indicative of higher testosterone, larger vocal-tract length, and larger overall body size (Fitch, 1997; Fitch & Giedd, 1999). By manipulating D₇ of male voices, Feinberg et al. (2005) mimicked the effect of altering vocal tract length and presumed body size. Although they found that women judged male voices with shorter D₇ as voices belonging to larger, more masculine, and older men than those of higher D₇, they did not find a significant difference in voice attractiveness ratings. Puts et al. (2011) independently manipulated the F₀ and D₇ of female voices, and investigated how this impacted perceived attractiveness and flirtatiousness. They found that voices with higher D₇ or F₀ were both rated as more attractive and flirtatious by male and female listeners, that males preferred voices of higher D₇ or F₀ particularly in the context of short-term sexual relationship, and that manipulation of D₇ had a larger main effect than F₀. This may suggest a tendency for
males to be more attracted to the voices of women with smaller body sizes or lower testosterone, particularly in the context of a short-term mate.

Hormones other than testosterone can also affect acoustic properties of the voice and the perception of voice attractiveness. Human vocal folds have receptors for androgens, estrogens, and progesterone (Newman, Butler, Hammond & Gray, 2000). Increased progesterone levels can cause production of a thicker and more acidic mucus within the vocal folds leading to dryness of the laryngeal muscle and edema of the vocal folds themselves (Abitbol et al., 1999). During pre-ovulatory and late-luteal phases, the interaction of estrogen and progesterone can modify laryngeal mucosa, altering vocal acoustic properties (Abitbol et al., 1999). Men and women rate female voices as most attractive when their estrogen levels are high relative to their progesterone levels, a hormonal balance that naturally occurs before and during ovulation (Puts et al., 2013). Given the effects of hormones on the voice, researchers continue to investigate how the voice may change throughout the menstrual cycle.

Although jitter and shimmer naturally fluctuate, high levels of jitter and shimmer can be a sign of laryngeal pathologies such as vocal fold polyps, edema or paralysis (Zhang & Jiang, 2008). However, the extent to which people perceive voices with high levels of jitter or shimmer as unhealthy is not clear in the literature. Most studies of vocal acoustic analysis have found no significant change in jitter or shimmer as a factor of cycle phase (Bryant & Haselton, 2009; Çelik et al. 2013; Fischer et al. 2011). However, Shoup-Knox and Ostrander (unpublished data) found that naturally cycling high-fertility women exhibit lower levels of shimmer than the same women at low-fertility, and found no cyclical change among women taking hormonal contraceptives. Without taking phase of
cycle into account, levels of both jitter and shimmer are lower among females that take oral hormonal contraceptives compared to naturally cycling females, suggesting that hormones may affect these properties of the voice (Amir, Kishon-Rabin & Muchnik, 2002).

Bryant and Haselton (2009) found that females at high-fertility exhibited voices of higher average F0 than the same females exhibited during their luteal phase. Fischer et al. (2011) recorded female voices every day over the course of a menstrual cycle and did not replicate this finding, but found that F0 was marginally significantly higher in the days preceding ovulation, and the F0 of their participants was actually lowest during ovulation. Through analyzing F0, HNR, jitter and shimmer, the only significant difference Fischer et al. (2011) found based on cycle phase was that the HNR was higher during ovulation than menstruation. Men and women rate voices with higher HNR values as more attractive than voices with lower HNR values (Bruckert et al., 2010). Taken together, these studies suggest that higher HNR and F0 exhibited during or preceding ovulation could affect perception of attractiveness or signal fertility.

Pipitone and Gallup (2008) found that the attractiveness ratings of voice recordings of naturally cycling high-fertility females were higher than recordings of the same females at low-fertility. However, there was no relationship between cycle phase and voice attractiveness ratings of recordings of females that were taking hormonal contraceptives, suggesting that perceptual differences were due to the effects of sex hormones on voice production. In this study, both males and females rated voices of the high-fertility women as more attractive, potentially implying that both males and females are attune to vocal fertility cues. Women exhibit voices of the highest perceived quality around the time of
ovulation, versus lowest perceived quality in their premenstrual phase, based on perceived grade, roughness, breathiness, asthenia, and strain (Çelik et al., 2013). Men judge female voices recorded during menstruation to be of lower quality than the same female voices recorded during other phases (Pipitone & Gallup, 2011). Additionally, male and female listeners rate voices of women with lower progesterone levels as more attractive (Puts et al., 2013), suggesting that voices produced during the follicular phase and ovulation should naturally be more attractive than voices produced during the luteal phase.

The human voice is a distinct and unique feature between individuals. Properties of sound within a spoken voice can fluctuate not only by intention, but also as a product of hormonal interaction with the anatomical structures that produce speech. Perhaps most interesting is not the fact that hormones can alter the voice, but that these changes alter human perception of attractiveness and may serve as fertility cues. Changes in the voice across the phases of the menstrual cycle, as well as perceptions thereof, may reflect an evolutionary mechanism that promotes reproductive success. Because males and females alike recognize the difference in attractiveness across the cycle, it could also be a contributing factor to both male and female mate-guarding and female intrasexual competition.

**Intrasexual Competition and Fertility**

Although human females do exhibit signs of ovulation, these signs are not as overt as those that other species exhibit. Because of this, researchers assume that human estrus was selected against and women evolved to conceal any cues to fertility (Alexander & Noonan, 1979). Some researchers have asserted that this concealment of fertility supports a dual-mating strategy, whereby a female could mate with males of higher genetic quality
Sexual selection affects mating strategies when possessing beneficial phylogenetic characteristics leads to a higher likelihood of obtaining a mate and procreating. Because of this natural process, intersexual competition takes place whereby a member of one sex chooses a particular member of the opposite sex to mate with, based on the displays of high genetic quality and desirable phylogenetic traits. Due to intersexual competition, intrasexual competition arises whereby members of the same sex will compete with one another to increase the likelihood of being chosen by members of the opposite sex. For most species, the majority of research regarding intrasexual competition has revolved around the males. However, research has started to illustrate human intrasexual competition among females as well. Buss (1988) found sex differences in human intrasexual competition such that while males display strength, athleticism, or resources more often, females employ tactics such as wearing makeup and jewelry, altering their appearance, flirting or acting promiscuous. Rosvall (2011) suggests that female intrasexual competition increases when the ratio of females to males is biased towards females or when mating opportunities are limited, and that the competition should increase in the presence of males that provide direct benefits. Given that obtaining a mate with the direct benefits of desirable inheritable traits is only evolutionarily effective during fertile phases while fertile, and retain a different long-term partner through sexual activity while not in the fertile phase (e.g. Benshoof & Thornhill, 1979; Strassman, 1981). Although a human estrus is not advertised per se, it may be extreme to say that women completely conceal fertility. The degree to which fertility cues affect sexual selection, as well as female intrasexual competition, is a subject of past and ongoing research.
PHYSIOLOGICAL RESPONSES TO FERTILITY CUES

of the menstrual cycle, some research on human intrasexual competition has begun to focus on changes in competitive behavior among females while at high-fertility.

Women at high-fertility choose clothing and ornamentation that is more competitively attractive than women at low-fertility (Beall & Tracy, 2013; Durante, Griskevicius, Hill, Perilloux & Li, 2010; Durante, Li & Haselton, 2008; Eisenbruch, Simmons & Roney, 2015; Haselton, Mortezaie, Pillsworth, Bleske-Rechek & Frederick, 2007). Ornamentation can be a form of intersexual competition when it enables a person to have more power to choose their desired mate. However, it can also manifest itself as intrasexual competition when it leads to a higher likelihood of being chosen by a mate through rendering someone more desirable than their same-sex rivals. Reddening of the skin on certain areas of the body (i.e. buttocks or vulva) indicates estrus in many primates, and culturally the color red has become associated with sexual symbols such as the hearts of Valentine’s Day or the lights of “red-light districts” (for further review see Elliot & Maier, 2007; Prokop & Hromada, 2013). The color red has been shown to increase males’ attraction to females (Elliot & Niesta, 2008), and during fertile windows, females wear pink or red 2-3 times more often than during other phases (Beall & Tracy, 2013; Eisenbruch et al., 2015). Women wear more revealing and sexier attire while fertile than when the same women are in their luteal phase, and when asked to draw what they would wear to a social event they draw pictures of more revealing and provocative clothing during their fertile windows (Durante et al., 2008). Additionally, men and women judge fertile females to wear nicer and more fashionable clothing that shows more skin when shown pictures of females taken during their fertile phase compared to those taken during their late-luteal phase (Haselton et al., 2007).
Schmitt and Buss (1996) studied intrasexual competition in terms of self-promotion tactics as well as competitor derogation tactics that women judged to be most effective in mating contexts. They found that women cited acting flirtatious, acting seductively, displaying exclusivity, sexualizing one’s appearance, making sexual propositions and actually having sex as the most effective self-promotion tactics. Females judged calling a rival sexually unavailable or promiscuous, questioning a rival’s fidelity, and derogating a rival’s appearance or attractiveness as the most effective competitor derogation tactics. Females derogate the fidelity of other females wearing red more than females wearing white, after also rating the women wearing red to be more sexually receptive (Pazda, Prokop & Elliot, 2014). Fisher (2004) found that mid-cycle females rated the attractiveness of other women as lower compared to the ratings of females in their early-follicular or late-luteal phases. This finding implies that, when closer to peak fertility, women may be more likely to compete intrasexually through derogating their rivals, and may use fertility cues to determine their targets.

Researchers have investigated the effect of priming women at high-fertility with pictures of other women and observing the subsequent responses to further illustrate intrasexual competition. When primed with a picture of an attractive female, women at high-fertility purchase significantly more clothing, shoes and accessories judged to be sexy than after being primed with unattractive females, unattractive males, or attractive males (Durante et al., 2010). When shown pictures of a variety of functional items as well as a variety of products that signal status, females remember significantly more status products around ovulation than in other phases (Lens, Driesmans, Pandelaere & Janssens, 2012). These studies imply that not only are females more prone to compete by dressing
attractively while fertile, particularly in the presence of an attractive female, but also are more attentive to the similar efforts of rival competitors.

The dual-mating strategy suggests that that not only should females be more competitive during fertile phases, but also that they should become selectively competitive for males of high genetic quality. Puts (2005) found that females preferred men with voices of a lower F₀ as they approached peak fertility, but only preferred these voices in terms of a short-term rather than long-term mating context. Cantú et al. (2014) observed an increase in instances of flirtatious behavior directed towards men judged to be desirable as short-term mates among women at high-fertility, compared to when they were at low-fertility. Females also report higher levels of sexual attraction to, and fantasy about, males other than their primary partners during ovulation than they do during their luteal phase (Gangestad, Thornhill & Garver, 2002).

Given the evidence that fertile women have the tendency to have more extra-pair sexual desires, it may be that, in their presence other women could be threatened in their own mating context, exhibit heightened intrasexual competition, and increase their own mate-guarding tactics. Women display higher levels of mate guarding tactics in reaction to females wearing red than females wearing green (Pazda et al., 2014), which may imply that females recognize wearing red as a cue to fertility. Puts et al. (2013) found that when women rated photos of other women’s faces on measures of flirtatiousness, progesterone levels of the women in the photos negatively predicted flirtatiousness ratings. This suggests that women may be judged as more flirtatious when in their follicular phase or during ovulation relative to their luteal phase. This also implies that females may be able to discriminate when a competitor is most of a threat to mate-seeking behavior based on
face alone, and this detection may influence their own behavior. In fact, fertile females are more likely to withhold resources from attractive females than unattractive females (Lucas & Koff, 2013), indicating that sexually competitive behavior can be modified by how threatening a competitor is perceived.

Men may also detect behavioral changes in their female partners and attempt to guard them more closely when they are fertile. Women report higher levels of mate-guarding tactics such as hypervigilance, monopolization of time, and attentiveness exhibited by their partners when they are at high-fertility relative to when they are in their luteal phases (Gangestad et al., 2002). Additionally, less attractive males increase their mate-guarding behaviors more than attractive males while their partners are at high-fertility (Pillsworth & Haselton, 2006). If a dual-mating strategy exists, it would be evolutionarily advantageous for males of lower attractiveness, and perhaps genetic quality, to mate-guard their partners more closely around peak fertility. Haselton and Gangestad (2006) found an increase in jealous and possessive mate behaviors towards mid-cycle females, but also found that women reported greater interest in going to places where they may meet men, as well as feeling more sexually attractive while fertile compared to when in their luteal phase. Taken together, these studies suggest that women are more likely to put themselves in situations where mate-seeking is possible when at high-fertility, and that men are able to detect this change and more closely guard them.

Compared to men, women report much greater distress when a rival has a more attractive face or body than themselves (Buss, Shackelford, Choe, Buunk & Dijkstra, 2000). Given that faces (Bobst & Lobmaier, 2012), voices (Pipitone & Gallup, 2008; Shoup-Knox & Pipitone, 2015), body odors (Cerdina-Molina et al., 2013; Miller & Maner,
2010; Singh & Bronstad, 2001) and even gait (Gueguen, 2012) of fertile phase women are judged as more attractive than those of women in non-fertile phases, it should follow suit that women would be more distressed and perhaps more competitive when there are fertile females present. There is now reason to believe that at a physiological level, females react to certain cues to other females’ fertility. Shoup-Knox and Pipitone (2015) found that the skin conductance response of females listening to voices of naturally cycling women at high-fertility is elevated compared to the skin conductance response to voices of those same women at low-fertility. Heightened skin conductance response is an indication of sympathetic nervous system arousal that often indicates a response to threat. Additionally, following exposure to the body odor of women at high-fertility, females display higher testosterone levels than the levels displayed by females exposed to the odor of women at low-fertility (Maner & McNulty, 2013). Taken together, these findings show that females are react to fertility cues of other females at a physiological level. They also show that females respond in fashions indicative of a reaction to threat and with an alteration of testosterone level, a sex hormone related to competitive behavior.

Although research regarding human female intrasexual competition has not been exhaustively explored, there is already evidence of different forms of competitive behaviors as well as factors that influence their expression. Given the preliminary research relating cycle phase to jealousy, intrasexual derogation, choice of ornamentation and product purchases, it seems that there is a relationship between fertility and levels of intrasexual competition expressed. Furthermore, given the research that suggests females can detect cues of fertility in other females, there is reason to believe that women could perceive an ovulating female as a threat, and this threat could provoke higher levels of
intrasexual competition within the observer. Further research is necessary to investigate how females detect the fertility of other females, if there is an effect of this detection on intrasexually competitive behaviors, and if there are physiological reactions to this detection that may prime competitive behaviors. In order to interpret how physiological responses may prime downstream behavioral tendencies, in the context of intrasexual competition, some basic information regarding endocrine responses and the sympathetic nervous system should be understood.

**Sympathetic Nervous System Activity and Endocrine Responses**

The autonomic nervous system (ANS) of the human body controls many processes that often go unnoticed. The ANS makes homeostatic adjustments in many different physiological systems, and does so without the voluntary control of the individual. The ANS is characterized by two branches, the sympathetic nervous system (SNS) and the parasympathetic nervous system. The sympathetic division is typically known as the system responsible for arousal, or “fight or flight” responses, whereas the parasympathetic division is known as being responsible for counteracting the SNS, or “rest and digest” periods. The SNS becomes active in response to a variety of stimuli that cause psychological arousal, including threatening stimuli, novel stimuli, and stimuli that elicit strong emotions (e.g. Kreibig, 2010). Several methods can be used to measure sympathetic nervous system arousal. Arguably, the most common method is through monitoring electrodermal activity.

Electrodermal activity is the change in electrical conductivity or electrical resistance across the surface of an individual’s skin. Human skin has a basal level of conductivity known as a tonic skin conductance level (SCL), whereas the increased
conductivity of human skin in response to SNS arousal is known as the skin conductance response (SCR). In response to SNS activity, eccrine glands release sweat into ducts beneath the surface of the skin, which fill with sweat, lowering electrical resistance of the skin and allowing current to flow more freely. Conductance levels and changes in conductivity are measured in units of the µSiemen (µS), and an elicited SCR is generally quantified as being an increase of between 0.1µS and 1µS. SCRs are typically observed within a 1-4 second latency window after a stimuli is presented (for review of electrodermal activity, see: Dawson, Schell, & Filion, 2007). Electrodermal activity is a very common measure in evaluating the presence and strength of sympathetic nervous system arousal, and heightened activity is interpreted as a response to strong emotions including threat perception.

Responses to threat and stress can also be gauged by monitoring endocrine activity. Neuroendocrine responses to threat and stress function predominantly through the release of epinephrine and cortisol. While epinephrine release will activate the SNS, cortisol facilitates SNS functioning by mobilizing glucose and enhancing cardiovascular functioning (see Knight & Mehta, 2014 for review). While a large amount of research relative to cortisol responses has focused on psychosocial stress, researchers have also investigated the joint effects of testosterone and cortisol in response to competition.

Salvador and Costa (2009) conducted a meta-analysis showing the overall trend for testosterone to increase in response to competition, and for there to be a larger increase exhibited post-competition in winners than in losers. Humans also exhibit an anticipatory rise in both testosterone and cortisol prior to competition (Booth, Shelley, Mazur, Tharp & Kittok, 1989; Suay et al., 1999). Specific to women, studies have shown elevated
testosterone and cortisol in anticipation of competition (Bateup, Booth, Shirtcliff & Granger, 2002; Oliveira, Gouveia & Oliveira, 2009), but there is some conflict in the literature. Edwards and Kurlander (2010) found only an anticipatory rise in testosterone, but not cortisol, among women preparing for competition. Contrary to most competition research regarding testosterone, Mazur, Susman and Edelbrock (1996) investigated sex differences in response to a video game competition and found that cortisol was significantly elevated post-competition for both men and women, but testosterone was only elevated in men.

Collapsing across sexes, elevated testosterone heightens attention to threat (see Carré & Olmstead, 2015) and increases the likelihood of making risky choices (Stanton, Liening & Schultheiss, 2011). Mehta and Josephs (2006) found that elevated testosterone in response to losing a competition increases the likelihood of continuing to compete across both sexes. Additionally, Mehta and Josephs (2010) found that, across both sexes, higher basal testosterone paired with lower basal cortisol increased the willingness to compete. Although, none of the aforementioned studies focused on competition in terms of intrasexual competition, there is reason to believe that basal testosterone and testosterone responses are associated with both intersexual and intrasexual competition.

Although originally studied among birds, the challenge hypothesis (Wingfield, Hegner, Dufty & Ball, 1990) has been extended to humans in terms of how testosterone may affect intrasexual competition and mate seeking behaviors. Archer (2006) describes how the challenge hypothesis posits that among men, testosterone: increases due to sexual arousal, increases aggression, is lower among paternal men, is correlated with measures of dominance, and increases the likelihood of intrasexual competition. He then outlines how
the challenge hypothesis may also apply to women, while noting that it has not yet been exhaustively researched.

Sexual attraction and intersexual interaction influence both testosterone and cortisol, and this may affect mate-seeking behaviors. Roney, Lukaszewski and Simmons (2007) report increased testosterone and cortisol among men after the mere presence of a young female confederate. Among women, imagining a sexual encounter induces an increase in testosterone, but not cortisol (Goldey & van Anders, 2011). In one of the few testosterone studies that considered cycle phase, researchers found that in response to video footage of an attractive man both testosterone and cortisol increased in naturally cycling women (Lopez, Hay & Conklin, 2009). However, when women were at high-fertility only testosterone reflected an increase in response to the video of the attractive man.

Although there is not a vast amount of research regarding how cortisol and testosterone responses differ as a factor of cycle phase, preliminary research suggests that there may be minor differences in basal levels throughout the cycle. In terms of response to stressful stimuli, research suggests that women exhibit heightened cortisol responses during their luteal phase compared to their follicular phase (Kirschbaum, Kudielka, Gaab, Schommer & Hellhammer, 1999). Although Liening, Stanton, Saini and Schultheiss (2010) found no within-subject difference in either basal testosterone or cortisol to be a factor of cycle phase, others have found that testosterone may fluctuate throughout the cycle, and peak either during the early luteal phase (Dabbs & de La Rue, 1991) or during ovulation (Bui et al., 2013). Evidence of systematic cyclical fluctuations in testosterone or cortisol is not consistent in the literature.
Considering previous research implicating the roles of testosterone and cortisol in response to threat, competition, stress, and intrasexual competition, it is reasonable to question whether detection of fertility cues may elicit a response in one or both of these hormones. If the challenge hypothesis is applicable to women, it is reasonable to suspect that increased testosterone may heighten women’s propensity to exhibit aggression or other forms of intrasexual competition. Additionally, if the theory of a dual-mating strategy holds true and detection of fertility poses a discreet threat, it is reasonable to suspect an increase in cortisol following detection. Furthermore, given the debate in the literature regarding any cyclical variation in these hormones, it is of interest to further investigate whether basal levels of either hormone vary based on fertility status.

**Current Directions**

The current study will investigate if women exhibit a different sympathetic nervous system response to recordings of the voices of high-fertility women compared to low-fertility women, if they exhibit an endocrine response to the voices, and if the observers’ fertility status moderates these responses. To date, to my knowledge, no studies have investigated physiological responses to fertility cues based on both the fertility of the observer and the observed. By presenting vocal stimuli produced by naturally cycling high-fertility and low-fertility females to both naturally cycling high-fertility and low-fertility listeners, we can observe if physiological responses to fertility cues are dependent on the fertility status of the listeners themselves. Including voices provided by women on hormonal contraceptives, at cycle days analogous to high- and low-fertility, serves as a control to strengthen the implication that hormonal fluctuations of the speaker are responsible for altered vocal production and reactions of the listener.
Through monitoring response to threat based on measuring electrodermal activity, response to stress in measuring changes in cortisol, and anticipatory response to competition in measuring changes in testosterone, this research may present a more cohesive narrative on the impact of the detection of fertility cues on threat perception and intrasexual competition. It is hypothesized that detection of vocal fertility cues will elicit a heightened activation of the SNS, as indicated by heightened SCRs in response to naturally cycling high-fertility voices compared to naturally cycling low-fertility voices, whereas no differences will be observed in response to voices of women on hormonal contraceptives at analogous days in their cycles. It is hypothesized that detection of subtle indicators of fertility will elicit a stress response, as evidenced by an increase in cortisol, as well as an endocrine response that may prime competitive behavior, as evidenced by an increase in testosterone. It is also hypothesized that all of these physiological reactions to detection of intrasexually competitive rivals will be exaggerated when participants are at high-fertility themselves.

Method

Participants

Twenty-four naturally cycling women were recruited through distribution of flyers on the campus of James Madison University (following approval of materials and procedures by the Institutional Review Board of James Madison University), and given $20 compensation for participation in the study. Participants underwent an initial meeting in which they were screened for age ($M=19.9$ years, $SD=1.83$), regularity of menstrual cycle, plans on becoming pregnant, current and past use of hormonal contraceptives, relationship status, sexual orientation, and medication use (see Appendix B). Only
participants that were regularly cycling, heterosexual, not planning on becoming pregnant, not on medication that directly affects cortisol or testosterone, and who had not taken hormonal contraceptives within the past 90 days were retained for the study.

The experimenter issued participants 10 LH test strips (Wondfo USA Co., Willowbrook, I.L.), and explained how to properly test for ovulation. When an LH surge was detected, participants contacted the researchers and their first trial was scheduled either within two days of \((M=1.16\) days, \(SD=.64)\) or roughly 12 days following \((M=10.92\) days, \(SD=1.74)\) the positive result. Participants’ second trial was scheduled in the opposite fashion of their first, either within two days of their next positive result, or roughly 12 days following their first positive result. We attempted to counterbalance the participants’ phase during their first trial. However, given scheduling difficulties, 20 participants completed their first trial while ovulating and second trial while in their luteal phase, and only four participants completed their first trial during their luteal phase and second trial while ovulating. To control for diurnal decline in cortisol and testosterone, researchers attempted to schedule participants at the same time in the afternoon for both trials.

**Materials**

A playlist of voices obtained in a previous study (Pipitone & Gallup, 2008), consisting of 20 female voices counting from 1-10 at high-fertility and low-fertility, was used as the experimental stimuli. Ten of the women who provided voice samples were naturally cycling, and 10 of the women were currently using hormonal birth control. Participants listened to 40 individual recordings, in a randomized order, two from each female recorded at both high- and low- fertility (or analogous days in their cycle if on hormonal contraceptives). Experimenters provided each participant with a voice
attractiveness rating scale (see Appendix C), and a participant questionnaire was administered at the end of each trial to screen for variables that could affect endocrinology or SNS activity (see Appendix D) (for review of confounding variables, see: Al-Dujaili & Sharp, 2012; Badrick et al., 2008; Edwards, Evans, Hucklebridge & Clow, 2001; Granger, Hibel, Fortunado & Kapelewski, 2009; Granger, Shirtcliff, Booth, Kivlighan & Schwartz, 2004; Gibson et al., 1999; Hansen, Garde & Persson, 2008; Kirschbaum, Strasburger & Langkrär, 1993; Lovallo, Al’Absi, Blick, Whitsetts & Wilson, 1996; Luger et al., 1987; Nicolson, 2008).

**Apparatuses**

All electrodermal activity was recorded by use of a PowerLab 26T® and accompanying LabChart® software (ADInstruments, Sydney, Australia). Changes in electrodermal activity relative to the presentation of each stimulus was also generated through use of the LabChart® software. All salivary cortisol and testosterone measurements were analyzed using enzyme-linked immunoassay kits obtained through Salimetrics® (State College, P.A.) and a Bio-Rad® Model 680 Microplate Reader with accompanying Microplate Manager® 6 software (Hercules, C.A.). Audio playlists were compiled through use of VLC Media Player 2.2.4 (VideoLAN, Paris, France) and played through an AudioBox™ Studio One® interface with accompanying high-definition headphones (PreSonus Audio Electronics Inc., Baton Rouge, L.A.).

**Procedure**

Upon arrival to the lab, participants rinsed their mouths with water, allowed several minutes to pass, and provided a baseline saliva sample of roughly 1.8mL by passively drooling through a saliva collection aid (Salimetrics, State College, P.A.) into a
polypropylene cryovial. Experimenters temporarily stored samples in a non-commercial grade freezer. Experimenters then attached participants to the galvanic skin response monitor by adhering skin conductance electrodes to the index finger and the ring finger of their non-dominant hand. Experimenters informed participants that they would be listening to a series of voices counting from 1-10 and to rate the voices on a scale of 1-100 on how attractive they perceive the voice to be (1 being very unattractive, and 100 being very attractive). Experimenters gave participants headphones to listen to the stimuli, and volume was held constant between participants and trials. Experimenters recorded a 1-minute baseline reading of SCL before beginning the playlist of voices, and kept temporal record with reference to the ongoing SCL monitoring such that responses to individual voices were distinguishable. Exactly five minutes and 20 minutes following the end of the playlist presentation, participants provided the second and third saliva samples as described previously. Timing of saliva collection was based on the expected latency for endocrine responses to be evident in saliva (e.g. Dickerson & Kemeny, 2004; Kirschbaum & Hellhammer, 1989). Experimenters gave participants a questionnaire for further screening and use in analyses, and issued compensation at the end of each trial. Experimenters then transferred all saliva samples to a commercial-grade freezer to be stored at -80°C.

Following the completion of all trials, and collection of all saliva samples, the saliva samples were analyzed using competitive enzyme linked immunosorbent assay (ELISA) kits for both cortisol and testosterone (Salimetrics®, State College, P.A.), according to manufacturer’s instruction. In brief, the researcher thawed the samples at room temperature, and centrifuged them for 15 minutes to remove mucins and potential
contaminants (e.g. food particles). Following centrifugation, 96-well microtitre plates were loaded with saliva samples, standardized concentrations of cortisol or testosterone, as well as control wells containing no testosterone or cortisol. Assay diluent containing hormones (cortisol or testosterone) conjugated with enzymes was added to each well before the plate was shaken on a plate rotator and allowed to incubate. The researcher then added tetramethylbenzidine substrate to all wells before rotating the plate again and allowing time for incubation. Last, the researcher added a stop solution, allowed time for the reaction to be stopped, and within 10 minutes obtained absorption and concentration values using a plate reader and accompanying software. Researchers analyzed all three samples obtained during any given trial using the same assay plate, to avoid any variation in standard and control comparison values between assay kits.

Results

Endocrine Analyses

The intra-assay coefficients of variation (CV) were 15.13% for cortisol and 9.13% for testosterone, and the inter-assay CVs were 7.78% for cortisol and 11.08% for testosterone. Shapiro-Wilk’s tests of normality revealed that salivary hormone concentrations were positively skewed in all three samples of cortisol (baseline: \( W(48) = .88, p < .001 \); 5-minute: \( W(48) = .871, p < .001 \); 20-minute: \( W(48) = .836, p < .001 \)), and two out of three samples of testosterone (baseline: \( W(48) = .926, p < .05 \); 5-minute: \( W(48) = .985, p = .802 \); 20-minute: \( W(48) = .946, p < .05 \)). Hence, concentration levels of both hormones were transformed using Box-Cox power transformations (Box & Cox, 1964; see also Miller & Plessow, 2012; Osborne, 2010) in order to approximate normality before proceeding with analyses. Baseline cortisol levels did not systematically differ as a factor
of fertility status ($t(23)=1.15, p=.26$), nor did testosterone levels ($t(23)=-.108, p=.915$), therefore no ceiling effects were anticipated or statistically controlled for. Although bivariate correlations did reveal a relationship between hours since awakening and baseline hormone levels (cortisol: $r=-.417, p=.004$; testosterone: $r=-.155, p=.298$), hours since awakening did not differ within participants between trials while ovulating ($M=7.61$, $SD=2.86$) and during their luteal phase ($M=7.58$, $SD=3.07$) ($t(23)=.061, p=.952$), so no attempts were made to control for the diurnal decline in either hormone.

Cortisol levels of listeners were analyzed using a 2 (fertility status) x 3 (time of sample) repeated-measures ANOVA. Collapsing across time of sample, mean cortisol levels did not differ between when participants were ovulating ($M=.207\mu g/dL, SD=.11$) and when they were in their luteal phase ($M=.229\mu g/dL, SD=.16$), $F(1, 23)<1$. Cortisol levels were not found to differ between baseline ($M=.21\mu g/dL, SD=.14$), 5-minutes post stimuli ($M=.23 \mu g/dL, SD=.15$), and 20-minutes post stimuli ($M=.21 \mu g/dL, SD=.12$), $F(2, 46)=1.183, p=.315, \eta^2_p=.049$. Mauchly’s test indicated that sphericity had been violated for the interaction of fertility status and time of sample ($\chi^2=7.467, p=.024$), therefore degrees of freedom were adjusted using Greenhouse-Geisser estimates of sphericity ($\varepsilon=.777$). Cortisol response was not conditional upon fertility status, as indicated by lack of a significant interaction, $F(1.553, 46)=2.419, p=.115, \eta^2_p=.095$ (see Appendix E).

Testosterone levels of listeners were analyzed using a 2 (fertility status) x 3 (time of sample) repeated-measures ANOVA. Collapsing across time of sample, mean testosterone levels did not differ between when participants were ovulating ($M=61.61pg/mL, SD=21.01$) and when they were in their luteal phase ($M=63.75pg/mL, SD=21.93$) ($F(1, 23)=.341, p=.565, \eta^2_p=.015$). Collapsing across fertility status of the
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Listener, testosterone levels differed between baseline ($M=55.72$ pg/mL, $SD=17.88$), 5-minutes post stimuli ($M=66.53$ pg/mL, $SD=.15$), and 20-minutes post stimuli ($M=65.12$ pg/mL, $SD=23.85$), $F(2, 46)=12.019$, $p<.001$, $\eta_p^2=.343$. Mauchly’s test indicated that sphericity had been violated for the interaction of fertility status and time of sample ($\chi^2=7.919$, $p=.019$), therefore degrees of freedom were adjusted using Greenhouse-Geisser estimates of sphericity ($\epsilon=.768$). Testosterone response was not moderated by fertility status, as indicated by lack of a significant interaction, $F(1.536, 46)=.219$, $p=.746$, $\eta_p^2=.009$ (see Appendix F). Post hoc analyses revealed that baseline samples had significantly lower concentrations of testosterone than samples collected at 5-minutes post-stimuli ($p<.001$) and 20-minutes post-stimuli ($p=.013$), however, the 5-minute samples and 20-minute samples did not differ from one another ($p>.05$) (see Appendix G).

Skin Conductance Response Analyses

Upon visual inspection of electrodermal activity, it was clear that most participants exhibited a relatively extreme SCR to the onset of the first voice in the playlist. In 27 of the 48 trials, this response exceeded two standard deviations above the mean response of each participant. We attributed this to a startle response rather than a response to the actual stimulus. Hence, these data were considered outliers and removed from the sample. The voice removed was one of a woman taking hormonal contraceptives, leaving the remaining data to reflect responses to 10 naturally cycling women, both at high- and low-fertility, and nine women on hormonal contraceptives, at analogous days in their menstrual cycles. Because the analyses conducted compared listeners’ SCRs to the voices of women at high-fertility compared to the same woman’s voice at low-fertility, the data in reaction to the second recording of the woman whose recording was first in the playlist was also
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removed. Room temperature ($M=72.47^\circ$F, $SD=.63$) did not systematically vary between trials ($t(20)=-.623, p=.540$) nor did humidity ($M=32.29$, $SD=9.78$), $t(20)=.592, p=.56$, hence neither were expected to affect tonic SCL or SCRs.

Skin conductance responses were quantified by obtaining the maximum SCL and minimum SCL throughout the duration of each stimulus and comparing these to the SCL at the onset of the stimulus. For cases in which maximum SCL exceeded SCL at onset, the maximum SCL was subtracted from the SCL at the onset of each voice and retained for analysis. For cases in which the maximum SCL did not exceed the SCL at onset, the minimum SCL was subtracted from the SCL at the onset of each voice and retained for analysis. Mean SCR values were calculated for each voice type (high-fertility naturally cycling, low-fertility naturally cycling, high-fertility hormonal contraceptive, low-fertility hormonal contraceptive) and retained for analysis.

Skin conductance responses were analyzed using a 2 (fertility status of participant) x 4 (fertility status of voice) repeated-measures ANOVA. Collapsing across voice type, SCRs did not differ between when the participant was ovulating ($M=.47\mu S$, $SD=.70$) and when they were in their luteal phase ($M=.42\mu S$, $SD=.62$), $F(1, 23)<1$. Mauchly’s test indicated that sphericity had been violated for the main effect of voice type ($\chi^2=18.201, p=.003$) and the interaction of voice type and fertility status ($\chi^2=25.593, p<.001$), therefore degrees of freedom were adjusted using Greenhouse-Geisser estimates of sphericity ($\varepsilon=.668$ voice type; $\varepsilon=.583$ interaction). SCRs were not found to differ as a factor of the fertility status of the voice provider ($F(2.064, 69)=.310, p=.818, \eta^2_p=.013$). SCR was also not moderated by fertility status of the participant, as indicated by lack of a significant interaction, $F(1.75, 69)=.179, p=.911, \eta^2_p=.008$ (see Appendix H).
Voice Perception Analyses

Lacking temporally specific evidence that the any physiological responses present were specific to the voices of high-fertility naturally cycling voices, I further assessed whether perceptual differences in voice attractiveness was robust to this sample. Voice attractiveness ratings from one participant were excluded from analysis due to assigning all voices the same rating during both trials, leaving data from 23 participants. Collapsing across type of voice, raw voice attractiveness ratings did not differ between when participants were ovulating ($M=36.78$, $SD=10.97$) and when they were in their luteal phase ($M=35.28$, $SD=9.59$), $t(22)=.753$, $p=.459$. To control for individual differences in response variability, all ratings were $z$-scored prior to analysis. Mean $z$-scored attractiveness ratings were calculated for each voice type (high-fertility naturally cycling, low-fertility naturally cycling, high-fertility hormonal contraceptive, low-fertility hormonal contraceptive) and retained for analysis.

In order to assess whether voice attractiveness ratings differed as a factor of the fertility status of the provider, and if these differences were moderated by the fertility status of the listener, a 2 (fertility status of participant) x 4 (fertility status of voice) repeated-measures ANOVA was employed. Mauchly’s test indicated that sphericity had been violated for the main effect of voice type ($\chi^2=21.293$, $p=.001$), therefore degrees of freedom were adjusted using Greenhouse-Geisser estimates of sphericity ($\varepsilon=.603$). Voice attractiveness ratings were found to differ as a factor of voice type ($F(7.809, 66)=4.487$, $p=.02$, $\eta_p^2=.169$), but were not conditional upon the fertility status of the listener as evidenced by the lack of a significant interaction ($F(3, 66)=2.743$, $p=.05$, $\eta_p^2=.11$). Post-hoc analyses revealed that naturally cycling high-fertility voices were rated as more
attractive than naturally cycling low-fertility voices ($p=.001$), but there was no difference in attractiveness ratings of voices from women using hormonal contraceptives between high-fertility and low-fertility recordings ($p=.277$) (see appendix I).

Although the interaction was only marginally significant ($p=.05$), exploratory analyses revealed that the effect size for the difference between ratings of naturally cycling high-fertility and low-fertility voices was considerably larger when the listeners were ovulating ($\eta^2_\text{p}=.543$) than when the listeners were in their luteal phase ($\eta^2_\text{p}=.251$). Additionally, the mean difference between voice attractiveness ratings of naturally cycling high-fertility and low-fertility women was more exaggerated when the listeners were ovulating ($MD=.332$) than when the participants were in their luteal phase ($MD=.181$). The effect size for the difference, and actual mean differences between ratings of women on hormonal contraceptives at “high-fertility” and “low-fertility” also differed between when the listeners were ovulating ($\eta^2_\text{p}=.258$, $MD=.150$) compared to when they were in their luteal phase ($\eta^2_\text{p}=.014$, $MD=.039$), however these differences were not as exaggerated.

Additional exploratory analyses were conducted in order to assess if there may be a relationship between testosterone levels and derogation of potential rivals, given research implying that testosterone relates to willingness to compete (i.e. Mehta & Josephs, 2010) and rival derogation is thought to be an effective tactic for women to employ when competing with other women in mating contexts (i.e. Schmitt & Buss, 1996). In order to investigate, bivariate correlations were conducted between raw voice attractiveness ratings for each type of voice, as well as all voices combined, and baseline testosterone levels. Bivariate correlations between average voice attractiveness ratings,
ratings specific to voice types, and difference scores reflecting changes in testosterone relative to baseline at 5-minutes and 20-minutes post-stimuli were also conducted to probe the relationship between testosterone reactivity and rival derogation. If such relationships existed, we would expect that heightened basal testosterone, and heightened testosterone reactivity would be associated with lower attractiveness ratings. No significant relationships were found between baseline testosterone, or differences in testosterone following stimuli presentation and the average voice attractiveness ratings or attractiveness ratings specific to fertility status of the voice provider ($r’s<.250$, $p’s>.09$).

**Discussion**

The current study was the first to examine how physiological reactions to human fertility cues are influenced by the fertility of the observer. Although reactions to a variety of stimuli have been investigated as a factor of fertility, physiological reactions to stimuli representative of potential threats to reproductive success have not been explored in this context. Although this study was limited in the power to detect some of these cyclical shifts in response patterns due to a relatively small sample size, preliminary findings and trends in our results provide justification for these questions to be more thoroughly examined.

We did not find that women exhibited heightened SCR amplitude in response to fertility detection as a factor of their own fertility. Previous research suggests that women may exhibit increased SCR amplitude in response to neutral stimuli during ovulation (Gomez-Amor, Martinez-Selva, Roman, Zamora & Sastre, 1990a; Gomez-Amor, Martinez-Selva, Roman, Zamora & Sastre, 1990b). Our data can neither substantiate nor refute these findings, and we would not venture to classify the vocal stimuli presented as
positive, negative or neutral. Contrary to expectations and previous findings (i.e. Shoup-Knox & Pipitone, 2015), skin conductance responses of the women in this study were not heightened specifically in reaction to voices of high-fertility women relative to the voices of the same women at low-fertility. Regardless of the fact there were no differences in SCR between voice types, it should not be overlooked that on average, women exhibited SCRs of magnitude that would be considered elicited (as opposed to non-specific fluctuations) (see Dawson, Schell & Filion, 2007), and would index greater overall arousal. Although the results do not imply that fertility cues were necessarily the source of heightened arousal, they do show that listening to female voices and rating their attractiveness elicited sympathetic nervous system activation. Further, while not statistically significant, average reactivity to each individual voice type was higher when women were ovulating compared to when they were in their luteal phase.

Although there were no differences in SNS activity as a factor of voice type, this does not negate the fact that women perceived the voices of high-fertility naturally cycling women as more attractive than the voices of the same women at low-fertility. This contributes to the body of literature that posits that vocal fertility cues may affect perceptions of attractiveness. Additionally, the difference in attractiveness ratings of naturally cycling voices was more exaggerated when listeners were at high-fertility. This may imply that alterations in vocal acoustics that are affected by hormonal state become more salient to women when they are ovulating, and, potentially, that ovulating women become more attentive to any number of markers of attractiveness. The fact that there were no significant perceptual differences in the attractiveness of voices of women on
hormonal contraceptives throughout different phases of their cycles further implies that cyclical variation in voice attractiveness is affected by variation in hormonal state.

The current data supports previous findings (Liening et al., 2010) that basal levels of cortisol and testosterone do not systematically differ throughout phases of high- and low-fertility. Although some suggest that women exhibit heightened cortisol responses during their luteal phase, relative to their follicular phase (Kirschbaum et al., 1999), we did not see this trend in our results. This is not to claim that women’s cortisol responses do not differ throughout the cycle. Based on salivary analyses, it was not evident that our stimuli elicited an observable stress response that would be suitable to compare between phases. More overt and perceptually salient cues of intrasexual competition may be required in order to adequately address whether cycle phase influences endocrine response to stressors relative to threat in the context of mate selection or mate retention.

Although cortisol levels remained relatively stable before and after the presentation of stimuli, testosterone levels rose following the procedure and presentation of stimuli. It is possible that subtle indicators of fertility that can be expressed through alterations of the voice were not salient enough to elicit an endocrine response to stress. However, some aspect of the procedure or stimuli was effective in heightening testosterone release. It is difficult, lacking a physiological response with more temporal specificity, to propose that heightened testosterone was a factor of only fertility cue detection. Given anticipation of competition heightens testosterone levels (Bateup et al., 2002; Oliveira et al., 2009), testosterone may have risen in reaction to the detection of vocal fertility cues and discreet assumptions regarding rival competitiveness. Elevated testosterone also heightens attention to threat (e.g. Carré & Olmstead, 2015), and
testosterone levels may have risen as a factor of introducing stimuli representative of intrasexual competition, and thereby primed women to be more attentive to attractive vocal characteristics. However, it is also possible that the procedure of rating the attractiveness of other women affected alternative cognitive mechanisms influencing testosterone. One could argue that women undergoing this procedure would naturally be contemplating how attractive their own voice was relative to the stimuli, which could be a covert competition in it of itself.

The challenge hypothesis (Wingfield et al., 1990; see also Archer, 2006) proposes that high testosterone levels among males should increase in response to sexual stimuli and heighten the likelihood of exhibiting intrasexual competition. Although the extension of these reactions and behavioral effects have not been exhaustively researched among females, research suggestions that testosterone heightens women’s willingness to compete in domains outside of mating contexts (i.e. Bateup et al, 2002; Oliveira et al., 2009; Edwards et al., 2010), that sexual stimuli elicits testosterone release (Goldey et al., 2011) and that endocrine responses to sexual stimuli may vary as a factor of fertility status (Lopez et al., 2009). Our results do not bear evidence of cyclical differences in testosterone responses, however, they may provide additional evidence that the challenge hypothesis extends to women. Regardless of whether heightened testosterone was in response to framing voice attractiveness sexually, or to detection of competitive rivals, the extension of the challenge hypothesis applies. Using low voice attractiveness ratings as an index for intrasexual competition via rival derogation, there were no definitive answers as to whether heightened testosterone levels could prime this form of intrasexual competition. However, it is not unlikely that testosterone affects women similarly to men.
in terms of priming intrasexual competition, and that high levels of testosterone may be related to an increased frequency of overt derogation of sexual rivals among females in more natural environments.

It is interesting that women exhibited the most marked increase in testosterone five minutes following the end of the stimuli (roughly 12 minutes after the onset), rather than continuing to rise until 20 minutes post-stimuli (roughly 27 minutes after onset) (see Appendix G). Although elicited testosterone reactions are reflected in salivary testosterone concentrations 15 minutes after presentation of stimuli (Hellhammer, Hubert & Schürmeyer, 1985), it is less consistent in the literature when the peak testosterone response would be evidenced in saliva. This introduces difficulty with definitively asserting what aspect of the stimuli elicited the testosterone response, and suggests that future research may either incorporate blood serum sampling or obtain saliva samples at additional time intervals after stimulus presentation to observe the rise and fall of testosterone. Nevertheless, either listening to female voices of differing fertility, rating the attractiveness of other women, or a combination thereof seems to have precipitated the release of testosterone in women at high- and low-fertility. This suggests that merely being exposed to other women and gauging their attractiveness may physiologically prime women to behave more competitively.

**Limitations**

This study was limited by both a small sample size, and the inability to properly counterbalance trial order between participants. Uncontrollable scheduling difficulties rendered efforts towards counterbalancing futile, therefore, trends towards potential interactions between cycle phase and physiological or perceptual responses should be
interpreted with caution, as there is the possibility of an order effect. Additionally, without individually presenting voices of naturally cycling women at high-fertility and low-fertility during separate trials, we are limited our ability to ascribe testosterone responses to an individual voice type, or more specifically, detection of vocal fertility cues.

Unfortunately, tonic SCL before the onset of vocal stimuli was not recorded, such that if there was a ceiling effect influencing SCR amplitude or variability, we were unable to detect or control for this potential confound. In addition, the voices were played continuously, which did not allow SCLs to return to baseline in between voices, and may have led to carry-over effects and violated independence of observations. Future studies should consider incorporating an interval of white noise in between stimuli to both allow for a return to baseline and include noise to avoid a startle response in reaction to the stimulus to follow. It should also be mentioned that the ratio of females to males in the population from which our sample was derived is biased towards females, which should increase the frequency and extent of intrasexually competitive behavior (Rosvall, 2011). It could be the case that there was a lack of SNS activation in response to subtle fertility cues of the voice because our participants were desensitized to subtle cues in the presence of more overt signs of fertility or sexual receptivity.

Although limited in some areas, the use of LH strips to detect ovulation strengthened the ability of this study to firmly assert that we were conducting trials while women were ovulating. Many research designs used in other studies have estimated fertility by incorporating backward or forward counting methods, and assumed women were at high-fertility based on number of days since or following their menses, using a typical 28-day cycle as a reference. Although this is a common practice, and it is likely
relatively accurate to estimate high-fertility in most women, it does not provide any true evidence that participants were undergoing any alterations to their hormonal state that accompany ovulation. By design, we were able to clearly identify when women were at high-fertility, regardless of cycle length, and schedule trials accordingly.

**Future Directions**

Becoming increasingly attentive to the attractiveness of potential competitors during ovulation could be evolutionarily adaptive if this tendency also precipitated behaviors such as enhancing one’s own attractiveness or distancing one’s mate from more attractive rivals. Although we found a trend in women’s responses to naturally cycling female voices that may illustrate increased attentiveness to attractiveness or attentiveness to fertility cues when female observers were at high-fertility themselves, it was not statistically significant and should be further investigated. Considering that women purchase more sexually competitive products when primed with attractive females (Durante et al., 2010) and are more attentive to status symbols (Lens et al., 2012) specifically when at high-fertility, further research is warranted to identify exactly what types of stimuli become more salient at high-fertility, and how this shift in attention may promote reproductive success.

Future research should investigate whether women have heightened SNS reactivity around ovulation in response to stimuli representative of women that are intrasexually competitive, regardless of if they are more competitive due to outward indicators of fertility. If indeed, there is heightened reactivity during ovulation, it may be the case that women become physiologically primed to be hypervigilant at high-fertility in response to a generalized class of stimuli, rather than specific cues. This is not to claim, however, that
if enough cues of attractiveness or fertility were present women’s responses would not become more exaggerated.

Our results also merit further research to identify whether the observed increase in testosterone was due to detection of vocal fertility cues or a downstream effect of listening to all voices and gauging attractiveness. If testosterone responses are specific to exposure to cues of high-fertility, it is reasonable to suspect that women would exhibit a higher propensity towards derogating other women at high-fertility, and enhancing their own sexual attractiveness in their presence. However, it is unclear, given the results of the current study, if women would also have to consciously assess the attractiveness of another before an endocrine response would be elicited. Additional measures of downstream competitor derogation, as well as controls to tease apart the effects of assessing attractiveness and detection of fertility should be incorporated into future research designs.

Conclusion

Women exhibit cyclical shifts in their internal endocrine environment that are accompanied by shifts in physical morphology, attractiveness, desire, perception, and behavior. Although theories regarding the functions of these cyclical changes have been presented within and outside of this study, there have been very few researchers that have investigated the underlying physiological mechanisms that trigger these differences. In order to better understand how women choose mates, react to rival mate-seeking competitors, and interpret threats to current relationships, there is a need for continuing to incorporate measurements of physiological responses to stimuli, as opposed to solely perceptual or behavioral differences.
Although there is now conflict in the literature as to whether detection of fertility cues elicits SNS activation among females (i.e. Shoup-Knox & Pipitone, 2015), perceptual differences in vocal attractiveness remains a robust finding, and may be influenced by the fertility of the listener. While seemingly unaffected by the fertility of the observer, testosterone responses may be elicited by detection of fertility cues, or as a downstream effect of assessing the attractiveness of a potential intrasexual competitor. Furthermore, how potential cortisol responses induced by threats within mating contexts may be moderated by the fertility status of the observer remains an unanswered question. Female reaction to fertility cues, how they affect mate-seeking and mate-guarding behaviors, and particularly how or if these reactions to fertility cues are affected by the fertility status of the observer are yet to be clearly defined and should be further investigated in light of how physiological reactions may prime downstream behavior.
Figure 1. Typical hormone fluctuations throughout the menstrual cycle (adapted from Gilbert, 2013).
Appendix B

Intake Criteria Questionnaire

1. What is your age? ___________

2. Is your menstrual cycle regular?  □ Yes  □ No

   If yes, approximately how many days pass between the onset of your menses (the first day of your “period”)? ________________

3. Are you pregnant or planning to become pregnant?  □ Yes  □ No

4. Are you currently using any hormonal contraceptives (birth control, including intrauterine devices)?  □ Yes  □ No

5. Have you used hormonal contraceptives within the past 90 days?  □ Yes  □ No

6. Are you planning to begin using hormonal contraceptives within 60 days?  □ Yes  □ No

7. Do you frequently smoke or vaporize?  □ Yes  □ No

   If yes, which?  □ Smoke  □ Vaporize  □ Both

8. Are you currently in a committed relationship?  □ Yes  □ No
9. What is your primary sexual orientation?
   - Heterosexual
   - Homosexual
   - Bisexual
   - Other: _____________________
   - Prefer not to answer

10. Are you taking any medications (including any over-the-counter medications, prescription medications, inhalers for asthma or allergies, insulin, nicotine replacements, etc.) on a regular basis?  
    - Yes  
    - No  
    - Prefer not to answer

    If yes, please list:

    ______________________________________________________

    ______________________________________________________

    ______________________________________________________

    ______________________________________________________

    ______________________________________________________
Appendix C

Voice Rating Scale

1. How attractive do you think this person’s voice is?

<table>
<thead>
<tr>
<th>1</th>
<th>50</th>
<th>100</th>
</tr>
</thead>
<tbody>
<tr>
<td>very unattractive</td>
<td>average</td>
<td>very attractive</td>
</tr>
</tbody>
</table>

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
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<th></th>
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<tbody>
<tr>
<td></td>
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</table>
Appendix D

Participant Questionnaire

Have you consumed alcohol within the past 24 hours?  □ Yes  □ No
If yes, how long before you came to the trial? ________________
If yes, how many drinks? ________________

Do you consume alcohol daily or almost daily?  □ Yes  □ No
If yes, approximately how many drinks per day? ________________

Do you frequently smoke or vaporize?  □ Yes  □ No

How long has it been since you ingested nicotine? ________________ or □ Not Applicable
(this includes nicotine replacement therapies, i.e. patches, gums, etc.)

Did you brush your teeth within an hour of coming to the trial?  □ Yes  □ No
If yes, approximately how long before arriving? ________________

Do you have gum disease?  □ Yes  □ No

Have you ingested caffeine within the past 3 hours?  □ Yes  □ No
If yes, how long before you came to the trial? ________________
If yes, how many caffeinated drinks/pills? ________________
If yes, do you consume caffeine on a regular basis?  □ Yes  □ No

Are you currently on any medication?  □ Yes  □ No  □ Prefer not to answer
(this includes over-the-counter medications, as well as inhalers, insulin, etc.)
If yes, please list: ____________________________________________

Have you participated in intense exercise today?  □ Yes  □ No
If yes, how long before you came to the trial? ________________

What time did you wake up today? ________________

Did you nap in between waking up and coming to the trial?  □ Yes  □ No
If yes, when did you nap? ________________

Did you eat a meal within 2 hours of coming to the trial?  □ Yes  □ No
If yes, how long before arriving did you finish eating? ________________

What time did you come to the trial today? ________________
Table 1

*Descriptive statistics of cortisol levels (in μg/dL)*

<table>
<thead>
<tr>
<th>Participant Fertility Status</th>
<th>Baseline</th>
<th>5-minutes post-stimuli</th>
<th>20-minutes post-stimuli</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ovulating</td>
<td>.22 (.13)</td>
<td>.21 (.11)</td>
<td>.19 (.07)</td>
</tr>
<tr>
<td>Luteal Phase</td>
<td>.21 (.15)</td>
<td>.25 (.18)</td>
<td>.23 (.15)</td>
</tr>
</tbody>
</table>
Figure 2. Salivary testosterone levels of ovulating and luteal phase participants before and following stimuli. (Error bars indicate one standard error of the mean.)
Figure 3. Salivary testosterone levels before and following stimuli, collapsing across cycle phase. (Error bars indicate one standard error of the mean. *Significantly different than baseline, $p<.05$)
Table 2

*Descriptive statistics of skin conductance responses (in μS) by type of voice and fertility status of listener*

<table>
<thead>
<tr>
<th>Participant Fertility Status</th>
<th>Naturally cycling high-fertility</th>
<th>Naturally cycling low-fertility</th>
<th>Hormonal contraceptive user at “high-fertility”</th>
<th>Hormonal contraceptive user at “low-fertility”</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ovulating</td>
<td>.466 (.67)</td>
<td>.434 (.48)</td>
<td>.542 (.80)</td>
<td>.447 (.76)</td>
</tr>
<tr>
<td>Luteal Phase</td>
<td>.359 (.70)</td>
<td>.425 (.66)</td>
<td>.461 (.64)</td>
<td>.425 (.47)</td>
</tr>
</tbody>
</table>
Figure 4. Voice attractiveness ratings (z-scored) across voices of differing fertility for participants while ovulating and during their luteal phase. (Error bars indicate one standard error of the mean. *p<.05)
References


