FACULTY OF SCIENCE
Charles University

Department of Philosophy and History of Science

Theoretical and Evolutionary Biology

The evolved information processing design of the human mating mind

Ayten Yesim Semchenko, M.S., MSc.

Doctoral dissertation

Supervisor: Doc. Mgr. Karel Kleisner, Ph.D.

Prague 2023

I declare that I carried out this doctoral thesis independently, and only with the cited sources, literature and other professional sources. It has not been used to obtain another or the same degree.

I understand that my work relates to the rights and obligations under the Act No. 121/2000 Sb., the Copyright Act, as amended, in particular the fact that the Charles University has the right to conclude a license agreement on the use of this work as a school work pursuant to Section 60 subsection 1 of the Copyright Act.

In .... date ....

Author's signature

Acknowledgment

I am deeply grateful to Dr.Karel Kleisner for accepting to be my supervisor and for supporting me throughout my studies. I am also immensely grateful for the support I received from Dr.David M.G. Lewis. Not only that he had accepted me as part of his research group, but also he has unofficially co-supervised me. He has also inspired me to be resilient and to be someone that follows her dreams despite many obstacles that life may present. I am also thankful for my incredibly supportive and loving husband, Anton Semchenko, for bearing with me in my most difficult times in this journey. His love and support has surely given me a lot of strength to stand tall against the adversities in life. I am grateful for my mother, who has loved me unconditionally and has been a great help during various obstacles I had to overcome. I am in great debt to my friends for absorbing negativity and supporting me in difficult times as well as celebrating each publication with me. I am also very lucky that our paths have crossed with our dog, Gina. She has since been the joy in our house. Lastly, I am grateful to my favorite writer, Neil Gaiman for reminding me that the dreams are most difficult to kill even if they are considered fragile for many. So, I will end my acknowledgment with a quote from his book, Fragile Things:

"....it occurs to me that the pecularity of most things we think of as fragile is how tough they truly are... Hearts may break, but hearts are the toughest muscles able to pump for a lifetime, seventy times a minute, and scarcely falter along the way. Even dreams, the most delicate and intangible of things, can prove remarkably difficult to kill."

Title: The evolved information processing design of the human mating mind

Author: Ayten Yesim Semchenko

Department: Department of Philosophy and History of Science

Study Programme: Theoretical and Evolutionary Biology

Supervisor: Doc. Mgr. Karel Kleisner, Ph.D.

Abstract:

In this dissertation, I investigated the psychological adaptations designed to overcome the challenge of mate acquisition through its sub-problems such as (not) missing an opportunity to interact with a potentially suitable partner, identifying mates who exhibit specific fitness-relevant cues, identifying mates that are available to us, and identifying (right) ways of appearance-enhancement. In an attempt to unravel the psychological adaptations designed to solve the stated sub-problems of mate acquisition, I studied the effect of the theoretically-anchored inputs such as biological sex, incomplete visual information, mating context, lumbar curvature angle, and back arching behavior. Through investigating the effects of those inputs (e.g., mating context and lumbar curvature angle), I found outputs consistent with the proposed psychological adaptations (e.g., male preference for an intermediate lumbar curvature angle in women) designed to solve the sub-problems of mate acquisition (e.g., identifying mates with the specific fitness-enhancing trait). Furthermore, these findings indicated that our approach to studying the human mating mind led to accurately identified inputs producing the predicted outputs.

Keywords: evolutionary psychology, human mating, mate acquisition, psychological adaptations

Titul: Evolučně odvozené procesy zpracování informací účastnící se výběru partnera u lidí

Autor: Ayten Yesim Semchenko

Katedra: Katedra filozofie a dějin vědy

Studijní program: Teoretická a evoluční biologie

Vedoucí: Doc. Mgr. Karel Kleisner, Ph.D.

Abstrakt:

V disertaci se věnuji zkoumání psychologických adaptací směřujících k překonání potíží se získáním partnera/partnerky. Postupuji metodou výzkumu částečných problémů, jako je (ne)promeškání příležitosti k interakci s potenciálně vhodným partnere/partnerkou, identifikace potenciálních partnerů/partnerek, kteří vykazují znaky spojované s fitness, identifikace partnerů/partnerek, kteří jsou dostupní, a určení (vhodných) způsobů umělého zlepšení vzhledu. V rámci snahy o lepší porozumění psychologickým adaptacím, jejichž cílem je řešit výše zmíněné dílčí překážky v získání partnera/partnerky, jsem studoval efekt teoreticky ukotvených vstupů jako je biologické pohlaví, neúplné vizuální informace, kontext páření, úhel zakřivení bederní páteře i úmyslné prohýbání zad. Studium efektu těchto vstupních faktorů (např. kontextu hledání partnera nebo zakřivení bederní páteře) mi umožnilo identifikovat výstupy konzistentní s navrhovanými psychologickými adaptacemi (např. mužská preference pro středně velký úhel zakřivení bederní páteře u žen), které se vyvinuly proto, aby pomohly při řešení dílčích problémů při získávání partnera/partnerky (např. identifikace potenciálního partnera/partnerky s daným rysem, který přispívá ke specifické fitness).Tato zjištění navíc ukázala, že náš přístup k výzkumu lidské mysli ve vztahu k rozmnožování vedlo ke správně určeným vstupům, tedy takovým, které vedly k předpovídaným výstupům.

Klíčová slova: evoluční psychologie, lidské epigamní interakce, získávání partnera/partnerky, psychologické adaptace

Contents

Preface

There are three chapters in this dissertation. In the first chapter, I provide a brief theoretical background about evolution, the products of natural and sexual selection (i.e., adaptations, byproducts, and noises), human mating literature, and an information processing approach to the psychological adaptations designed to overcome the challenges of mate acquisition. In the second chapter, I briefly introduced the previous literature about the adaptive problems related to mate acquisition such as the problem of missing opportunities to interact with a potentially suitable partner and the problem of identifying mates exhibiting specific fitness-relevant cues, together with my own studies. Lastly, I laid out the summary of my findings as the conclusion of this dissertation.

In the process of creating this dissertation, it is true that I learned a lot from literature and from the research experience. But most importantly, my critical thinking skills have been developed further, allowing me to broaden my horizon. Therefore, it is not wrong to say not only I created this dissertation, but also it shaped me. I hope that when you read this dissertation, it will stimulate thoughts in you and that you will thoroughly enjoy it.

1. Evolution and human mating

Acquiring a mate is required for human reproduction, hence, it has an utmost importance for our continuation. However, it is potentially accompanied with various problems throughout our evolutionary history such as the problem of (not) missing an opportunity to interact with a suitable mate under uncertainty, and psychological adaptations are likely to evolve to overcome those problems. However, before delving into the adaptive problems associated with mate acquisition, I would like to briefly introduce evolution, natural and sexual selection, and the products of the selection processes (i.e., adaptations, byproducts of adaptations, and noises) to be able to provide a more solid theoretical background.

1.1 A brief introduction to evolution

Evolution can be defined as the change in heritable traits among organisms. When these changes progress into a direction increasing the organisms' survival and/or reproduction, they can be selected over time through natural (Darwin, 1859) and/or sexual selection (Darwin, 1871). [1]

1.1.1 The products of natural and/or sexual selection

Natural and/or sexual selection produces adaptations, byproducts of adaptations, noises, or any combination of these processes over time (Leca, 2020). Before defining and exemplifying the products of natural and/or sexual selection, it is important to note that adaptations and byproducts of adaptations are the consequences of selection processes, while noises may or may or may not be so.

---

[1] I fully recognize that the account for selection processes is simplified here. There are invaluable scientists such as Mendel (Weiling, 1991), or Maynard Smith (Charlesworth, 2004) who contributed to the understanding of selection by shedding light on various subjects such as genetics or mathematical biology. However, to keep the dissertation concise, I will not lay out all the processes behind the selection mechanisms in evolutionary theories.

Adaptations

Both a process of heritable alterations resulting in a functional trait and the trait itself is labelled as adaptation. The word function in the previous sentence refers to the function of increasing organisms' survival and/or reproductive success. To understand an adaptation, we can take a closer look at bird tails as they are important in maintaining stability and making maneuvers to turn, potentially affecting birds' survival. Birds that live in environments requiring more maneuvers, and longer tails can lower the probability of accidents due to not being able to turn efficiently, while for open country birds, having a longer tail may not give sufficient additional advantage. In line with this articulation, Thomas & Balmford (1995) found that open country birds have shorter tails while birds living in more cluttered environments needing more maneuvers have longer tails. Therefore, the length of a bird's tail can indicate the birds' adaptation to its environment through natural selection.

A more recent example could come from the Chernobyl accident site. In 1986, radioactive materials were spread in Chernobyl from a nuclear station due to an accident (Blakemore, 2019). Buracco & Orizaola (2022) found that the tree frogs in the exclusion zone, which had higher radiation level compared to the other zones, had a darker dorsal skin compared to the tree frogs in the other areas. Melanin, which can cause darker coloration, might work against the damage caused by radiation (Zhang et al., 2022). Other potential reasons for darker skin such as body condition and oxidative status were found to be unrelated to the darker skin coloration of the tree frogs in the exclusion zone. Furthermore, the differences in skin color seemed to be connected to the historical radiation levels rather than the current levels. Therefore, Buracco & Orizaola (2022) concluded that darker colors for the dorsal skin might have been selected around the time of accident as it can reduce the radiation damage. In other words, darker skin color can be the tree frogs' adaptation to the radioactive environment.

Adaptations through natural selection, however, did not offer explanation for every trait, especially the ones that reduce the chances of survival for some animals. The infamous example would be the colorful and heavy feathers of peacocks hindering their survival and at the same, increasing peacocks' chances to be selected by peahens. Therefore, those bright feathers can be adaptive as they potentially increase peacocks' reproductive success. This phenomenon is labelled as sexual selection (Darwin, 1871). To explain it simply, the traits that maximize reproductive success (i.e., adaptive traits) might be selected in nature. Sexual selection has two phases, namely, intrasexual and intersexual selection. When same-sex individuals compete (e.g., male-to-male competition) with one another to be chosen by the opposite sex, it is called intrasexual selection and when the individuals choose mates from the opposite sex (e.g., female choice), it is called intersexual selection. In the intrasexual selection, rival assessment skills can be *adaptive* as assessing how the rival looks (i.e., morphological cues) and what it does (i.e., behavioral cues) can potentially give an advantage to the assessor in the competition. For example, peacocks' gaze patterns were investigated and it was found that they selectively pay attention to the rival feathers and wings (i.e., morphological cues) and their displays (i.e., behavioral cues), indicating a possible rival assessment through both morphological cues and behavioral cues (Yorzinski et al., 2017). Indeed, both morphological and behavioral cues are found to play a part in peahens' choice of peacocks (Loyau & Sorci, 2005), therefore peacocks' selective attention towards these cues, which might be *an adaptation*, can truly help them assess their rivals.

As exemplified above, adaptations can be in numerous forms such as morphological (i.e., peacocks' bright feathers), behavioral (e.g., display of the bright feathers), and psychological (e.g., peacocks' selective attention towards other peacocks' bright feathers and their displays). In this dissertation, I will focus on psychological adaptations against the challenge of human mate acquisition. However, before moving on with that focus, it is important to clearly define what byproducts and residual noises are in order to be able to establish and test plausible hypotheses about whether a trait is an adaptation or not.

Byproducts (of Adaptations)

Byproducts are the traits that couples with adaptations (Tooby & Cosmides, 2016), or as Al-Shawaf et al. (2021a) put it, they are the "*side effects*" of adaptations. According to Leca (2020), there are three types of byproducts which are 1) spandrels, 2) exaptation type I, and 3) exaptation type II. Spandrels are the fitness-neutral byproducts of adaptations (Leca, 2020). In other words, the traits that are classified as spandrels have never contributed to organisms' fitness. For example, male nipples are considered to be spandrels (Kelly et al., 2018). It is articulated that female nipples are adaptive as they are functional for feeding offspring, contributing to reproductive success of the mother and survival of the offspring. Men have nipples because both sexes share the same embyrological development until the eighth week and nipples start developing around the fifth week (Vorherr, 1974; Lloyd, 2013). The second type of byproducts named as exaptation type I indicates the traits that stem from *a pre-existing adaptations* which later became a fitness increasing feature for another function. The common example would be bird feathers as they were first evolved for their thermoregulatory functions and later were co-opted for flight enabling usage (Ostrom, 1974). The last type of the byproducts labelled as exaptation type II covers the traits that comes from *a pre-existing spandrel* co-opted for a fitness-enhancing use. For example, sutures in the skull may have been the spandrels for skeleton shaping process for many vertebrates such as birds and reptiles. However, those sutures may ease birthing of large headed mammals through narrower birth canals (Gould & Vrba, 1982; Leca, 2020).

It is important to note that there is a disagreement in the literature about the categorization of exaptations. For example, Al-Shawaf et al. (2021a) articulates that they are a sub-category of adaptations whereas Leca (2020) introduced them as the sub-category of byproducts. Al-Shawaf et al. (2021a) considers exaptations as adaptations because in their words, '*no function is eternal*'. As long as the stated function gained under the pressures of the evolutionary past rather than the current pressures, exaptations are adaptations. Furthermore, categorizations of byproducts also differ in the literature. For example, Al-Shawaf et al. (2021a) categorizes byproducts from a different perspective than Leca (2020), as Al-Shawaf et al. (2021a) make the distinction between the obligate and facultative byproducts. Accordingly, most morphological and physiological byproducts are obligate (i.e., inevitable side effects of adaptations) while most psychological byproducts are facultative (i.e., potential side effects of adaptations).

Noises

Noises are *random variations* that are not necessarily dependent on adaptive traits or byproducts (Al-Shawaf et al., 2021b). The variation in the shape of bellybutton (i.e., inner or outer) can be an example of a noise (Buss et al., 1998).

Above, I summarized the products of natural and sexual selection, which are adaptations, byproducts of adaptations, and (possibly) noises. In this dissertation, however, I focused on one type of adaptation, which is the psychological adaptations designed to solve the problem of mate acquisition. Cosmides & Tooby (1992) articulated that adaptations can be understood with an information-processing approach because brains are like computers, they process information. Accordingly, the designer of the brain is not an engineer but natural and sexual selection (Cosmides & Tooby, 1992). The hypotheses regarding psychological adaptations are studied by testing how the predicted outputs are sensitive to the inputs. I explained two of the theoretically-anchored inputs (i.e., biological sex, mating contexts) which I used in my studies in the following section as part of the introduction to human mating literature. The remaining inputs (e.g., lumbar curvature angle and incomplete visual information) were laid out in the next chapter.

1.2 A brief introduction to human mating

Darwin (1871) articulated that the bright ornaments of most male animals can be explained by male-to-male competition (i.e., intrasexual selection) and female choice (i.e., intersexual selection). However, he did not really explain the reason why females were choosier. In the Victorian era, gender division was sharp and women were confined to domestic and supportive roles (Digby, 1992). Taken together, the idea that women choose men was not very popular and alternative explanations were articulated (Zuk & Simmons, 2018). For example, Wallace (1891) was amongst the people who were against the idea of a female choice (Darwin, 1871), and he explained the male's colored ornamentation by the vital energy surplus (i.e., males have more energy than females). At that time, the theories accounting for male ornamentation and the dispute whether female choice exists and plays a role in such ornamentations were theoretical. An empirical mating experiment with Drosophila flies that Bateman (1948) published showed us that male flies had higher variability in reproductive success than female flies. This effect was associated with costlier gamete production for females than it is for males, potentially making females choosier than males. As a result of that higher female choosiness, males had more variable reproductive success than females. The findings indicating higher variation in male reproductive success compared to female reproductive success and the association of male reproductive success with finding females are supported by a number of other studies such as Jacobs (1955) with dragonflies and Koivisto (1965) with black grouse. Built upon those studies, a cardinal theory for understanding human mating, the Parental Investment Theory (Robert, 1972) was articulated. Accordingly, the sex that contributes to the progeny/offspring development more is the choosier sex. In humans, because gestation, placentation, and lactation happen in the female body, women compared to men invest more as part of a minimum obligatory parenthood, and therefore, they are expected to be choosier. Two decades after Robert (1972), Buss & Schmitt (1993) articulated the Sexual Strategies Theory. Accordingly, heterosexual men and women have faced both similar and different adaptive challenges during our evolutionary history in different mating contexts (i.e., short-term uncommitted, long-term committed) and developed mating strategies accordingly. In other words, mating context and biological sex are the two features of the SST (Buss, 2017) and they interact with one another to a certain extent. Before starting with the first main feature, I would like to point out that these two features are not the only ones affecting human sexual strategies. Sex ratio (e.g., Schacht & Borgerhoff Mulder, 2015; Kramer et al., 2017; Maner & Ackerman, 2020), culture (e.g., Shan et al., 2012), socio-economic status (e.g., Karney, 2021), and socio-sexual orientation (e.g., Ostovich & Sabini, 2004) are among the examples of other features that potentially affect mating strategies. To exemplify how sex ratio can affect human mating strategies, Schacht & Borgerhoff Mulder (2015) reported that only when there are more women than men in the society, men are more prone to uncommitted mating. Another example might come from the effect of socioeconomic status on human mating as Karney (2021)'s review shows us that the probability of divorce among couples who have a higher socioeconomic status (SES) was lower than couples whose SES is lower. Therefore, I acknowledge that in addition to sex and mating context, other factors also affect our mating strategies. However, to be concise, through this thesis, I focus on mating context and sex as they are among the inputs that I studied throughout my research.

1.2.1 The two features of human mating

Biological sex

Adaptive challenges that ancestral men and women faced might have varied based on their sex (Buss & Schmitt, 1993). The difference in reproductive systems and body features between men and women can affect mating strategies (Buss, 2016, 2019). For example, the reason why for the asymmetrical minimum obligatory parental investment is the differences in the reproductive system. Because men's minimum investment requirement is considerably less than women's, it is articulated that having a higher number of sexual partners would benefit men more than women (e.g., Buss & Schmitt, 1993; Buss, 2017; Buss & Schmitt, 2019). Women, on the other hand, cannot have more children if they are already pregnant, possibly making them choosier. There are studies also suggesting that women are choosier than men in the short-term mating context. For instance, on dating apps, women on average get more matches than men do (e.g., Tyson et al., 2016; Timmermans & Courtois, 2018). However, I acknowledge that men wanting more sexual partners than women may be a simplified conclusion. As discussed in the earlier section (in the long-term mating context section), humans are rather considered serial monogamists (De La Croix & Mariani, 2015). Therefore, although men on average might want to have a higher number of sexual partners than women, not every man, at any point in time, would follow a short-term mating strategy and desire a higher number of sexual partners than women do. In line with that articulation, Pedersen et al. (2002) found that men on average desire a higher number of sexual partners than women do before settling down, and the majority of their participants intended to settle down at some point. Therefore, they concluded that humans are not typical short-term mating seekers. Yet Fenigstein & Preston (2007) replicated the finding that men on average desire a higher number of sexual partners than women do. In addition, they investigated how perceived risks affect those desires. They found that when women were presented with no risk, women still did not want to have a higher number of sexual partners. Men, on the other hand, when presented with no risk, desired a higher number of sexual partners than women do. One reason why that might be, as discussed before, that women may not benefit from having multiple partners as much as men do. Therefore, even though, there are no costs in the presented scenario, there might not be an added benefit for women which potentially leads to a sex-differentiated level of desire for the number of sexual partners.

Moving to the differences in body features affecting mating strategies, women are on average smaller than men (Touraille & Gouyon, 2008) which can potentially make women physically disadvantaged against predators or aggressive men. Having physical protection can increase both women's and their offspring's survival. Relatedly, studies suggest that a psychological adaptation that women perceive men who are strong, formidable (e.g., Sell et al., 2017; Butovskaya et al., 2022) and taller men than themselves (e.g., Pawlowski et al., 2000; Nettle, 2002; Stulp et al., 2013) as more attractive. However, these findings are not universal, as the associated costs and benefits might differ from situation to situation. Continuing with the same example, having a strong man can mean having physical protection from outside dangers however, it can also increase the potential for domestic violence. Therefore, a trade-off approach considering costs and benefits in a given environment might be more appropriate for understanding mating strategies (Gangestad & Simpson, 2000). For example, if the environment is rather dangerous, the cost of potential domestic violence might be worth the benefit of having physical protection. Indeed, Snyder et al. (2011) found that women's fear of crime is associated with the preference for formidable mates.

Mating context

According to SST, there are two main mating contexts which are long-term committed and short-term uncommitted mating.

Long-term committed mating context

The typical human mating is suggested to be serial monogamy even though it is possible to observe monogamy, polygyny, and polyamory across human societies. However, even in polygynous societies, most marriages are monogamous (see Schacht & Kramer, 2019, for a review), and remarrying also occurs where divorce is allowed indicating serial monogamy (De La Croix & Mariani, 2015). Therefore, it can be said that long-term committed mating is one of the main human mating strategies. The theoretical reasons why long-term mating might have evolved in the first place are not without debate due to the possible effects of other variables such as culture or socioeconomic status. Among the candidate explanations, enhancing offspring survival through paternal care or increasing paternity certainty can be listed (e.g., Buss & Schmitt, 1993, 2019). Concerning the potential benefit of long-term bonding through paternal care, whether paternal care adds any advantage to child survival is a debatable topic in the literature. For example, a review conducted by Sear & Mace (2008) found that only one-third of studies indicated the added value of paternal care in child survival while grandmothers seem to play a bigger part. Since nonmaternal help happens in human societies (e.g., Kramer, 2010; Bogin et al., 2014), the sufficiency of the added benefit of fathers might be open to discussion. Another function of long-term mating can be increasing paternity certainty. Studies indeed indicate that extra pair paternities (epp) are rather low, usually varying between 1% to 2% (see Larmuseau et al., 2016, for a review)) among couples. Similarly, a review conducted by Anderson (2006) reported that the nonpaternity rates vary between 1.7 to 3%. However, the epp rates also seem to be affected by environment, socioeconomic status (SES), and culture. To exemplify the effect of environment and culture, higher rates (around 6%) of epp were recorded among urban and low SES families (Larmuseau et al., 2019). As for the effect of culture, in the Himba society with the rate of epp was 17 percent (Scelza, 2011). However, that rate was zero among love-match marriages, suggesting a specific effect of culture, in which explicit female choice could not be sufficiently exercised, on epp. Therefore, even though the rates vary from culture to culture, in general, epp rate is low among humans and that might have been achieved through long-term pair-bonded, committed mating. However, overall, even though the exact reasons why long-term mating evolved is still in debate, long-term committed mating is one of the main mating strategies of humans.

Short-term uncommitted mating context

Long-term committed mating is not the only strategy for humans, there are also uncommitted mating practices such as one-night stands and booty calls (e.g., Wentland & Reissing, 2011, 2014). In Wentland & Reissing (2014)'s study, one night stands were defined as sex between strangers where alcohol and drugs are usually involved, and there is no expectation of meeting again. Booty calls were described as a mating practice in which at least one party is under the influence of alcohol or drugs and this person calls another with the intention of having sex (Wentland & Reissing, 2014).[2] For men, such low commitment mating gives the advantage of increasing the number of women that they can copulate and potentially increase their reproductive success. In line with this reasoning, studies indeed show that on average men want a higher number of sexual partners than women (e.g., Buss & Schmitt, 1993; McBurney et al., 2005). For women, short-term uncommitted mating can establish instant resource gain (e.g., Buss, 2017; Buss & Schmitt, 2019). To exemplify instant resource gain, gift-giving behaviors can be examined. Gift-giving in relationships can have a number of meanings such as an indication of love and commitment, or a token for sex (Poulin, 2007). Therefore, gift-giving is not exclusive to short-term uncommitted mating, however, it seems to be part of it too. Furthermore, literature shows us that gift-giving in heterosexual relationships is heavily done by men (e.g., Saad & Gill, 2003; Jonason et al., 2019) rather than women, and men use gift-giving to woo their partners

---

[2] It is important to note that Wentland & Reissing (2014) found that most participants (over 81%) correctly matched the definitions with the given relationship types.

and women are aware of this tactic.

In sum, I briefly introduced both committed and uncommitted mating contexts above, I recognize that commitment may not be the only distinguishing feature of mating contexts. A cross-cultural study attempting to comprehensively account for all variations in relationships and their features could unravel variations in the mating contexts, perhaps further than commitment. However, to the best of our knowledge supported by a review in relationship typology studies (Vojt et al., 2020), there is no such cross-cultural study to this day. In other words, my current use of commitment as an important contextual feature to distinguish human mating contexts does not mean that I do not recognize the possibility of other crucial variations in relationships and their features. It is only that with our current knowledge in the literature, we study human mating in two main relationship contexts (i.e., long-term uncommitted, and short-term committed).

2. The adaptive problem of mate acquisition

In this chapter, I will focus on four adaptive problems of mate acquisition, which are 1) the problem of missing opportunities to interact with a potentially suitable mate, 2) the problem of identifying mates that are available, 3) the problem of identifying mates exhibiting specific fitness-related cues, and 4) the problem of identifying (right) ways for appearance-enhancement.[1] I will briefly introduce these adaptive problems and identify the problem-specific inputs (e.g., incomplete visual cues and lumbar curvature angle) to study them. I will also present my own studies in which I tested the effects of these problem-specific inputs along with the other theoretically-anchored input(s) (i.e., sex and mating contexts) that were discussed in Chapter 1.

2.1 The problem of missing opportunities to interact with potentially suitable mates

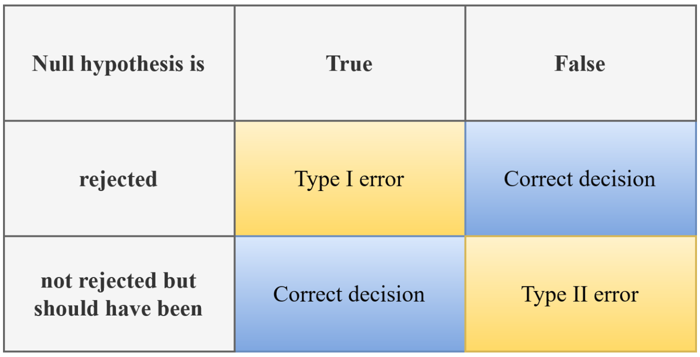
2.1.1 The initial person perception (outcome), biological sex (input), incomplete visual information (input)

Our ancestors might have experienced situations where it is difficult to judge the attractiveness of the potential mate, hence, faced the problem of missing opportunities to interact with a potentially suitable mate under uncertainty. To potentially exemplify such a situation, we can focus on the use of red ochre, a mineral with a staining red color. Red ochre has been used by neanderthals and humans for various purposes such as adornment, celebratory and medicinal pur-

---

[1] I am aware that there are other potential sub-problems of mate acquisition such as the problem of mate scarcity. However, given the time constraint of the doctoral studies, I had to limit my focus. I tried to investigate the problems that was not overstudied. However, for sure, if time allowed, I could have worked on more *not* oversaturated problem fields.

poses, and as a group identity (e.g., Roebroeks et al., 2012; Duarte, 2014; Rifkin, 2015; Huntley, 2021). The use of red ochre might have made it harder to judge a potential mate's attractiveness under the uncertainty created by body paints, particularly if one sees the other for the first time. Exogamic unions (i.e., finding a partner outside of the group), which are evidenced by genetic analysis, (Chapais, 2013; Knipper et al., 2017), would leave room for adaptations about initial person perception under uncertainty. In short, body paint use and exogamy together suggest that we might have had to judge attractiveness under uncertainty throughout our history and likely evolved cognitive adaptations accordingly. In other words, for the goal of being able to identify a fit partner when there is incomplete visual information available, our minds could have evolved certain algorithms depending on the differential cost-benefit analysis of the potential outcomes. Yet, there are only a few studies investigating such algorithms and their findings are sex-differentiated as they find that men showed a stronger positivity bias (i.e., overperception of the attractiveness of the uncertain opposite-sex images) when rating female images under uncertainty compared to women rating male images under uncertainty. I would like to note here that Yonemura et al. (2013)'s method of analysis may not be ideal. They used *on-average* attractiveness ratings as their dependent variable. In other words, instead of comparing each participant's ratings given to certain (i.e., front-view first) and uncertain condition (i.e., back-view first), they used an average score for each stimuli in each condition (i.e., certain and uncertain). As explained by Lewis et al. (2023), this method of analysis, to say the least, is questionable, because it is not ideal to compare one's rating of attractiveness with study sample's average rating as there can be variation between individuals. Concerning their results, they found that males rated female images as more attractive from the back-view than they did from the front view in each conditions. Females also showed a positivity bias (i.e., overperception of the uncertain images' attractiveness) but it was not as pronounced. Another study, conducted by Orghian & Hidalgo (2020) showed that when both men and women had an access to only partial physical information about the person in the image, they rated the incomplete information version as more attractive than the complete version. Much like Yonemura et al. (2013), they found that this effect is more evident in men than it is in women. Although their method for incomplete information was quite comprehensive (they used various methods such as small images, images where only one-third of the image was seen, and blurred images), their method of analysis was similarly questionable. They also used *on-average* ratings of attractiveness as the dependent variable in their analysis. In short, the positivity bias reported in the literature is at least partially in line with the following theoretical reasoning. If a man under uncertainty, identifies the woman as unattractive when in fact she was attractive (type II error, false negative, see Figure 2.1.1), the cost would be higher than identifying the woman as attractive when she was unattractive (type I error, false positive).



Null hypothesis is	**True**	**False**
rejected	Type I error	Correct decision
not rejected but should have been	Correct decision	Type II error

Figure 2.1.1: Error types in hypothesis testing. *(CC-By-Attribution 4.0 International)*

For women, however, the cost of committing type II error is lower compared to the cost of committing type I error due to the asymmetrical minimum parental obligations which was detailed in Chapter 1. Therefore, women would not be expected to show positivity bias. On the contrary, they may show negativity bias (i.e., underperceiving the attractiveness of uncertain opposite-sex images) under uncertainty as type I error is costlier for them. This expectation of a negative bias is the reason why I claimed that the findings discussed earlier are partially in line with the theoretical reasoning. According to the Error Management Theory (EMT), when type I error and type II error is asymmetrical in our evolutionary history, psychological adaptations such as biases could have evolved (Haselton & Buss, 2000). With that theory, Haselton & Buss (2000) accounted for the reason why men have overperception bias towards women's sexual intent and they accurately predicted women's underestimation of male commitment. Both findings may be accounted for by the asymmetrical minimum parental investment obligation. Because men invest less, it would be costlier for them to not identify sexually available women (type II error) than misidentifying unavailable women as available (type I error). For the latter prediction, it is costlier for a woman to misidentify a man who is not willing to commit (type I error) than to misidentify a man who is willing to commit (type II error). The EMT can be used to understand our evolved mating biases when there is an asymmetry between type I and type II error costs. However, as pointed out before, there are only a handful of studies conducted in this area. We, (Lewis et al., 2022) conducted a study where female and male facial images were blurred and their attractiveness was rated by the opposite-sex participants. With this study, we had a chance to investigate the evolutionary algorithms with the goal of identifying fit partners under uncertainty, and whether those algorithms are sensitive to the input of biological sex or not. For example, for men, the candidate algorithms can be: 1) When uncertain, always add x constant to guess potential mate's attractiveness or 2) When uncertain, always assume that the potential mate is attractive. In the first algorithm, male perception of female attractiveness under uncertainty would not change by female's true attractiveness as the constant X would be added. In the second algorithm, however, by assuming each women is attractive, we should observe an overperception effect varying by the true attractiveness of the woman (Lewis et al., 2022). Our results showed that men rated female images as more attractive in the blurred condition than in the clear condition, and women did the opposite. It is important to note that our dependent variable was not *on-average* attractiveness rating. In our model, we analysed the attractiveness rating difference for *each* participant. We also used target's revealed attractiveness calculated by averaging the attractiveness ratings of the clear images in the blurred-first condition for each target as an input in our analysis. We found that the effect of uncertainty (i.e., blurriness) had a significant interaction with the target's true attractiveness. Therefore, we conducted a follow-up analyses by categorizing target images' attractiveness into two, attractive and unattractive to better understand the algorithms. If the rating was above the midpoint of the scale, it was classified as attractive, and if below, then as unattractive. We showed that men rated female images as more attractive when those images were unattractive, but that bias did not exist for the attractive female images. Attractive women were still perceived as attractive. Women underestimated the attractiveness of attractive men but they did not perceive unattractive men as less attractive. In other words, our results indicated that the second algorithm explained above was valid for men and the same algorithm with opposite direction (i.e., When uncertain, always assume that the potential mate is *unattractive*) was valid for women. These findings are *similar* to the previous studies (Yonemura et al., 2013; Orghian & Hidalgo, 2020) as they also found that men overperceive female attractiveness under uncertainty. However, they did not find underperception bias among female raters for the male images. The reason why might be that they used on-average attractiveness ratings as the dependent variable.

2.1.2 An adaptation or a byproduct?

The sex-differentiated biases about the perception of attractiveness under uncertainty might be an adaptation to not miss the opportunity to interact with a potentially suitable partner. However, it might also be a byproduct of another adaptation about initial person perception. In other words, it is harder to judge other characteristics such as intelligence or kindness quickly compared to physical attractiveness from the initial perception. Our current findings might be reflecting the byproducts of adaptive biases to evaluate those characteristics (Lewis et al., 2022). Future studies are needed to investigate this further.

2.1.3 Lewis, Al-Shawaf, Semchenko, & Evans, 2022

The author created the study stimuli, prepared the survey, collected, processed, and analyzed all data.

Evolution and Human Behavior 43 (2022) 87–96

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.elsevier.com/locate/ens

Error Management Theory and biased first impressions: How do people perceive potential mates under conditions of uncertainty?

David M.G. Lewis [a,b,*], Laith Al-Shawaf [c], Ayten Yesim Semchenko [d], Kortnee C. Evans [a]

[a] *College of Science, Health, Engineering, and Education, Murdoch University, Australia*
[b] *Centre for Healthy Ageing, Health Futures Institute, Murdoch University, Australia*
[c] *Psychology Department, University of Colorado Colorado Springs, USA*
[d] *Faculty of Science, Charles University, Czech Republic*

ARTICLE INFO

Keywords:
Error Management Theory
Cognitive biases
Human mating
Person perception
Algorithm
Levels of analysis

ABSTRACT

People must make inferences about a potential mate's desirability based on incomplete information. Under such uncertainty, there are two possible errors: people could overperceive a mate's desirability, which might lead to regrettable mating behavior, or they could underperceive the mate's desirability, which might lead to missing a valuable opportunity. How do people balance the risks of these errors, and do men and women respond differently? Based on an analysis of the relative costs of these two types of error, we generated two new hypotheses about biases in initial person perception: the Male Overperception of Attractiveness Bias (MOAB) and the Female Underperception of Attractive Bias (FUAB). Participants ($N = 398$), who were recruited via social media, an email distribution list, and snowball sampling, rated the attractiveness of unfamiliar opposite-sex targets twice: once from a blurred image, and once from a clear image. By randomizing order of presentation (blurred first vs. clear first), we isolated the unique effects of *uncertainty*—which was only present when the participant saw the blurred image first. As predicted, men *over*perceived women's attractiveness, on average. By contrast, as predicted, women *under*perceived men's attractiveness, on average. Because multiple possible decision rules could produce these effects, the effects do not reveal the algorithm responsible for them. We explicitly addressed this level of analysis by identifying multiple candidate algorithms and testing the divergent predictions they yield. This suggested the existence of more nuanced biases: men overperceived the attractiveness of unattractive (but not attractive) women, whereas women underperceived the attractiveness of attractive (but not unattractive) men. These findings highlight the importance of incorporating algorithm in analyses of cognitive biases.

Imagine you're with your friends in a dimly illuminated bar, and you catch only a brief glimpse of someone as they walk past you. Was that person as attractive as they seemed to be? It's now later in the evening, and your friends want to leave. Do you leave with your friends without giving that person another thought? Or do you feel like you need to approach that person? Can you anticipate the pangs of regret if you don't?

Because people have only incomplete information about potential mates, they must make inferences about potential mates' desirability under conditions of uncertainty. Under these conditions of uncertainty, there are two possible inferential errors. One could infer that the potential mate is more desirable than they actually are, which may lead to a regrettable mating decision. Alternatively, one could underperceive the potential mate's desirability, which could lead to missing out on a valuable opportunity. How do people balance these risks? And do men and women respond differently to this uncertainty?

1. Signal Detection Theory and Error Management Theory

Signal Detection Theory (Green & Swets, 1966) articulates that, when making decisions under uncertainty, two general types of error can occur – false positives and false negatives (Type I and Type II errors, respectively). It is impossible for a decision-making system to concurrently reduce both errors, as decreasing the likelihood of one directly results in an increase in the likelihood of the other (Green & Swets, 1966). When the costs of the two error types within a decision are

---

* Corresponding author at: Psychology, Murdoch University, 90 South Street, Murdoch, WA 6150, Australia.
E-mail address: davidlewis@utexas.edu (D.M.G. Lewis).

https://doi.org/10.1016/j.evolhumbehav.2021.10.001
Received 24 August 2020; Received in revised form 13 July 2021; Accepted 15 October 2021

asymmetrical, an engineered system should be designed in such a way that it minimizes the net costs of the errors over the sample space of instances, even if this does not minimize the system's error rate (Green & Swets, 1966). For example, it is costlier for a smoke alarm to fail to detect an actual fire (a "miss", also known as a false negative or Type II error) than it is for a smoke alarm to go off when there is no real fire present (a "false alarm", also known as a false positive or Type I error). For this reason, smoke alarm systems are *designed to be biased* toward false positive errors (Schifiliti & Pucci, 1996). Despite this often leading to us regretting burnt toast, we readily accept this outcome because a false positive is much less costly than a false negative. This design increases error *rates,* but it is superior in terms of the net *costs* incurred over the sample space of instances (Green & Swets, 1966).

Error Management Theory (EMT; Haselton & Buss, 2000) extends this logic from human-engineered information-processing systems to evolved information-processing systems: the psychological mechanisms of the human mind. EMT proposes that, because the outcomes relevant to selection are fitness costs – not error rates – selection should have shaped information-processing adaptations to minimize the net costs of inferential errors, even if this resulted in systems that commit a greater number of errors. This suggests that, when there was a recurrent asymmetry in the fitness costs of the two types of inferential error, selection should have shaped psychological mechanisms that are biased toward committing the less costly error.

2. EMT and evolved biases in person perception

EMT is a "middle-level" evolutionary theory (Buss, 1995) that both (1) can account for known, but previously unexplained, phenomena and (2) has led to the discovery of previously unknown inferential biases. For example, sex differences in perceptions of sexual intent, wherein men perceive greater sexual intent in women than women do in men, were documented at least as early as 1982 (Abbey, 1982). At the time, the causal origins of this phenomenon were not well understood, and attributed variously to proximate explanations such as a general oversexualization of the world by men, media exposure of women acting shy despite sexual interest, and men projecting their own levels of sexual interest onto women (see Haselton & Buss, 2000).

However, the phenomenon was neatly explained by the EMT framework advanced by Haselton and Buss (2000). Ancestrally, a key limiting factor on men's reproductive success was their access to fertile mates (Symons, 1979). Because of this, missed sexual opportunities were highly costly for men. In estimating women's sexual intent, a false negative – inferring that a woman was uninterested when she actually was interested – could have resulted in the substantial fitness costs of a lost sexual opportunity and decreased reproductive success. By contrast, a false positive – inferring that a woman was sexually interested when she was not – could have included the social embarrassment of rejection and wasted courtship effort, but these have comparatively minor effects on men's fitness (see Abbey, 1987; Perilloux, Easton, & Buss, 2012).

Based on this asymmetry in the two possible inferential errors, Haselton and Buss (2000) hypothesized that men possess intention-reading adaptations that are designed to make the less costly error – to over-infer women's sexual intent – in order to minimize the frequency of missed sexual opportunities. In support of this hypothesis, numerous studies have demonstrated that men overestimate women's sexual intent, a phenomenon now known as the 'sexual overperception bias' (e.g., Haselton & Buss, 2000; Haselton, 2003; Henningsen, 2004; Mongeau & Johnson, 1995; for nuanced analyses and discussion, see Henningsen & Henningsen, 2010; Henningsen, Henningsen, McWorthy, McWorthy, & McWorthy, 2011; Koenig, Kirkpatrick, & Ketelaar, 2007).

EMT has also been used to predict *previously unknown inferential biases*, such as women's systematic tendency to underperceive men's commitment intent: the commitment-skepticism bias (Haselton & Buss, 2000). Due to internal gestation, women's minimum obligatory parental investment is massive: nine months of pregnancy, which is frequently accompanied by multiple years of lactation, breastfeeding, and child-rearing. This results in an unwanted pregnancy being a particularly pronounced problem for women (Goetz & Shackelford, 2009). Although underestimating a man's commitment intent would have carried costs, these would have been dramatically outweighed by the costs of *over*-estimating a man's intention to commit. Being abandoned by a man following sexual relations could have resulted in the woman incurring the costs of an unwanted pregnancy and raising a child without an investing mate (Buss, 1994), which is associated with decreased offspring survival (Hurtado & Hill, 1992). The woman also could have suffered reputational damage (Buss, 1994) and, crucially, reductions in her mate value (Buss, 1994) and future reproductive potential (Hurtado & Hill, 1992). Based on this, Haselton and Buss (2000) hypothesized that that women possess intention-reading adaptations designed to make the less costly error: underestimating men's commitment intent. This hypothesis has received empirical support in several studies (e.g., Cyrus, Schwarz, & Hassebrauck, 2011; Haselton & Buss, 2000).

3. Error Management Theory: prospects and limitations

This previous literature has articulated the logic of EMT and demonstrated the theory's empirical merit. However, as a middle-level theory based on first principles, EMT has tremendous predictive power and broad scope. Some of its strengths remain largely untapped.

First, EMT is a rich fount of a priori hypotheses. Yet, the EMT work that is perhaps best known – Haselton and Buss's (2000) account of men's overperception of women's sexual interest – was (openly) designed to explain known findings rather than predict new ones. Although observation-driven research is a fundamental component of science, the fact that the seminal EMT research was observation-driven may be unfortunate, because evolutionary approaches to psychology have long been subjected to unwarranted accusations of 'just-so' storytelling (e.g., Gould, 1978). This allegation, which reflects a fundamental misunderstanding of the enterprise of evolutionary psychology, has been headed off multiple times in the scholarly literature (see Confer et al., 2010; Lewis, Al-Shawaf, Conroy-Beam, Asao, & Buss, 2017 for recent discussions; see also Al-Shawaf, 2020 for an essay devoted to this issue). Nonetheless, this allegation can be most easily avoided when the phenomenon of interest is discovered after a priori theorizing about its existence, as in the case of the commitment-skepticism bias (see Haselton & Buss, 2000). When such discoveries are made on the basis of a priori hypotheses, it becomes abundantly clear that the just-so charge falls flat. In the current study, we used EMT to generate several novel hypotheses, thereby demonstrating the theory's a priori predictive power.

Second, EMT's principles apply to all domains of inferential procedures, granting it incredibly broad scope (Al-Shawaf, Lewis, & Evans, 2021). EMT can be used to generate hypotheses across diverse domains, from auditory perception (e.g., Neuhoff, 2001) to visual perception (e.g., Jackson & Cormack, 2007) to mating cognition (Haselton & Buss, 2000). Moreover, because there are many inferential procedures *within* each of these domains, EMT may be used to generate numerous hypotheses within each domain. This is certainly true of mating cognition.

In human mating, inferences can occur at numerous stages, from initial person perception through relationship maintenance to breakups and attributions about their causes. Yet, to date, EMT-inspired research on human mating has focused heavily on inferences made post-interaction—thereby neglecting an important component of human mating psychology: the inferences that occur *before* potential mates interact. These pre-interaction inferences are critical; by motivating individuals to engage in approach or avoidance behavior, they may influence the likelihood of interactions occurring at all (Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008). Because inferential errors can be made in these crucial pre-interaction phases, we might expect selection to have favored psychological mechanisms that are biased toward producing the less costly error in these initial information-processing stages. To our knowledge, this aspect of human mating – inferential errors in pre-interaction decision-making – has never been explored. Here, we advance the overarching hypothesis that selection should have favored inferential biases in initial perceptions of potential mates' desirability, and that these biases should be sex-differentiated.

4. Error Management Theory and sex differences in perceiving attractiveness

Perceptions of attractiveness are powerful determinants of approach and avoidance behavior (Hatfield, Roberts, & Schmidt, 1980). This has implications for the inferential procedures that the mind uses when information about a potential mate is limited, unavailable, or otherwise uncertain. Because perceiving a target as unattractive motivates avoidance behavior, mistakenly inferring that a potential mate is unattractive carries the cost of missing a potentially valuable opportunity. Conversely, erroneously inferring that a target is a desirable mate when they are *not* could lead to negative consequences as well, including (for example) injudicious sexual relations.

To generate predictions about whether humans' psychological mechanisms will be systematically biased toward one of these errors, we must consider the cost asymmetry between the two errors. Moreover, because the costs of these errors may differ for men and women, these cost asymmetries – and the resulting inferential biases – may be sex-differentiated. For example, in the commitment-skepticism bias, the costly investment of pregnancy is not endured by men. This renders overestimation of commitment intent much costlier for women than for men. Consequently, women exhibit the commitment-skepticism bias, but men do not (Haselton & Buss, 2000; Henningsen & Henningsen, 2010).

4.1. Male (over)perceptions of female attractiveness

Because a key limiting factor on ancestral men's reproductive success was their ability to have sexual intercourse with fertile women (Symons, 1979), forgoing potentially valuable mating opportunities would have carried substantial fitness costs for men. Errors of commission also would have carried costs, but these likely would have been comparatively smaller. The exact costs of injudicious mating behavior cannot be known, but they would have been mitigated by the fact that men's minimum obligatory parental investment is substantially lower than women's. Injudicious mating might have resulted in a man producing offspring with a woman that he did not want to commit to or invest in, but this would not necessarily have prevented him from engaging in other mating effort, including mating with and producing offspring with other women. On balance and on average, for men, a missed sexual opportunity likely was costlier than injudicious sexual behavior (Fig. 1, top panel) (Haselton & Buss, 2000; Haselton & Nettle, 2006; Symons, 1979). Consequently, we should expect men's minds to minimize inferential errors that result in forgoing valuable mating opportunities (see Haselton & Buss, 2000). In the current context, if the downstream costs of mistakenly inferring that a woman was *unattractive* were greater than the costs of wrongly inferring that a woman was *attractive*, selection should have favored inferential procedures in the male mind biased toward overperceiving women's attractiveness under conditions of uncertainty.

Hypothesis 1. The Male Overperception of Attractiveness Bias (MOAB): Under conditions of uncertainty, men will overestimate women's attractiveness, on average.

4.2. Female (under)perceptions of male attractiveness

For women, on the other hand, the asymmetry in the cost matrix is different, and may even be reversed. The large metabolic and time investment required from women for successful reproduction (Goetz & Shackelford, 2009) means that engaging in injudicious mating behavior would have been substantially costlier, on average, for women than for men. Additionally, the ability to have intercourse with members of the opposite sex would not have been a limiting factor on women's reproductive success to the same extent that it constrained men's reproductive success (Symons, 1979). The cost matrix is therefore different: forgoing a mating opportunity would have carried greater costs for men than for women, whereas errors of commission would have carried higher costs for women than for men. Although the exact costs of forgoing a mating opportunity and of engaging in injudicious mating behavior cannot be known, this a priori analysis suggests that, for ancestral women, the costs of commission exceeded the costs of omission (Fig. 1, bottom panel) (Haselton & Buss, 2000). If this is true, then we should expect women's minds to have evolved to be biased toward inferential errors that result in forgone mating opportunities rather than errors of commission. In the current context, if the downstream costs of mistakenly inferring that a man was *attractive* were greater than the costs of wrongly inferring that a man was *unattractive*, selection should have favored inferential procedures in the female mind biased toward *under*perceiving men's attractiveness under conditions of uncertainty.

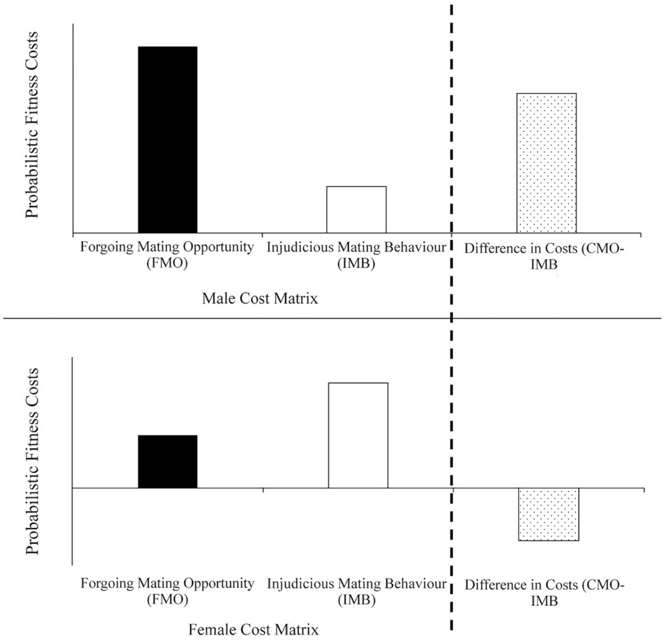


Fig. 1. A conceptual illustration of the relative costs of forgoing a mating opportunity and engaging in injudicious mating behavior among men (top), among women (bottom), and between men and women (top right vs. bottom right).

Hypothesis 2. The Female Underperception of Attractiveness Bias (FUAB): Under conditions of uncertainty, women will underestimate men's attractiveness, on average.

5. EMT and decision rules: the integration of heuristics and evolved biases

EMT is a powerful framework for generating a priori hypotheses across diverse domains, but the research it inspires needs further refining (see McKay & Efferson, 2010; see also Al-Shawaf, 2016). Certain content in the seminal work introducing EMT – "Errors may be evidence of evolved adaptive biases, not simplifying heuristics" (Haselton & Buss, 2000, p. 90) – could be construed to mean that evolved biases and heuristics are competing explanations. They are not, and this was not the emphasis of statements such as these. Rather, the focus of these statements was to contrast (1) the EMT view that the biases reflected evolved, adaptive design with (2) the prevalent view that dismissed such biases as “illusions” (Piatelli-Palmarini, 1994) or “fallacies” (Tversky & Kahneman, 1974). As a theory about cognition and information processing, heuristics are integral to EMT.

One of the foundations of cognitive science is that a complete analysis of an information-processing system includes the specification of its (1) *function*, as well as the (2) *algorithm* and (3) *implementation* by which it achieves that function (McClamrock, 1991; see also Marr, 1982). By articulating why selection should have favored inferential systems that lead men, on average, to overestimate women’s sexual intent, and women, on average, to underestimate men’s commitment intent, the seminal EMT work thoroughly addressed *function* – “What is the goal […], why is it appropriate, and what is the logic of the strategy […]?” (Marr, 1982, p. 25). However, this and subsequent excellent theoretical work on EMT (e.g., Haselton & Nettle, 2006) has tended not to emphasize these distinct levels of analysis of an information-processing system. Consequently, it has either explicitly conflated these levels of analysis (see McKay & Efferson, 2010 for discussion) or simply neglected one or multiple of them. Here, we focus on the *algorithmic* level (Marr, 1982)—the information-processing decision rules by which the mind may systematically produce biased inferences.

This is a crucial level of analysis for EMT. Because there are multiple possible decision rules that could produce a given bias, we cannot claim to know how “decisions are actually made” (Shafir & Tversky, 1995, p. 77) without knowledge of the specific rule used. The sexual overperception bias illustrates this well. For example, the heuristic of “estimate a woman’s sexual intent based on cues detected, and add constant X to that estimate in case cues of interest were missed” would yield an on-average overperception of women’s sexual intent. But so too would a very different heuristic: “when uncertain about a woman’s sexual intent, assume she is sexually interested.” That the same effect can be produced by two different algorithms tells us that we cannot resolve the cognitive architecture of the human mind from the effect itself. As McKay and Efferson write, inferences about cognitive architecture based on such effects can be “radically underdetermined” (McKay & Efferson, 2010, p. 313). Ultimately, the issue is that articulating the hypothesized *function* of an information-processing system does not answer questions about *algorithm*. These distinct levels of analysis, and the need to address both as part of a comprehensive analysis of an information-processing system, are foundational concepts in cognitive science (Marr, 1982).

The algorithm level of analysis can be seamlessly integrated into EMT work. First, researchers can identify *candidate algorithms* that could plausibly achieve the proposed *function* of the information-processing system. Second, researchers can specify the quantitative effects predicted by each of these decision rules, with an emphasis on identifying *divergent* predictions generated based on the different candidate algorithms (see Lewis et al., 2017). Third, researchers can then design studies capable of testing for these predicted effects to discriminate between alternative candidate algorithms. We illustrate this approach by applying it to the MOAB hypothesis: the novel hypothesis advanced here that selection favored inferential procedures in the male mind biased toward perceiving women as attractive under conditions of uncertainty.

6. One function, multiple possible algorithms

There are multiple possible algorithms that could serve the same function of preventing men from missing potentially valuable mating opportunities, and which would generate an on-average overperception of women’s attractiveness. One possible heuristic would be: “estimate a woman’s attractiveness based on available information, but, if available information is limited or other otherwise uncertain, add constant X to that estimate” (Algorithm A). Another candidate decision rule would be: “when uncertain whether a woman is attractive, assume that she is attractive” (Algorithm B). We could elaborate many more candidate heuristics, but the point is this: multiple different algorithms could serve the same relevant function. All would produce an on-average overperception of women’s attractiveness.

The fact that multiple algorithms would generate an on-average overperception of women’s attractiveness tells us that this overall quantitative effect leaves inferences about algorithm underdetermined. To adjudicate between different candidate algorithms, we must specify the unique quantitative effects predicted by each. Algorithm A entails adding a fixed value to the estimate for all women. The quantitative effects of this algorithm do not vary as a function of the women’s actual attractiveness (Fig. 2, left panel). By contrast, Algorithm B – “when uncertain whether a woman is attractive, assume that she is attractive” – will produce quantitative effects that vary as a function of the woman’s actual attractiveness. This algorithm will generate overestimates of the attractiveness of unattractive women, but (roughly) accurate estimates of the attractiveness of attractive women (Fig. 2, right panel).

To our knowledge, no EMT research to date has sought to identify the actual algorithms underlying the biases. The second goal of our study was therefore to test the distinct effects predicted by different candidate algorithms, alongside the primary goal of testing for previously undiscovered, sex-differentiated biases in the perception of attractiveness.

7. The current study

We tested for these proposed inferential biases in response to uncertainty using a within-subjects, within-target design. We had male and female participants view and rate the attractiveness of unfamiliar opposite-sex targets twice: once from a blurred image, and once from a clear image. By randomizing order of presentation (blurred first vs. clear first), we isolated the unique effects of *uncertainty*—which was only present when the participant saw the blurred image first. That is, when a participant viewed a target’s clear image before the target’s blurred image, the blurred image did not reflect uncertainty, but *when the participant viewed the blurred image before seeing the clear image*, the participant had to make assessments of the target’s attractiveness under uncertainty. If *uncertainty* is the key variable (not merely blurring or order alone), then the effect of blurring should be moderated by order of presentation: if *uncertainty* is the key variable, then blurring should interact with order. Our study design enabled us to test this key idea.

The recording of the participants’ ratings of the targets’ clear images also enabled us to test the algorithmic structure of the potential bias. If the underlying algorithm uniformly underestimates or overestimates targets’ attractiveness under conditions of uncertainty (as in the case of Algorithm A above), then the magnitude of the bias should *not* vary as a function of the targets’ “true” attractiveness (i.e., their revealed attractiveness, as indexed by participants’ ratings of their clear images). Alternatively, if the decision rule is simply to assume that a target is unattractive or attractive under conditions of uncertainty (as in the case of Algorithm B above), then the magnitude of the bias should vary as a function of the targets’ attractiveness. Our design enabled us to test for these different quantitative effects predicted by distinct algorithms, and thereby begin to map the information-processing architecture underlying these hypothesized biases.

8. Method

8.1. Ethics statement

This study was approved by the [REDACTED FOR PEER REVIEW] institutional review board (Approval number: 2018/02).

8.2. Participants

Three hundred and ninety-eight subjects (211 heterosexual women: $M_{age} = 26.1$, $SD_{age} = 4.34$; 187 heterosexual men: $M_{age} = 26.5$, $SD_{age} = 4.77$) participated in the current study between May and November 2018. Participants were recruited by advertising the study to

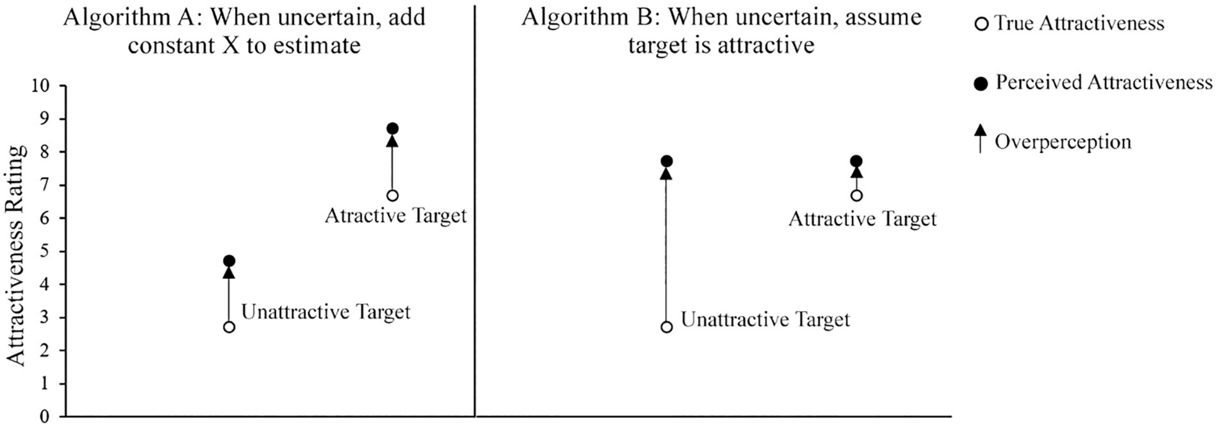


Fig. 2. Different candidate algorithms. The left panel (Algorithm A) depicts a decision rule in which the mind responds to uncertainty by adding a constant value X to its uncertain estimate; this generates an overperception of target attractiveness that does not vary with the target's true attractiveness. The right panel (Algorithm B) depicts a decision rule in which the mind responds to uncertainty by inferring that the target is attractive; this results in the magnitude of the overperception effect varying as a function of the target's true attractiveness.

a distribution list of individuals interested in participating in research. Participants completed the measures described below as part of a longer survey, which was shared via email and completed remotely online via the Qualtrics survey software platform. The sample came from the Czech Republic (86%), Slovakia (10%), Turkey (2%), Russia (1%), and other countries (1%).

8.3. Materials

Forty-eight target images (24 female, 24 male) were drawn from the Chicago Face Database (CFD; Ma, Correll, & Wittenbrink, 2015), a resource developed for scientific research that provides standardized, high-resolution images of both male and female faces. Access to the database along with the references to the faces used can be found at https://osf.io/qw57v/.

To operationalize the construct of uncertainty about a person's physical appearance, we created a second version of each target image by using the Gaussian Blur function in Gimp (open-source raster graphic editor; settings: X = 18, Y = 18; see Fig. 3). This yielded 96 total images: a "clear" image and a "blurred" image of each of the 48 targets.

8.4. Procedure

We employed a within-subjects, within-target design in which participants rated the attractiveness of each opposite-sex target two times. Each participant rated the original, unmodified ("clear") image of the target as well as the Gaussian-blurred version of the target's image.

Participants were presented with one image at a time, and asked to rate the attractiveness of the individual shown on an 11-point scale (0 = Very unattractive, 10 = Very attractive). Each target was presented in a single block (i.e., the target's clear and blurred image appeared on consecutive pages). The order of presentation (clear image first vs. blurred image first) was randomized for each target for each participant.

This design isolated the effect of *uncertainty* from any effects of blurring or order alone. When a participant viewed a target's clear image before the target's blurred image, the blurred image did not reflect uncertainty. However, when the participant viewed the target's blurred image *before* seeing the target's clear image, the participant had to assess the target's attractiveness under conditions of uncertainty.

Order of presentation of targets was randomized across participants.

9. Results

The aim of the current study was to test for inferential biases in the perception of potential mates' attractiveness under conditions of uncertainty. The specific study data capable of testing for these biases were those in which the participant first saw the blurred image of a target (uncertain condition) and then saw the clear image of that target (certain condition). For those data in which the order of presentation was reversed – when the participant viewed the target's blurred image after the clear image – the blurred image no longer reflected uncertainty, as the participant already had clear information about the target (i.e., had already seen the clear image of the target).

For this reason, the specific study data appropriate for testing hypotheses about inferential biases under uncertainty were the "blurred-first" data—those data corresponding to when the participant saw the blurred image of a target before the clear image. The clear-first data were nonetheless a key part of study design because they enabled us to test whether the effects of blur depended on order. If *uncertainty* is the key variable – not order or blurriness per se – then we should expect the effect of blur to be moderated by order: when seen first, the blurred images reflect uncertainty, whereas, when seen second, they do not. This is the core logic of our study design. Our first analyses tested these ideas by assessing (1) whether there was a simple effect of order, (2) whether blurriness influenced perceptions of attractiveness independent of any effect of order and, crucially, (3) whether any effect of blurriness was moderated by order.

Fig. 3. Example study stimuli.

For all analyses, we fit study data (available, along with code, at https://osf.io/qw57v/) to linear mixed-effect models using the *lmerTest* (Version 3.1–2; Kuznetsova, Brockhoff, & Christensen, 2017) package in *R* (R Core Team, 2020). These models enabled us to nest the attractiveness ratings within participants and targets to account for the within-subject, within-target design. Random intercepts for participants were entered to control for differences between participants in their baseline perceptions of attractiveness, and random intercepts were entered for targets to control for baseline differences in attractiveness between targets. This enabled us to better isolate the effects of order, blur, and *uncertainty* (i.e., the unique effect when the blurred image appeared first, captured by the order × blur interaction).

9.1. *The effect of uncertainty*

To conduct the key test of whether any effect of blurriness was moderated by order – which it should be if *uncertainty* has unique effects – we fit all study data to a linear mixed model in which attractiveness ratings were predicted from the fixed effects of order, blurriness, and, crucially, the interaction between these effects. Precisely as expected if *uncertainty* is the key variable – not order or blurriness alone – the interaction between blurriness and order was significant, $b = -0.16$, $SE = 0.04$, $p < .001$. This indicated that the effect of blurriness on participants' perceptions of targets' attractiveness depended on whether the participant saw the blurred image of the target first – the *uncertainty* condition – or second, after seeing the clear image of the target. This is consistent with the hypothesis that uncertainty exerted unique effects on participants' perceptions. To directly probe these effects, we focused subsequent analyses on the specific subset of study data in which participants made assessments of the targets' attractiveness under uncertainty: when they saw the blurred image of the target first.

9.2. *Biases under uncertainty: sex differences*

Our next analyses tested for (1) biases under uncertainty and (2) sex differences in any such biases by testing the effects of uncertainty, participant sex, and the interaction between uncertainty and participant sex. If neither men nor women exhibit any inferential bias under uncertainty, then this test should yield no effect of uncertainty *and* no interaction between uncertainty and participant sex. If both sexes possess the same bias, then we should expect to observe an effect of uncertainty, but no interaction between uncertainty and participant sex. However, if at least one sex possesses a bias and the other sex possesses a different bias (or does not possess a bias at all), then we should expect to observe an interaction between uncertainty and participant sex in predicting perceptions of attractiveness. This is precisely what we observed: participant sex interacted with uncertainty to predict perceptions of attractiveness, $b = 0.27$, $SE = 0.06$, $p < .001$. This demonstrated that men and women responded differently to uncertainty.

We therefore conducted separate analyses on the effect of uncertainty among male and female participants. These analyses would tell us whether (1) both sexes had a bias in the same direction, but one sex had a stronger bias, (2) one sex had a bias and the other did not, or (3) both sexes exhibited a bias, but in opposite directions. The study hypotheses predicted that these biases would be in opposite directions: Hypothesis 1 – the male overperception of attractiveness bias (MOAB) – predicted that men would *over*perceive women's attractiveness under uncertainty, and Hypothesis 2 – the female underperception of attractiveness bias (FUAB) – predicted that women would *under*perceive men's attractiveness under uncertainty.

9.2.1. *Men's attractiveness overperception bias*

In line with the MOAB hypothesis, an analysis of the effect of uncertainty on men's perceptions of the female targets revealed a male tendency to overperceive women's attractiveness under conditions of uncertainty, $b = 0.13$, $SE = 0.04$, $p = .001$ (Fig. 4).

9.2.2. *Women's attractiveness underperception bias*

In line with the FUAB hypothesis, an analysis of the effect of uncertainty on women's perceptions of the male targets revealed a female tendency to *under*perceive men's attractiveness under conditions of uncertainty, $b = -0.14$, $SE = 0.04$, $p < .001$ (Fig. 4).

9.3. *The information-processing architecture of the bias: the algorithm*

These findings suggest male and female tendencies to over- and underperceive, respectively, the attractiveness of opposite-sex individuals under conditions of uncertainty. However, these on-average effects leave ambiguity about the structure of the heuristics responsible for these biases. Several different possible decision rules could produce these on-average effects, so further analyses are needed to adjudicate between different algorithms. For example, for men, the algorithm could be: "if uncertain, increase the estimate of the target's attractiveness by constant *X*" (Algorithm A). Alternatively, it could be: "if uncertain, assume the target is attractive" (Algorithm B). Both possibilities would yield the observed average effect of men overperceiving women's attractiveness. However, they lead to different predictions when taking into account variation in the actual attractiveness of the targets. The first algorithm would produce a uniform bias whose magnitude does not vary of a function of the target's actual attractiveness (Fig. 2, left panel). The second algorithm, by contrast, would produce a bias whose magnitude was inversely related to the target's actual attractiveness (Fig. 2, right panel).

If the observed biases are underlain by an information-processing structure like Algorithm A, then the effect of uncertainty should *not* be moderated by the targets' attractiveness. On the other hand, if the information-processing architecture underlying the bias is better described by Algorithm B, then target attractiveness should moderate the effect of uncertainty.

We therefore conducted additional analyses that incorporated the targets' attractiveness in the model. This enabled us to test for different quantitative effects of uncertainty at different levels of target attractiveness, and thereby gain a clearer picture of the information-processing structure of the algorithm responsible for producing the on-average bias. For these analyses, we operationalized each target's attractiveness as their "revealed" attractiveness: the average attractiveness rating given to the target when their clear image was revealed to participants (i.e., after the participants had seen the target's blurred image).

9.3.1. *Systematic variation in men's overperception bias*

These analyses indicated that the effect of uncertainty on men's perceptions of female targets depended on the targets' attractiveness: uncertainty × target attractiveness interaction $b = -0.12$, $SE = 0.02$, $p < .001$. This meant that the effect of uncertainty on men's perceptions of women's attractiveness varied as a function of the women's actual attractiveness. We therefore conducted follow-up analyses to probe this systematic variation as a function of target attractiveness. For the purpose of these analyses, we categorized female targets as being attractive ($M_{\text{attractiveness}} = 6.12$, $SD_{\text{attractiveness}} = 0.67$) or unattractive ($M_{\text{attractiveness}} = 2.69$, $SD_{\text{attractiveness}} = 1.63$) based on whether the average rating given to the target's clear image by all opposite-sex participants was above or below the midpoint of the response scale for the study (i.e., 5; 0 = Very unattractive, 10 = Very attractive).

Uncertainty had no effect on men's perceptions of attractive women, $b = -0.11$, $SE = 0.07$, *ns.*[1] This indicated that men perceived attractive

---

[1] Because random intercepts for targets had been included to control for between-target differences in attractiveness, but this analysis pertained to only attractive targets, we removed the random intercept term for targets. We did this for all analyses pertaining to only attractive targets or only unattractive targets.

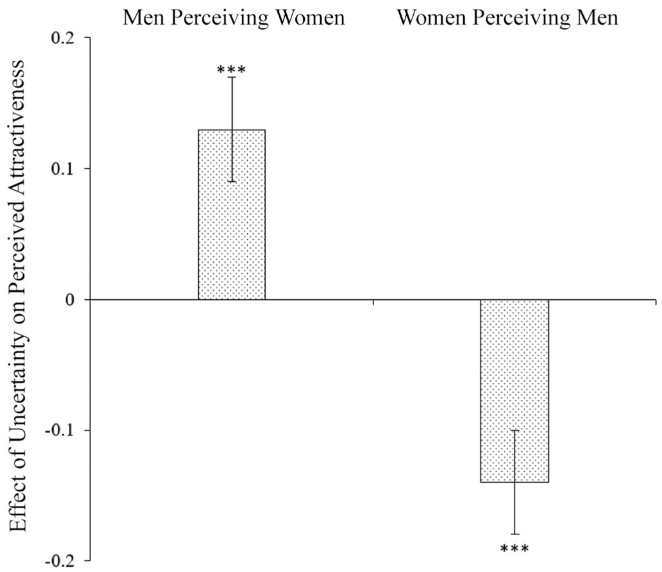


Fig. 4. Sex differences in response to uncertainty. Bars display the mean difference between participants' perceptions of targets' attractiveness under uncertainty versus certainty. Positive values indicate a bias to *over*perceive attractiveness under uncertainty, whereas negative values indicate a bias to *under*estimate attractiveness under uncertainty. Men (left) exhibited a bias to *over*perceive women's attractiveness under uncertainty, whereas women (right) did the opposite: women responded to uncertain information by *under*estimating men's attractiveness. *Note.* Error bars = ±1*SE*. *** $p < .001$.

women to be attractive, even if they had only incomplete, uncertain information about the women (Fig. 5). Conversely, uncertainty was associated with a positive bias in men's perceptions of unattractive women, $b = 0.33$, $SE = 0.08$, $p < .001$. This indicated that, when men viewed unattractive women but were uncertain about their physical appearance, they exhibited a bias to overperceive their attractiveness (Fig. 5). This finding – that the magnitude of the bias varied as a function of the targets' attractiveness – is less consistent with Algorithm A ("if uncertain, increase the estimate of the target's attractiveness by constant *X*") and more consistent with Algorithm B ("if uncertain, assume the target is attractive"), but future research is needed to tease apart and test the different predictions generated by these and additional candidate algorithms.

9.3.2. Systematic variation in women's underperception bias

We conducted parallel analyses on the data from female participants. For women, the algorithm underlying the on-average effect of *under*perceiving men's attractiveness could be: "if uncertain, decrease the estimate of the target's attractiveness by a constant *X*" (Algorithm C). Alternatively, it could be: "if uncertain, assume the target is unattractive" (Algorithm D). As with men, both heuristics would yield the observed main effect, but they lead to divergent predictions with respect to variation in the attractiveness of the targets. The first algorithm would decrease the attractiveness of *all* targets. The second algorithm, on the other hand, would produce a bias whose magnitude varied with the targets' actual attractiveness. If the observed biases are underlain by an information-processing structure like Algorithm C, then the effect of uncertainty should *not* be moderated by the targets' attractiveness. On the other hand, if Algorithm D better characterizes the relevant information-processing architecture, then target attractiveness should moderate the effect of uncertainty.

These analyses again revealed a significant interaction between the effects of uncertainty and target attractiveness – but in the *opposite* direction to that observed among men: $b = -0.17$, $SE = 0.03$, $p < .001$. This indicated that the effect of uncertainty on women's perceptions of men's attractiveness varied as a function of whether the men were attractive or unattractive. We therefore conducted a subsequent set of analyses in which we tested the effect of uncertainty on women's perceptions of attractive and unattractive men separately. As with the categorization of female targets, we categorized male targets as being attractive ($M_{\text{attractiveness}} = 6.11$, $SD_{\text{attractiveness}} = 0.48$) or unattractive ($M_{\text{attractiveness}} = 2.96$, $SD_{\text{attractiveness}} = 1.04$) based on whether the average rating given to the target's clear image by all opposite-sex participants was above or below the midpoint of the response scale for the study (i.e., 5; 0 = Very unattractive, 10 = Very attractive).

Whereas uncertainty had no effect on men's perceptions of attractive women, uncertainty was associated with a negative bias in women's perceptions of attractive men, $b = -0.67$, $SE = 0.09$, $p < .001$. This indicates that women responded to uncertain information about attractive men by exhibiting a bias to perceive them as less attractive (Fig. 5). On the other hand, uncertainty had no effect on women's perceptions of unattractive men, $b = -0.03$, $SE = 0.05$, $p = .52$. This indicates that

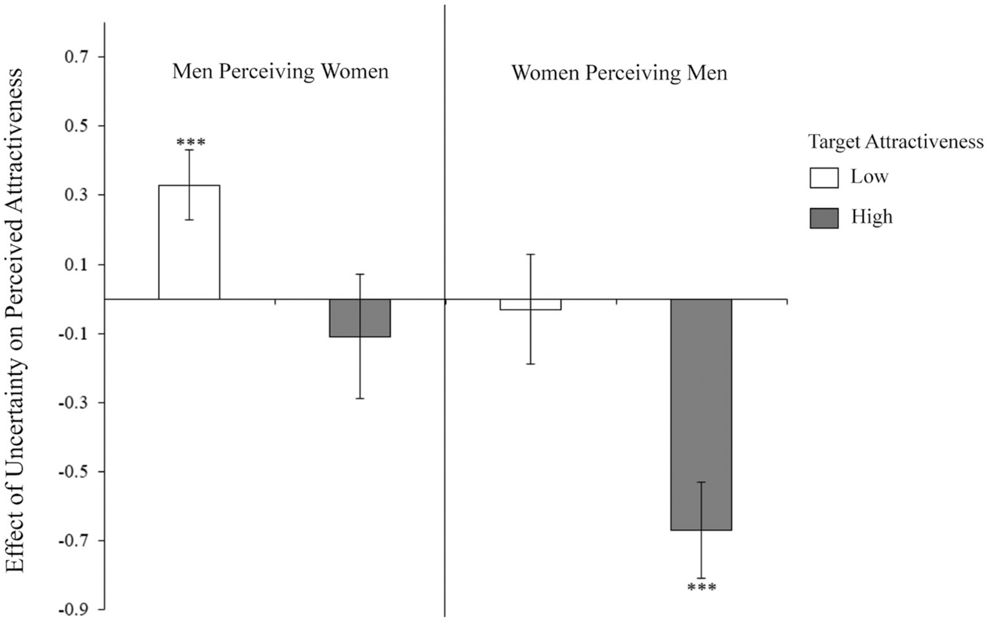


Fig. 5. Investigating the heuristic structure of the inferential biases. Bars display the mean difference between participants' perceptions of targets' attractiveness under uncertainty versus certainty. Positive values indicate a bias to *over*perceive attractiveness under uncertainty, whereas negative values indicate a bias to *under*estimate attractiveness under uncertainty. Men responded to uncertain information about *unattractive* women (left side of left panel) by exhibiting a bias to *over*perceive their attractiveness, whereas there was no effect of uncertainty on men's perceptions of *attractive* women (right side of left panel): men perceived attractive women to be attractive under both certain and uncertain conditions. There was no effect of uncertainty on women's perceptions of *unattractive* men (left side of right panel) – women perceived unattractive men to be unattractive under both certain and uncertain conditions – but women responded to uncertain information about *attractive* men by exhibiting a bias to perceive them as *less* attractive (right side of right panel). *Note.* Error bars = ±1*SE*. *** $p < .001$.

women concluded that unattractive men were unattractive, even if they had only incomplete, uncertain information about the men (Fig. 5). This contrasts with the finding that men overperceived the attractiveness of unattractive women under conditions of uncertainty.

10. Discussion

The current study applied Error Management Theory to a new stage of social perception – initial person perception – to generate hypotheses about two previously unknown cognitive biases. We hypothesized that, on average, men would respond to uncertainty about women's attractiveness by *over*estimating their attractiveness. Second, we hypothesized that women, on average, would respond to uncertainty about men's attractiveness by *under*estimating their attractiveness. Both hypotheses were empirically supported.

We also advanced and tested a new approach for mapping the cognitive architecture responsible for these biases. Previous work on evolved cognitive biases, such as research on men's overperception of women's sexual interest, has heavily emphasized a between-sex difference. This is an important finding, but broad quantitative effects such as these cannot discriminate between multiple candidate decision rules, because multiple different algorithms are capable of producing the same outcome.

In the current paper, we show that identifying the divergent predictions yielded by different candidate algorithms may be useful for charting the cognitive architecture responsible for the bias under investigation. In the current study, we found the predicted on-average sex difference. However, we also probed the observed biases more deeply by testing for specific quantitative effects. These more specific analyses suggested that on-average effects may not reveal the information-processing architecture responsible for the biases. Men, on average, overperceived women's attractiveness, and women, on average, underperceived men's attractiveness. However, further analyses tentatively suggest that men exhibit a bias in the perception of unattractive (but not attractive) women, and women exhibit a bias in the perception of attractive (but not unattractive) men. Had we not directed explicit attention to algorithm, these potential features of the biases might have remained unknown.

This is a first attempt at investigating these biases, and we do not claim to have conclusively revealed their information-processing architecture. Rather, our emphasis here is that work on cognitive biases would benefit by explicitly considering the algorithmic level of analysis. To this end, we have advanced a simple approach and provided an initial demonstration of the value of this approach for discriminating between different candidate algorithms. We hope that research on cognitive biases becomes more explicit about the algorithmic level of analysis, and that the approach we have outlined here might make modest contributions toward mapping the information-processing architecture underlying these biases.

10.1. Sex-differentiated inferential biases or thresholds for activation?

One (ostensible) alternative explanation for the current study's findings is that men might have lower thresholds than women for engaging further with a potential mating opportunity. This threshold hypothesis might also be correct, but is not a *competing* explanation.

The threshold hypothesis generates predictions at a later stage of decision making: the stage of *responding* to a potential mate's perceived attractiveness by motivating (or failing to motivate) further engagement with the potential opportunity, *not* at the stage of *perceiving* attractiveness. In short, the threshold hypothesis does not generate predictions about biases in initial inferences about a potential mate's attractiveness.

Although the current study's findings cannot be readily accounted for by this threshold hypothesis, the threshold hypothesis might simultaneously be true. Sex differences in the relative costs and benefits of forgone mating opportunities and injudicious mating behavior could have selected for *both* (1) sex-differentiated biases at the stage of making inferences about a mate's desirability *and* (2) sex-differentiated thresholds for activation in response to those inferences. These are two distinct and potentially complementary hypothesized design features. Future research is needed to more clearly resolve whether men have different thresholds than women for engaging further with a potential mating opportunity.

10.2. Uncertainty in ancestral conditions

For selection to have favored the inferential biases proposed in the current study, there must have been recurrent scenarios in ancestral mating environments in which a potential mate's physical attractiveness could not have been determined with certainty. Several features of ancestral mating practices and behavior, such as the interaction of exogamy and appearance enhancement behavior, may have prevented perceivers from reliably obtaining *certain*—that is, *complete* and *accurate*—information about a potential mate's physical attractiveness.

Exogamy is the predominant marriage practice among numerous modern populations (e.g., see Marchi et al., 2018) and occurs in over 90% of human groups (Ember, Gonzalez, & McCloskey, 2021). Analyses of ancient DNA from multiple archaeological sites provide evidence of mating patterns predominantly characterized by women reaching reproductive maturity where they were born, but then mating with men from geographically distant groups (Knipper et al., 2017). In short, evidence suggests that ancestral men and women frequently were mated to individuals who were *not* part of their tribe or group (see also Walker, Hill, Flinn, & Ellsworth, 2011). This exogamy-linked reduction in prior interaction could have combined with physical appearance enhancement behavior to constrain individuals' ability to obtain complete and accurate information about potential mates.

Physical appearance enhancement behaviors, which range from cosmetics to clothing to combing hair (see Davis & Arnocky, 2020), are ubiquitous across both time and space: they occur in virtually every known culture (see Davis & Arnocky, 2020) and may date all the way back to the emergence of *Homo sapiens*, or perhaps even earlier (see Tacon, 2006).[2] Although specific appearance-enhancement behaviors may vary across cultures, these behaviors all have the same defining characteristic: they change or conceal the appearance of specific physical features (Lewis & Buss, 2021). In short, physical appearance enhancement behaviors – a human universal whose roots appear to trace back to the emergence of our species – reliably alter one's appearance such that it does *not* provide complete and accurate information about one's true physical phenotype. Indeed, in a sense that is the *purpose* and the point of appearance enhancement behaviors.

This combination of exogamy and physical appearance enhancement behavior may have resulted in ancestral humans frequently *not* having complete and accurate information about the physical phenotype of potential mates. Consequently, in some circumstances they may have had to make inferences about a potential mate's physical phenotype under conditions of uncertainty – in particular in initial stages of person perception.

It is important to note that the male overperception of attractiveness bias (MOAB) hypothesis does not propose that men's initial bias persists after further information acquisition, or that it necessarily forms the basis for men's final decision whether to mate with a woman. Instead, the MOAB hypothesis proposes that selection may have favored a bias in men to overperceive women's attractiveness in initial person perception; if initial perceptions of a mate's desirability are too low, this could

---

[2] To take just one example, evidence suggests that the application of red ochre, a cosmetic used by ancient Egyptians (see Caton, Lewis, Al-Shawaf, & Evans, 2021) and still used in traditional societies such as the Ovahimba of Namibia (Molefe, 2015), was a cultural practice among both *Homo sapiens* and *Homo neanderthalensis* at least a quarter of a *million* years ago (see Tacon, 2006).

result in disinterest and lack of motivation to gather additional information about them. Future research is needed to more clearly resolve whether men are more likely than women to engage in further information acquisition after being exposed briefly to incomplete information about a potential mate, and whether women more than men experience disinterest following these brief exposures.

10.2.1. An alternative, byproduct hypothesis

Compared to information about attractiveness, reliable information about *other* components of a person's mate value (e.g., intelligence, social status, kindness) may be even more difficult to glean from brief exposures or during early stages of social interaction. Consequently, selection could have shaped inferential procedures to systematically over- or under-infer the levels of these qualities under conditions of uncertainty.

This overarching hypothesis raises an intriguing possibility: the effects observed in the current study may be *byproducts* (see Park, 2007; see also Kurzban, Tooby, & Cosmides, 2001; Al-Shawaf, Lewis, Barbaro, & Wehbe, 2020). To the extent that reliable information about *other* mate value-relevant characteristics may have been difficult to obtain (in particular during initial interactions in the context of exogamy), selection could have shaped psychological mechanisms to make biased inferences about a potential mate's mate value under such conditions of uncertainty. These adaptations may not have evolved to make inferences about a potential mate's physical attractiveness per se. However, in modern dating environments in which unfamiliar individuals frequently interact, there can be a great deal of informational uncertainty surrounding a potential mate's true physical phenotype—whether due to selectively chosen photographs for an online dating profile or dim illumination in a bar or night club. In these modern environments, the activation of mechanisms that evolved to deal with informational uncertainty about a potential mate's mate value – but not *specifically* uncertainty about their physical attractiveness – may result in the biased inferences observed in the current study. In short, the biases observed in the current study may be incidental byproducts of psychological adaptations that evolved to solve a different adaptive problem. We think this byproduct hypothesis is a plausible alternative, and eagerly await future research that pits the adaptation and byproduct hypotheses against each other. More broadly, this highlights the importance and utility of considering both adaptation and byproduct hypotheses in psychological research (Lewis et al., 2017; see also Al-Shawaf et al., 2020).

11. Conclusion

In contrast to the plentiful literature on biases in interpersonal perception that occur *after* two potential mates have interacted, much less EMT-informed work exists on *pre*-interaction biases in initial person perception. The current study addressed the possibility of an EMT bias in first impressions, which, to our knowledge, no work has addressed before. In support of the MOAB hypothesis, we found preliminary evidence of a male tendency to overperceive women's attractiveness, and, in support of the FUAB hypothesis, we observed a female tendency to underperceive men's attractiveness.

We also presented and applied a method for testing different candidate algorithms. These analyses suggested that on-average effects, such as on-average sex differences, may fail to reveal the underlying information-processing architecture. We hope these findings encourage research on other cognitive biases to more explicitly address algorithm, and that the approach we have outlined here might make modest contributions toward the goal of mapping the information-processing architecture underlying these biases.

The findings in the current study provide preliminary evidence of first-impression biases. However, future work is needed to more firmly establish the robustness of these effects and more clearly resolve the information-processing architecture responsible for producing them. We eagerly await future research that discriminatively tests the adaptation and byproduct hypotheses presented here, and that investigates first-impression biases about other components of mate value. More broadly, we hope the current study inspires new EMT research in uncharted domains and promotes greater attention to the algorithmic level of analysis in research on cognitive biases.

Declarations of Competing Interest

None.

Funding acknowledgement

This research was supported in part by grant #1742218 from Charles University Grant Agency (GAUK) to A. Y. Semchenko.

Authors' note

D.M.G.L. generated the hypotheses, designed the study, and wrote the manuscript. A.Y.S. created the study materials and collected, prepared, and analyzed all study data. L.A.S. and K.C.E. contributed to manuscript writing.

Acknowledgements

The authors thank Tess Robertson and two anonymous reviewers for their constructive suggestions on a previous draft of this manuscript, as well as Meg Selma for her support in preparing this manuscript.

References

Abbey, A. (1982). Sex differences in attributions for friendly behavior: Do males misperceive females' friendliness? *Journal of Personality and Social Psychology, 42*, 830–838.

Abbey, A. (1987). Misperceptions of friendly behavior as sexual interest: A survey of naturally occurring incidents. *Psychology of Women Quarterly, 11*(2), 173–194.

Al-Shawaf, L. (2016). Could there be a male commitment skepticism bias and a female sexual overperception bias? Novel hypotheses based on Error Management Theory. *Evolutionary Psychological Science, 2*(3), 237–240.

Al-Shawaf, L. (2020, October 20). Evolutionary psychology: Predictively powerful or riddled with just-so stories? *Areo Magazine*. https://areomagazine.com/2020/10/20/evolutionary-psychology-predictively-powerful-or-riddled-with-just-so-stories/.

Al-Shawaf, L., Lewis, D. M. G., Barbaro, N., & Wehbe, Y. S. (2020). The products of evolution: Conceptual distinctions, evidentiary criteria, and empirical examples. In T. K. Shackelford (Ed.), *SAGE handbook of evolutionary psychology* (pp. 70–95). Sage.

Al-Shawaf, L., Lewis, D. M. G., & Evans, K. C. (2021). *Error Management Theory: Clarifications, revisions, and advances*. Manuscript in preparation.

Buss, D. M. (1994). *The evolution of desire: Strategies of human mating*. New York: Basic Books.

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

Caton, N. R., Lewis, D. M. G., Al-Shawaf, L., & Evans, K. C. (2021). Human intersexual courtship. In J. K. Mogilksi, & T. K. Shackelford (Eds.), *The Oxford handbook of evolutionary psychology and romantic relationships*. Oxford University Press.

Confer, J. C., Easton, J. A., Fleischman, D. S., Goetz, C. D., Lewis, D. M. G., Perilloux, C., & Buss, D. M. (2010). Evolutionary psychology: Controversies, questions, prospects, and limitations. *American Psychologist, 65*(2), 110.

Core Team, R. (2020). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Cyrus, K., Schwarz, S., & Hassebrauck, M. (2011). Systematic cognitive biases in courtship context: women's commitment–skepticism as a life-history strategy? *Evolution and Human Behavior, 32*(1), 13–20.

Ember, C. R., Gonzalez, B., & McCloskey, D. (2021). Marriage and family. In C. R. Ember (Ed.), *Explaining human culture* (Human Relations Area Files).

Goetz, A. T., & Shackelford, T. K. (2009). Sexual conflict in humans: Evolutionary consequences of asymmetric parental investment and paternity uncertainty. *Animal Biology, 59*, 449–456.

Gould, S. J. (1978). Sociobiology: The art of storytelling. *New Scientist, 16*, 530–533.

Green, D. M., & Swets, J. A. (1966). *Signal detection and psychophysics*. New York: Wiley.

Haselton, M. G. (2003). The sexual overperception bias: Evidence of a systematic bias in men from a survey of naturally occurring events. *Journal of Research in Personality, 37*(1), 34–47.

Haselton, M. G., & Buss, D. M. (2000). Error Management Theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology, 78*(1), 81–91.

Haselton, M. G., & Nettle, D. (2006). The paranoid optimist: An integrative evolutionary model of cognitive biases. *Personality and Social Psychology Review, 10*(1), 47–66.

Hatfield, E., Roberts, D., & Schmidt, L. (1980). The impact of sex and physical attractiveness on an initial social encounter. *Recherches de Psychologie Sociale, 2*, 27–40.

Henningsen, D. D. (2004). Flirting with meaning: An examination of miscommunication in flirting interactions. *Sex Roles, 50*(7–8), 481–489.

Henningsen, D. D., & Henningsen, M. L. M. (2010). Testing Error Management Theory: Exploring the commitment skepticism bias and the sexual overperception bias. *Human Communication Research, 36*(4), 618–634.

Henningsen, D. D., Henningsen, M. L. M., McWorthy, E., McWorthy, C., & McWorthy, L. (2011). Exploring the effects of sex and mode of presentation in perceptions of dating goals in video-dating. *Journal of Communication, 61*(4), 641–658. https://doi.org/10.1111/j.1460-2466.2011.01564.x

Hurtado, A. M., & Hill, K. R. (1992). Paternal effect on offspring survivorship among ache and Hiwi hunter-gatherers. In B. S. Hewlett, et al. (Eds.), *Father-child relations: Cultural and biosocial contexts* (pp. 31–55). New York: Aldine de Gruyter.

Jackson, R. E., & Cormack, L. K. (2007). Evolved navigation theory and the descent illusion. *Perception & Psychophysics, 69*(3), 353–362.

Knipper, C., Mittnik, A., Massy, K., Kociumaka, C., Kucukkalipci, I., Maus, M., Wittenborn, F., Metz, S. E., Staskiewicz, A., Krause, J., & Stockhammer, P. W. (2017). Female exogamy and gene pool diversification at the transition from the final Neolithic to the early bronze age in Central Europe. *Proceedings of the National Academy of Sciences of the United States of America, 114*(38), 10083–10088. https://doi.org/10.1073/pnas.1706355114

Koenig, B. L., Kirkpatrick, L. A., & Ketelaar, T. (2007). Misperception of sexual and romantic interests in opposite-sex friendships: Four hypotheses. *Personal Relationships, 14*, 411–429. https://doi.org/10.1111/j.1475-6811.2007.00163.x

Kurzban, R., Tooby, J., & Cosmides, L. (2001). Can race be erased? Coalitional computation and social categorization. *Proceedings of the National Academy of Sciences of the United States of America, 98*, 15387–15392. https://doi.org/10.1073/pnas.251541498

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software, 82*(13), 1–26.

Lewis, D. M. G., Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (2017). Evolutionary psychology: A how to guide. *American Psychologist, 72*(4), 353–373.

Lewis, D. M. G., & Buss, D. M. (2021). Appearance enhancement: A cue-based approach. *Archives of Sexual Behavior.*. https://doi.org/10.1007/s10508-021-01957-2

Ma, D. S., Correll, J., & Wittenbrink, B. (2015). The Chicago face database: A free stimulus set of faces and norming data. *Behavior Research Methods, 47*, 1122–1135.

Marchi, N., Mennecier, P., Georges, M., Lafosse, S., Hegay, T., Dorzhu, C., Chichlo, B., Ségurel, L., & Heyer, E. (2018). Close inbreeding and low genetic diversity in inner Asian human populations despite geographical exogamy. *Scientific Reports, 8*, 9397. https://doi.org/10.1038/s41598-018-27047-3

Marr, D. (1982). *Vision: A computational approach*. San Francisco: Freeman & Co.

McClamrock, R. (1991). Marr's three levels: A re-evaluation. *Minds and Machines, 1*(2), 185–196.

McKay, R., & Efferson, C. (2010). The subtleties of error management. *Evolution and Human Behavior, 31*(5), 309–319.

Molefe, O. (2015). *Physico-chemical characterization of African traditional cosmetics produced by the Ovahimba tribes of northern Namibia*. Dissertation. University of Witwatersrand. Available from: http://hdl.handle.net/10539/19285.

Mongeau, P. A., & Johnson, K. L. (1995). Predicting cross-sex first-date sexual expectations and involvement: Contextual and individual difference factors. *Personal Relationships, 2*(4), 301–312.

Neuhoff, J. G. (2001). An adaptive bias in the perception of looming auditory motion. *Ecological Psychology, 13*(2), 87–110.

Park, J. H. (2007). Distinguishing byproducts from non-adaptive effects of algorithmic adaptations. *Evolutionary Psychology, 5*, 47–51. https://doi.org/10.1177/147470490700500105

Perilloux, C., Easton, J. A., & Buss, D. M. (2012). The misperception of sexual interest. *Psychological Science, 23*(2), 146–151.

Piatelli-Palmarini, M. (1994). *Inevitable illusions*. New York: Wiley.

Schifiliti, R. P., & Pucci, W. E. (1996). *Fire detection modeling: State of the art*. Bloomfield, CT: Fire Detection Institute.

Shafir, E., & Tversky, A. (1995). Decision making. In E. E. Smith, & D. N. Osherson (Eds.) (2nd ed.,*, Vol. 3. Thinking: An invitation to cognitive science* (pp. 77–100). Cambridge, MA: MIT Press.

Symons, D. (1979). *The evolution of human sexuality*. New York, NY: Oxford University Press.

Tacon, P. S. C. (2006). Behaviourally modern at 300,000 BP. *Before Farming, 2*, 1–9. https://doi.org/10.3828/bfarm.2006.2.3

Tooby, J., Cosmides, L., Sell, A., Lieberman, D., & Sznycer, D. (2008). Internal regulatory variables and the design of human motivation: A computational and evolutionary approach. In A. J. Elliot (Ed.), *Handbook of approach and avoidance motivation* (pp. 251–271). Mahwah, NJ: Erlbaum.

Tversky, A., & Kahneman, D. (1974). Judgment under uncertainty: Heuristics and biases. *Science, 185*(4157), 1124–1131.

Walker, R. S., Hill, K. R., Flinn, M. V., & Ellsworth, R. M. (2011). Evolutionary history of hunter-gatherer marriage practices. *PLoS One, 6*(4), Article e19066. https://doi.org/10.1371/journal.pone.0019066

2.1.4 Our response to Brandner et al. (2022)

Brandner et al. (2022) published a commentary addressing our study above (i.e., Lewis et al., 2022). In their commentary, Brandner et al. (2022) claim that re-analysis of our data indicates a non-significant interaction between the effect of blurriness and sex. In other words, they suggested that our data shows no sex-differentiated bias of attractiveness perception under uncertainty. In their analysis, Brandner et al. (2022) used a three-way interaction between target attractiveness, blurriness, and sex. First, we had no theoretical reason for conducting this three-way interaction, though for exploratory purposes it can be done. As part of the output of this model, the interaction between blurriness and sex was insignificant. However, as explained in our response, when I conduct this analysis, the next step would be to remove the insignificant three-way interaction (i.e., backward step-wise analysis) and continue with the analysis (Engqvist, 2005). When I did so (i.e., removed the insignificant three-way interaction), the effect of blurriness and sex was significant, which is a finding that we reported earlier. Furthermore, as explained in our response (Lewis et al., 2023), Brandner et al. (2022) misrepresent our analysis by claiming that we used a dichotomized ratings of attractiveness. I would like to note that target's true attractiveness ratings were used as a continuous variable in our mixed-effect effect model. After I found a significant interaction between blurriness and target attractiveness, I divided the data into two, based on the target attractiveness ratings. However, I have not used target attractiveness as a dichotomical variable in any of the models. Therefore, even though this commentary had creative ideas, it also included rather basic mistakes and misunderstandings.

2.1.5 Lewis, Al-Shawaf, Semchenko, & Evans, 2023

The author analysed all data and reviewed the manuscript.

ARTICLE IN PRESS

Evolution and Human Behavior xxx (xxxx) xxx

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.elsevier.com/locate/ens

Creative ideas, but elementary mistakes: A reply to Brandner and colleagues to promote best practices in error management theory research

David M.G. Lewis[a,b,*], Laith Al-Shawaf[c,d], Ayten Yesim Semchenko[e], Kortnee C. Evans[a]

[a] Discipline of Psychology, Murdoch University, Australia
[b] Centre for Healthy Ageing, Health Futures Institute, Murdoch University, Australia
[c] Department of Psychology, University of Colorado Colorado Springs, Australia
[d] Lyda Hill Institute for Human Resilience, University of Colorado Colorado Springs, Australia
[e] Faculty of Science, Charles University, Czechia

ARTICLE INFO

Keywords
Error management theory
Signal detection theory
Sensitivity
Bias
Cognitive biases
Sexual overperception bias

ABSTRACT

In their commentary on our paper, Brandner et al. commit an elementary statistical mistake that leads to entirely erroneous conclusions. When this statistical error is corrected, the effects described in our original paper appear exactly as reported. In principle, we could end our reply there. However, ending our reply there would be a lost opportunity for promoting best practices in Error Management Theory (EMT) research. The commentators make several other missteps that present the opportunity to draw attention to important principles in EMT research and offer clarifications that we hope assist in the operationalization, design, and interpretation of EMT-inspired studies in the future. We discuss these points and provide several EMT research scenarios to help to illustrate a key principle. We hope this reply highlights some of the key elements of best practices in EMT research and sheds light on pitfalls that researchers must make sure to avoid.

> *If the interaction term is not statistically significant, it should be removed from the model and the analysis rerun without the interaction term. Failure to remove an interaction term that was not statistically significant also can lead to an incorrect conclusion (*Engqvist, 2005*).*
>
> \- Beck & Bliwise, 2014, p. 371

> *To conclude this brief review, which can be extracted from almost any statistical textbook […] nonsignificant […] interaction terms must be removed before re-running the final analysis.*
>
> \- Engqvist, 2005, pp. 968–969

In their commentary on our paper, Brandner, Brase, and Young (2022) make an elementary statistical mistake that leads them to entirely erroneous conclusions. In their reanalysis, they failed to remove the non-significant interaction before interpreting the lower-order effects. As captured by the epigraphs above, you cannot do this.

That's the crux of it: the commentators' erroneous conclusions are caused entirely by this fundamental statistical error. Appropriately removing the non-significant higher-order interaction leads to the exact results we reported in our original article (Lewis, Al-Shawaf, Semchenko, & Evans, 2022).

Specifically, when the non-significant three-way interaction between participant sex, target attractiveness, and uncertainty is correctly removed, there are two significant two-way interactions: (1) between the effect of uncertainty and participant sex, which reflects the sex-differentiated biases in response to uncertainty that we originally reported, and which were our primary research findings; and (2) between uncertainty and target attractiveness, which was our secondary research finding. In other words, appropriately removing the non-significant higher-order interaction yields precisely the results we reported in our original article. The interested reader is welcome to consult these analyses, including the commentators' analyses followed by the correct analyses, on the Open Science Framework: https://osf.io/dskp4/?view_only=d9e70dabc844416bbc06105d2a901905.

In principle, we could end our reply here.

Ending our reply there, however, would be a lost opportunity to promote best practices in Error Management Theory (EMT) research.

---

* Corresponding author at: Discipline of Psychology, Murdoch University, 90 South Street, Murdoch WA 6150, Australia.
E-mail address: davidlewis@utexas.edu (D.M.G. Lewis).

https://doi.org/10.1016/j.evolhumbehav.2023.01.009
Received 12 December 2022; Accepted 2 January 2023

Please cite this article as: David M.G. Lewis, *Evolution and Human Behavior*, https://doi.org/10.1016/j.evolhumbehav.2023.01.009

Brandner et al. make many other missteps in their commentary. These present an opportunity to draw attention to important principles in EMT research, identify pitfalls that researchers should avoid, and offer clarifications that we hope assist in the operationalization, design, and interpretation of EMT-inspired studies in the future.

1. Principle 1: The *Average* does not equal the *Truth*

Brandner and colleagues encourage EMT research to substitute a *sample average* where an *objective baseline true value* is needed. This recommendation is flawed, and following it would automatically invalidate the entire analytical approach: although not made explicit, the procedure they describe would inherently treat a participant's judgment as *wrong* if it differs from *the average of other people's judgments*. The two scenarios below illustrate the invalidity of this operationalization of error (and any analyses based on it).

Scenario 1: Imagine you are a researcher studying people's perceptions of the height of a vertical surface such as a cliff. You conduct a study in which you take participants to the top of a cliff with a known height: 50 ft. You have each participant estimate the cliff's height. One participant, Taylor, estimates that the cliff is 50 ft tall. The average of all other participants' estimates is 54 ft. Is Taylor's estimate *wrong* – that is, did Taylor underperceive the height of the cliff – because it differed from the *average of other people's perceptions*?

Of course not. It would be preposterous to substitute the average of other people's perceptions for the *objective true state of the world.* However, this is precisely what Brandner and colleagues recommend.

In Scenario 1 (the cliff), there is an *objective true value* that can be known. In such situations, that objective true value must always be the value against which people's judgments are compared to test for an under- or over-perception bias.

However, a great deal of EMT research is interested in people's judgments about phenomena for which *there is no demonstrable objective true value*. Scenario 2 describes an example of this, and illustrates why using a sample average as a stand-in for objective baseline truth is still deeply flawed in such scenarios.

Scenario 2: Imagine you are a researcher studying men's perceptions of the most attractive female waist-to-hip ratio (WHR). Fifty percent of your sample is from the United States, and the other 50% are Hadza men. If your data parallel those from previous research, the *average* preferred WHR will be approximately 0.8; American men rank a WHR of 0.7 as most attractive, whereas Hadza men rank a WHR of 0.9 as most attractive (see Marlowe & Wetsman, 2001; see also test 1 in Sugiyama, 2004). If a given participant prefers a WHR that differs from 0.8, should you consider that participant to have made an inferential "error"?

Of course not.

Moreover, if the proportions of US men and Hadza men in the sample change, then the average value will change. An extreme example of this would be if your sample consisted of 99 US men and one Hadza man. In such a case, if the US men and the Hadza man had preferences reflective of their population means, the average preferred WHR would be 0.702. Should you then conclude that the Hadza man's preference is an "error" because it deviates from the sample average? Again, most certainly not. The difference between an individual participant's judgment and the average of a sample of other people's judgments is a wholly invalid operationalization of "error."

To be clear, the problem here is not that the Hadza man's response is being compared to the average response of people from a different culture. **The issue is that it is not valid to operationalize "error" as the difference between a given individual's response and the average response from other people**, regardless of whether those other people are from the same or a different culture. For example, if the lone Hadza man preferred a WHR of 0.95 and thereby had a preference that differed from the average preference in his population, his preference would still not be an "error."

The key point is that it is deeply misguided to treat a sample average as if it is the value against which "error" can be established and assessed. Any EMT or SDT analyses that are based on such an operationalization will be invalid.

The scenarios elaborated above illustrate why this operationalization is unsound. We can also illustrate the invalidity of this operationalization of "error" using a more quotidian example: if you were given a slice of pizza and asked how delicious it was, would your answer be *wrong* if it differed from the *average of other people's responses*? Of course not. That operationalization of "error" is clearly incorrect and logically ungrounded.

Yet it is at the core of the commentators' recommendation (and it is also at the core of Brandner and colleagues' analyses in their 2021 paper in *EHB*; see Brandner, Pohlman, & Brase, 2021). This issue is important because further propagation of this approach would be detrimental for Error Management Theory research, and indeed for all research on cognitive biases. "Sample average" and "objective baseline true value" are not the same thing, and conflating them can invalidate all analyses and conclusions predicated on their conflation.

2. Principle 2: Distinguish between primary, secondary, and tertiary findings

In their commentary, Brandner et al. assert that "dichotomization produced a Type I error in the original analysis." This is incorrect and misleading in multiple ways.[1] First, it fails to identify the true cause of Brandner and colleagues' discrepant results: their fundamental statistical error, which we described at the beginning of this reply. Second, it misrepresents our analyses—without exception, when we entered target attractiveness as a predictor, we entered it as a continuous variable.[2] Third, it misleads the reader by discussing our *tertiary* analyses as if an alternative set of results at the tertiary stage of analysis could somehow undermine the primary findings or secondary findings.

In our study, we conducted primary, secondary, and tertiary analyses. The primary focus of our paper was to test the hypothesized MOAB and FUAB biases. We established the existence of these biases. These were our primary findings: on average, men overperceived women's attractiveness under conditions of uncertainty, whereas women on average *under*perceived men's attractiveness under uncertainty. Next, the secondary goal was to determine whether the magnitudes of these biases varied as a function of target attractiveness. We established that they did: the effect of uncertainty depended on target attractiveness, as indicated by the significant interactions between target attractiveness and uncertainty observed among both male and female participants.

We then conducted *exploratory tertiary analyses* to probe these interactions. The commentators frame the idea that we could have probed the observed interactions in a different manner as if that somehow calls into question the existence of those interactions, or even the existence of the biases. This is extremely misleading. No matter what analytical approach is used to probe the interactions between target attractiveness and uncertainty, and no matter what conclusions are drawn from those tertiary analyses, they have no bearing on the primary findings of (1) men on average overperceiving women's attractiveness under

---

[1] There were several other instances in which Brandner et al. (2022) inaccurately describe or misrepresent our original paper, including our operationalizations and analyses. In this reply, we do not belabor all those errors. Rather, we focus on the issues that we see as most important for promoting best practices in EMT research.

[2] In our original paper, there were occasions in which we described or presented attractiveness in a dichotomous manner (e.g., Fig. 2). However, this was for the purpose of visualization and the reader's ease of understanding; although we occasionally talked about attractiveness using terms like "attractive" and "not attractive," there was not a single analysis in which we entered attractiveness as a dichotomous predictor.

conditions of uncertainty (the MOAB), and (2) women on average overperceiving men's attractiveness under conditions of uncertainty (the FUAB). They *also* have no bearing on the secondary finding that the effect of uncertainty depended on target attractiveness. These primary and secondary findings stand alone.

3. Principle 3: Demand characteristics should only be invoked as an alternative explanation when they can actually account for study findings

In their commentary, Brandner et al. (2022) allude to demand characteristics as a possible alternative explanation for our findings. This gives us the opportunity to clarify how researchers can best think about demand characteristics as possible alternative explanations. The most important question is *whether or not the proposed demand characteristic can actually account for the observed findings*. The commentators' proposed demand characteristic cannot account for any of the key study findings, so it falls flat as an alternative explanation.

Brandner and colleagues propose the following demand characteristic: "a second iteration of the same face and question demands a different response." In principle, we agree with this possibility. However, this demand characteristic generates only one prediction: participants will change their response when presented with a target for the second time. This prediction fails to account for the study findings in multiple ways. First, this demand characteristic alternative only proposes that participants will change their responses, not that they will change their responses *systematically in one direction.* Second, the demand characteristic fails to account for the fact that men and women systematically changed their responses *in opposite directions.* Third and finally, nothing about the demand characteristic alternative suggests that these sex-differentiated tendencies *should vary as a function of the target's attractiveness.* In short, the demand characteristic alternative collapses entirely when placed under scrutiny.

The key take-home message is this: researchers should ensure that a possible demand characteristic is actually capable of accounting for the observed findings before invoking it as an alternative explanation.

4. Principle 4: Sensitivity is not a relevant evidentiary criterion for assessing EMT hypotheses

In principle, we are excited by Brandner et al.'s idea to integrate Signal Detection Theory and EMT. The problem is that their proposed integration of SDT with EMT is not conceptually or analytically appropriate. The "more general signal detection theory (SDT) hypothesis" of "evolutionary optimality" that they propose in their commentary is not a competing alternative to an EMT hypothesis. The commentators suggest that their "evolutionary optimality hypothesis" proposes that "in situations of relative certainty, the heuristic should favor accurate judgments." We agree with this idea. However, by definition, it pertains to conditions of certainty. That is not what EMT hypotheses are about; EMT hypotheses are explicitly (and exclusively) concerned with how humans make inferences under *uncertainty*. This means that the idea that inferential mechanisms should be accurate under conditions of certainty is not in competition with our EMT-inspired hypotheses (or *any* EMT hypothesis, for that matter).

Moreover, neither (1) sensitivity nor (2) the relative influence of sensitivity (versus bias) are valid evidentiary criteria for assessing EMT hypotheses. The commentators state: "sensitivity to stimuli was more influential on responses than bias […] To put it succinctly, the uncertainty manipulation was not strong enough to bypass the evolved heuristic of maximizing correctness." These statements do not help the reader think clearly about the relationship between sensitivity and bias. Selection could have favored psychological mechanisms that are highly sensitive and make accurate inferences about the world in the majority of instances, *and* still exhibit biases in line with Error Management Theory. Many psychological mechanisms likely are characterized by *both* of the following: (1) they are usually accurate, and (2) in the small subset of instances in which they make errors, those errors are systematically biased in one direction over the other. To say that a mechanism is characterized by an EMT bias is not to say that it is *often wrong*; it is to say that *when* it is wrong, it is systematically wrong in one direction more than the other (e.g., biased in the direction of the less costly error). That is the core of EMT.

In sum, future research should be clear that sensitivity is not a valid criterion for testing EMT hypotheses. EMT hypotheses do not generate predictions about sensitivity at all; they generate predictions exclusively about *bias* (and not about the relative influence of bias compared to sensitivity). Researchers should therefore not use sensitivity as a criterion for assessing EMT hypotheses.

5. Conclusion

For the sake of evolutionary psychology and cognitive psychology, it is important to encourage best practices in Error Management Theory research. For the reasons outlined above, the analyses proposed and/or conducted by Brandner and colleagues in their (2022) commentary and their (2021) paper in *EHB* do not represent best practices. We hope that our reply here has illuminated some of the foundational errors involved in this approach. Our goal has been to point out and discuss these issues in order to facilitate best practices for future EMT studies. In particular, we emphasize that a sample average does not equal an objective baseline true value: treating an individual participant's judgment as *wrong* because it differs from the average of other people's responses is a nonsensical operationalization of error, and should not be used in future EMT research.

With respect to the sex-differentiated biases that we reported in our original paper, by no means do we purport to have final answers. Future research will be needed to answer additional questions about these biases and the cognitive architecture responsible for producing them. Are the biases specific to over- and underperceptions of physical attractiveness, or do they pertain to other dimensions of mate value as well? What is the information-processing architecture of the algorithms responsible for producing them?

Our emphasis here is that these and other questions must be tackled through research that applies best practices. We hope this reply has illuminated some of the key elements of best practices in EMT research, as well as invalid approaches and pitfalls that researchers must make sure to avoid.

Declaration of Competing Interest

None.

References

Beck, C. W., & Bliwise, N. G. (2014). Interactions are critical. *CBE Life Sciences Education, 13*(3), 371–372. https://doi.org/10.1187/cbe.14-05-0086

Brandner, J. L., Brase, G. L., & Young, M. E. (2022). Size, scale, and design matter: Commentary on Lewis, Al-Shawaf, Semchenko, and Evans, (2022). *Evolution and Human Behavior*. https://doi.org/10.1016/j.evolhumbehav.2022.09.007

Brandner, J. L., Pohlman, J., & Brase, G. L. (2021). On hits and being hit on: Error management theory, signal detection theory, and the male sexual overperception bias. *Evolution and Human Behavior, 42*(4), 331–342. https://doi.org/10.1016/j.evolhumbehav.2021.01.002

Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour, 70*(4), 967–971. https://doi.org/10.1016/j.anbehav.2005.01.016

Lewis, D. M. G., Al-Shawaf, L., Semchenko, A. Y., & Evans, K. C. (2022). Error management theory and biased first impressions: How do people perceive potential mates under conditions of uncertainty? *Evolution and Human Behavior, 43*(2), 87–96. https://doi.org/10.1016/j.evolhumbehav.2021.10.001

Marlowe, F., & Wetsman, A. (2001). Preferred waist-to-hip ratio and ecology. *Personality and Individual Differences, 30*(3), 481–489. https://doi.org/10.1016/S0191-8869(00)00039-8

Sugiyama, L. S. (2004). Is beauty in the context-sensitive adaptations of the beholder? Shiwiar use of waist-to-hip ratio in assessments of female mate value. *Evolution and Human Behavior, 25*(1), 51–62. https://doi.org/10.1016/S1090-5138(03)00083-7

2.2 The problem of identifying mates that are available

One of the crucial skills for acquiring a mate is to be able identify available mates to avoid a number of potential costs such as wasting time and resources for unavailable mates or losing opportunities with available mates. The word *available* can have more than one meaning, that is, it can mean, one is in an exclusive relationship and yet may be open to have a relationship with someone else, or it can mean one is in an not-exclusive relationship or single and may be open to have a relationship. To start with the former case, Davies & Shackelford (2017) found that the success of poaching attempts (i.e., trying to lure someone away from their exclusive relationship, Davies et al., 2007) would be higher when the current relationship has a lower commitment. Furthermore, as the commitment of the current relationship increase, the poachers are expected to have higher mate value than the current partner. The potential reason why that might be is that the benefit of gaining a higher mate value partner when there is lower commitment might exceed the cost of being poached. Therefore, understanding the costs and benefits associated with mate poaching can be helpful for future studies investigating the indicators of availability in already mated individuals. Whenever the benefits exceed the cost of being poached, the potential availability of the mated individuals might increase as in the Davies & Shackelford (2017)'s findings. In other words, though other factors such as personality (e.g., the positive relationship between Dark Triad traits which are narcissism, machiavellianism, and psychopathy and being poached for men, Kardum et al. (2015) can also play a role, cost-benefit difference of being poached can be an indicator of potential availability, and psychological adaptations identifying those indicators might have developed. However, currently, even the definition of mate poaching in studies is inconsistent. For that reason, I first wanted to give a succinct overview of mate poaching studies as well as the cost and benefits associated with mate poaching in the following subsection, which could be inspiring for the future work. In the second subsection, however, I will focus on a potential cue to identify available mates *irrespective of* their (potential mates') relationship status.

2.2.1 Already mated individuals: Mate poaching

Research shows that mate poaching is not an uncommon behavior despite its potential costs such as damage to reputation or being in physical danger (Schmitt & Buss, 2001). Schmitt & Buss (2001) defined three perspectives in mate poaching which are poacher (i.e., people who poach), poached, and a poachee (i.e., people whose partners are being poached away). Such a categorization could help us differentiate and clearly understand the perspectives in the conducted studies. However, Schmitt & Buss (2001)'s poaching definition, luring someone away from their current relationship to a new relationship, was incomplete. For something to be counted as poaching, the existing relationship should be exclusive and the poachers should know about the relationship and its exclusivity (Davies et al., 2007). Davies et al. (2007) conducted a study with a definition including the exclusivity emphasis. Although they reported somewhat different frequencies of poaching experience, the difference between their frequency and Schmitt & Buss (2001) was not significantly different (Davies et al., 2019). For example, 80.8% of Schmitt & Buss (2001)'s participants successfully poach someone for a casual relationship while that frequency was 74.3% in Davies et al. (2019). However, we need to interpret this with caution because participants were not the same in those two studies. The issues with the (un)/clarity of its definition set aside, mate poaching seemed to be quite common among people. It should be noted that being common may not mean it is people's first choice in a given situation and studies investigating mate poaching intention seem to support that notion. For example, Davies et al. (2010) found that if people were presented with equally attractive potential partners, one mated and one unmated, they prefer the unmated one. Similarly, Ueda et al. (2017) reported that men had more desire to have a romantic relationship with women without a partner than the ones that were already mated. Furthermore, relationships started through mate poaching might lead to lower relationship satisfaction (Semchenko & Havlíček, 2021), and relatedly, people with a history as a poacher is more likely to cheat (Belu & O'Sullivan, 2019). Therefore, for a phenomenon, which does not seem to be the first choice for many and with a potentially poorer relationship outcome, to be quite common is puzzling. In order to get a succinct view, Semchenko & Havlíček (2021) wrote a chapter about the costs and benefits of mate poaching. Such a review work can be a good first step for future studies investigating the psychological adaptations to identify already-mated but available potential mates. Semchenko & Havlíček (2021) focused on various inputs such as biological sex, mating context, and cultural and environmental factors potentially affecting mate poaching costs and benefits. However, I would like to note that these three inputs may not be quite independent of one another. To exemplify the dependence between mating context, biological sex, and socio-economic status, Schmitt (2004) hypothesized and found that in more liberal regions (measured by the women's access to political and economical resources), sex differences in short-term mate poaching is smaller than in more traditional regions.

2.2.2 Semchenko & Havlicek, 2020

The author conducted a relevant literature review, conceptualized, and wrote the manuscript.

Costs and Benefits of Mate Poaching

Ayten Yesim Semchenko and Jan Havlíček
Faculty of Science, Charles University,
Prague, Czech Republic

Synonyms

Human mate poaching; Mate poaching; Sex differences in costs and benefits of mate poaching

Definition

Mate poaching is a behavior intended to lure someone away from their current romantic relationship to form either temporary or permanent relationships with them.

Introduction

Mate poaching appears to be a ubiquitous behavior found in various regions of the world. Schmitt et al. (2004) conducted a survey with 53 nations on 5 continents and found that more than half of men (56.9% for short-term relationships; 57.1% for long-term relationships) tried to poach a mate. The frequency of occurrences was somewhat lower for women (34.9% for short-term relationships; 43.6% for long-term relationships).

For both long- and short-term relationships, around 70% of men and women reported that someone attempted to poach them. The highest rates of mate poaching attempts in a long-term context were reported in the Americas and Europe (56.2–65.6% in men and 43.3–51.5% in women), and a similar pattern was observed in the short-term context (56.7–70.3% in men and 35.5–41.9% in women). In contrast, the lowest rates of mate poaching in the long-term context were found in South/Southeast Asia (38.9% in men and 17.4% in women), while lowest rates in the short-term context were found in East Asia (29.5% in men and 14.9% in women). Overall, women tried to poach men for long-term relationships more than short-term relationships, while the opposite was true for men. These findings might suggest that mate poaching pays off more for men, in short-term mating.

The potential costs and benefits of mate poaching depend on the perspective of the individual involved. In other words, the perspective of mate poacher, poached one (i.e., the target of the poaching), and poachee (i.e., an individual whose mates were lured away) should be taken into consideration when assessing costs and benefits. For instance, taking pride in conquest is a potential benefit, while having a ready competition with the poachee is a potential cost exclusively for the poacher (Schmitt and Buss 2001). Fearing physical danger from the poachee, however, can be a potential cost for both the poacher and the poached one (Schmitt and Buss 2001; Wilson

T. K. Shackelford, V. A. Weekes-Shackelford (eds.), *Encyclopedia of Evolutionary Psychological Science*,
https://doi.org/10.1007/978-3-319-16999-6_1748-1

and Daly 1996). The poachee, on the other hand, might pay the cost of losing a partner.

The costs and benefits associated with mate poaching can be examined on the ultimate and proximate levels. The ultimate level cost-benefit analysis of mate poaching takes both the adaptive challenges that our ancestors may have faced and the adaptive solutions to those problems into account. This level of analysis urges to ask the "why" question to find the evolutionary function of the behavior. The proximate level analysis, however, has to do with the "how" question, and it encompasses immediate assessment of the behavior (Tinbergen 1963; Hladký and Havlíček 2013; Stephen and Sulikowski 2019). In this type of analysis, the flow of events (i.e., response to "how" question) is directly observable, unlike ultimate level analysis. The main aim of this entry is to provide an overview of ultimate and proximate costs and benefits associated with mate poaching. Several factors, such as type of the relationship desired by the poacher, sex differences, gender equality, socioeconomic status, and sex ratio, can potentially affect the costs and benefits of mate poaching. Costs and benefits linked with mate poaching will be explained and exemplified through these factors.

The Relationship Types and Sex Differences

Mate poachers aim to establish either short-term (i.e., temporary) or long-term (i.e., permanent) relationships with the poached. The type of desired relationships affects the potential costs and benefits of mate poaching. For instance, several proximate costs such as guilt feelings, deception issues, dating isolation (i.e., having to hide when on a date), and family rejection were reported as costlier in poaching for a long-term relationship compared to a short-term relationship for both sexes (Schmitt and Buss 2001).

Furthermore, the type of relationship that is being encroached on might also affect the potential costs and benefits of mate poaching. Davies and Shackelford (2017) found that the poached person expected more resources and physical attractiveness (compared to their current partner) when they were married as opposed to cohabitating and when they were cohabitating as opposed to dating. Similarly, Schmitt and Buss (2001) reported that both men and women were perceived as less successful in poaching women/men who have committed relationships as opposed to uncommitted relationships. Therefore, target individuals' current relationship status and investment affected their perception of the trade-off between the cost and benefit of being poached.

Together with the relationship types, sex differences also play a crucial role in the potential costs and benefits associated with mate poaching. An ultimate benefit of mate poaching is an increase in reproductive success. For men, the minimum parental investment required is only the copulation time, while for women, it is at least 9 months of pregnancy (Trivers 1972). Therefore, men can increase their reproductive success by having a higher number of partners. Relatedly, Schmitt and Buss (2001) found that enjoying sexual variety was labeled by the participants as a potential (proximate) benefit of mate poaching for men. In line with that idea, men might see more benefit in poaching for short-term relationships than for long-term relationships as compared to women. Schmitt and Buss (2001) found that the percentage of men (64%) attempting to poach for a short-term relationship was higher than the percentage of women for the same purpose (49%).

More women (63%) than men reported to attempt poaching for a long-term relationship (52%). However, men, more than women, attempted to poach for both long- and short-term relationships in all regions (Schmitt et al. 2004). In line with this finding and compared to men, women perceived a higher cost of reputational damage and shame if they poach for short- or long-term sexual affairs or a new exclusive relationship (Davies et al. 2010).

Furthermore, Schmitt and Buss (2001) found that for short-term mate poaching, men perceived a greater benefit of taking pride in conquest, while women perceived the same benefit more than men in the long-term mate poaching context. Relatedly, men perceived more benefit of egoboosting in mate poaching for a short-term relationship when compared to women (Davies et al. 2010). Consistent with their tendency for short-term matings with a lower commitment, men found more benefit in enjoying a lack of responsibility and always having time off from a relationship compared to women (Schmitt and Buss 2001).

Men can increase their reproductive success by having physically attractive partners. Previous studies showed that female physical attractiveness (e.g., waist-to-hip ratio and lumbar curvature) might indicate fertility (Singh 1993; Lewis et al. 2015). Therefore, having a physically attractive partner is a potential proximate benefit for men both as a poacher and poached.

Throughout human evolutionary history, the particular cost of fathering someone else's offspring has exclusively applied to men (Buss and Schmitt 1993). Therefore, to ensure their fatherhood, men might show sexual proprietariness (Buss and Schmitt 1993). One potential consequence of male sexual proprietariness might be murder, including wife killings (Wilson and Daly 1996; Buss 2005). In other words, having a physical danger might be a potential proximate cost for both the male poacher and the poached female.

The cost of fearing physical danger was rated more highly for men than for women by the participants (Schmitt and Buss 2001). However, Davies et al. (2010) found that women who poached for an exclusive relationship saw a greater cost of being physically harmed by the poached partner. The difference between these two studies might be due to the variation in methods of perspective given (i.e., third-person perspective, Schmitt and Buss 2001; first-person perspective, Davies et al. 2010).

Women can increase their reproductive success by having men who are willing to and have the means to provide for themselves and their offspring. Therefore, gaining resources can be the proximate benefit for females. Schmitt and Buss (2001) found that gaining resources was attributed as a benefit for female poachers. Relatedly, resource depletion might be a proximate cost for men (Schmitt and Buss 2001).

For both sexes, most mate poaching attempts appear to result in success. Schmitt et al. (2004) found that over 65% of men and women reported successfully poaching a mate away as a short-term mate and a long-term mate. More than half of men reported to be either poached away as a short-term or as a long-term partner. Over 40% of women were successfully poached away as a short-term mate, except in South/Southeast Asia (28%) and Africa (26.9%). More than 42% of women were poached away as a long-term partner worldwide. Arnocky et al. (2013) found that the number of mate poaching attempts was a significant predictor of lifetime sex partners, lifetime casual sex partners, and lifetime dating partners. However, another study showed that relationships formed via poaching function rather poorly. There were lower levels of commitment and investment and less satisfaction, and the rates of infidelity were higher compared to the other relationships formed differently (Foster et al. 2014). The quality of the resulting relationships might also be affected by the friendship between the poacher and the poached. For instance, it was found that poachers were seen as less likely to commit infidelity when the poacher and the poached were friends. Furthermore, their relationships were considered more likely to last over a year (Mogilski and Wade 2013). Friendship might signal commitment. Therefore, the likelihood of experiencing the proximate cost of future infidelity might be reduced.

Having a pre-approved partner can increase reproductive success, especially for women. As mentioned above, women can increase their reproductive success by being with men who can and are willing to provide resources for them and for their offspring (Schmitt and Buss 2001). These characteristics may not be readily available from the visual cues. Therefore, by copying the preferences of other women and poaching a coupled men, women can lower the cost of selecting a mate (e.g., time being spent and choosing a mate low in quality). On the other hand, the female body can signal fertility more readily than the male body (Perilloux and Cloud 2019). Therefore, men can use physical cues to assess women's mate value. Furthermore, preferring women with partner can lead to an unwanted consequence of misdirecting parental investment (Hill and Buss 2008). Therefore, having a pre-approved partner can be a proximate benefit of mate poaching for women rather than men.

The results of studies on female mate copying, however, have shown contradictory results. It was found that women perceive the male targets presented with females as more attractive (Gouda-Vossos et al. 2018) and that mate copying is more common among young women compared to older women (Anderson and Surbey 2014). However, Parker and Burkley (2009) found that only single women showed a preference for the attached men compared to single men. In another study, women did not perceive engaged or in-a-relationship men as more attractive or as having higher socioeconomic status (Uller and Johansson 2003).

A study conducted with male participants tested the mate copying effect. The findings suggest that men perceived the female images with the title “with a partner” as socially more distant compared to the female images with the title “without a partner” (Ueda et al. 2017). The two-thirds of the participants indicated a lower desire to have a romantic relationship with the partnered females in the images. They also show that this effect was accompanied by the parietal cortex activation. The parietal cortex is associated with social distance evaluation, the analysis of the complex network of social relationships based on physical distance, such as close and distant friends (Yamakawa et al. 2009). The participants preferring females with partners, in contrast, had a higher orbitofrontal cortex activity (Ueda et al. 2017). This region of the brain is linked with risk-taking (Hsu et al. 2005) and with subjective ranking of visual objects (Lebreton et al. 2009).

In line with the studies discussed above, Davies et al. (2010) found that both men and women would be averse to mated individuals when they are equally attracted to single and already-mated ones. These findings collectively suggest that the costs of mate poaching might under many circumstances exceed the benefits for the poacher.

Cultural and Environmental Factors

Gender equality, socioeconomic status, and sex ratio might affect the cost-benefit assessment of mate poaching. For instance, Davies et al. (2010) found that the perceived cost of mate poaching was higher among women than men. This difference might explain why men attempt to poach more than women (Schmitt et al. 2004). In line with that logic, Schmitt et al. (2004) found that in gender-equal regions, sex differences tend to shrink for poaching a short-term partner. This finding mainly stemmed from the women’s increased poaching attempts. Furthermore, there was a negative correlation between men’s poaching attempts for long-term relationships and gender egalitarianism (i.e., equal access to political and economic power). Women’s mate poaching attempts were, on the other hand, positively correlated with gender egalitarianism. Furthermore, both men and women showed increased poaching attempts when women have more political power indexed by the proportion of women in parliament. There was a positive correlation between political equity (i.e., equal access to political power) and women’s both short- and long-term poaching attempts and their prevalence. Political equity was also positively associated with the occurrence of men’s short-term mate poaching attempts.

Socioeconomic status can also have an impact on the potential costs and benefits of mate poaching. Schmitt et al. (2004) found that men who engage in short-term mate poaching attempts more had a higher socioeconomic status in many regions (i.e., North America, Western Europe, the Middle East, and Africa). Women also showed a similar tendency in certain regions of Southern Europe, South/Southeast Asia, and East Asia. Furthermore, for both sexes, the successful short-term mate poaching attempts were positively related to the socioeconomic status of the participants. Men’s failure to resist short-term mate poaching attempts was also positively linked to socioeconomic status. Therefore, for both poacher and the poached, socioeconomic status affects the costs and benefits of mate poaching.

Lastly, sex ratio might also affect the costs and benefits associated with mate poaching. The available mating pool might shrink for the more prevalent sex when the sex ratio is skewed. This reduced availability might motivate mate poaching by potentially increasing the reproductive success of the more prevalent sex. In other words, the benefits of mate poaching might be higher for the more prevalent sex compared to the rarer sex. As expected, the prevalence of female mate poaching attempts was negatively linked to their sex ratio (Schmitt et al. 2004). However, when the male sex ratio was higher, men showed fewer attempts of mate poaching. Furthermore, in the regions where there is a surplus of women, mate poaching rates showed a trend to increase. Therefore, the potential effect of sex ratio on the cost-benefit assessment of mate poaching was only partially supported.

Future Directions

The number of studies on the costs and benefits of mate poaching is somewhat limited. Indirect evidence from uxoricide (i.e., wife killing), infidelity research, and mate copying research have been commonly used in the mate poaching literature. However, uxoricide or extra-pair affairs do not always encompass mate poaching. For instance, if a married woman pursues a single potential partner and eventually has an affair, it falls into the definition of an extra-pair affair but not of mate poaching. Similarly, mate copying does not necessarily indicate mate poaching behavior. It might merely show the preferences of same-sex individuals. Therefore, future studies are needed in order to have a better understanding of the costs and benefits of mate poaching behavior. Furthermore, to our knowledge, none of the studies directly investigating the cost-benefits associated with mate poaching used the interview method. Qualitative studies with in-depth interviews might shed light on proximate costs and benefits further by exploring variation in contexts of mate poaching behavior.

Conclusions

Mate poaching appears to be a widespread human experience. Almost 70% of people claim that someone attempted to poach them, and nearly half of them reported to fail resisting it. Although it is a ubiquitous experience, the findings suggest that mate poaching may not be the first preference of most people when seeking a mate, possibly due to its potential costs.

There are various potential ultimate and proximate costs and benefits associated with mate poaching. Having a higher reproductive success is a potential ultimate benefit, while taking pride in conquest, gaining resources, and enjoying a sexual variety are among the proximate benefits. The potential ultimate cost of mate poaching is a lowered reproductive success; while future infidelity concerns, ready competition with the poachee, and resource depletion are the examples of the proximate costs.

Several factors affect the cost-benefit assessment of mate poaching for both the poacher and the poached individual. The types of relationships desired by the poacher and the type of target relationship being encroached on, sex differences, cultural and environmental factors (i.e., gender equality, socioeconomic status, and sex ratio) are among those factors. Future studies are needed to have more in-depth information about the context of mate poaching. Having a detailed picture of the mate poaching context will lead to a better understanding of its costs and benefits.

Cross-References

- ▶ Human Courting
- ▶ Infidelity
- ▶ Mate Copying
- ▶ Mating Rivalry
- ▶ Personality and Mate Poaching

Acknowledgments Ayten Yesim Semchenko and Jan Havlíček are supported by Charles University Grant Agency grant GAUK No. 1742218.

References

Anderson, R. C., & Surbey, M. K. (2014). I want what she's having. Evidence of human mate copying. *Human Nature, 25*(3), 342–358. https://doi.org/10.1007/s12110-014-9202-7.

Arnocky, S., Sunderani, S., & Vaillancourt, T. (2013). Mate-poaching and mating success in humans. *Journal of Evolutionary Psychology, 11*(2), 65–83. https://doi.org/10.1556/JEP.11.2013.2.2.

Buss, D. M. (2005). *The murderer next door: Why the mind is designed to kill*. New York: Penguin Press.

Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review, 100*(2), 204–232. https://doi.org/10.1037/0033-295X.100.2.204.

Davies, A. P. C., & Shackelford, T. K. (2017). Don't you wish your partner was hot like me? The effectiveness of mate poaching across relationship types considering the relative mate-values of the poacher and the partner of the poached. *Personality and Individual Differences, 106*, 32–35. https://doi.org/10.1016/j.paid.2016.10.029.

Davies, A. P. C., Shackelford, T. K., & Hass, R. G. (2010). Sex differences in perceptions of benefits and costs of mate poaching. *Personality and Individual Differences, 49*, 441–445. https://doi.org/10.1016/j.paid.2010.04.014.

Foster, J. D., Jonason, P. K., Shrira, I., Campbell, W. K., Shiverdecker, L. K., & Varner, S. C. (2014). What do you get when you make somebody else's partner your own? An analysis of relationships formed via mate poaching. *Journal of Research in Personality, 52*, 78–90. https://doi.org/10.1016/j.jrp.2014.07.008.

Gouda-Vossos, A., Nakagawa, S., Dixson, B. J. W., & Brooks, R. C. (2018). Mate choice copying in humans: A systematic review and meta-analysis. *Adaptive Human Behavior and Physiology, 4*(4), 364–386. https://doi.org/10.1007/s40750-018-0099-y.

Hill, S. E., & Buss, D. M. (2008). The mere presence of opposite-sex others on judgements of sexual and romantic desirability: Opposite effects for men and women. *Personality and Psychology Bulletin, 34*(5), 635–647. https://doi.org/10.1177/0146167207313728.

Hladký, V., & Havlíček, J. (2013). Was Tinbergen an Aristotelian? Comparison of Tinbergen's four whys and Aristotle's four causes. *Human Ethology Bulletin, 28*, 3–11.

Hsu, M., Bhatt, M., Adolphs, R., Tranel, D., & Camerer, C. F. (2005). Neural systems responding to degrees of uncertainty in human decision-making. *Science, 310*(5754), 1680–1683. https://doi.org/10.1126/science.1115327.

Lebreton, M., Jorge, S., Michel, V., Thirion, B., & Pessiglione, M. (2009). An automatic valuation system in the human brain: Evidence from functional neuroimaging. *Neuron, 64*(3), 431–439. https://doi.org/10.1016/j.neuron.2009.09.040.

Lewis, D. M. G., Russell, E. M., Al-Shawaf, L., & Buss, D. M. (2015). Lumbar curvature: A previously undiscovered standard of attractiveness. *Evolution and Human Behavior, 36*(5), 345–350. https://doi.org/10.1016/j.evolhumbehav.2015.01.007.

Mogilski, J., & Wade, T. J. (2013). Friendship as a relationship infiltration tactic during human mate poaching. *Evolutionary Psychology, 11*(4), 926–943. https://doi.org/10.1177/147470491301100415.

Parker, J., & Burkley, M. (2009). Who's chasing whom? The impact of gender and relationship status on mate poaching. *Journal of Experimental Social Psychology, 45*(4), 1016–1019. https://doi.org/10.1016/j.jesp.2009.04.022.

Perilloux, C., & Cloud, J. M. (2019). Mate-by-numbers: Budget, mating context, and sex predict preferences for facial and bodily traits. *Evolutionary Psychological Science, 5*(3), 294–299. https://doi.org/10.1007/s40806-019-00187-z.

Schmitt, D., & Buss, D. M. (2001). Human mate poaching: Tactics and temptations for infiltrating existing mateships. *Journal of Personality and Social Psychology, 80*(6), 894–917. https://doi.org/10.1037/0022-3514.80.6.894.

Schmitt, D. P., et al. (2004). Patterns and universals of mate poaching across 53 nations: The effects of sex, culture, and personality on romantically attracting another person's partner. *Journal of Personality and Social Psychology, 86*(4), 560–584. https://doi.org/10.1037/0022-3514.86.4.560.

Singh, D. (1993). Adaptive significance of female physical attractiveness. Role of waist-to-hip ratio. *Journal of Personality and Social Psychology, 65*(2), 293–307. https://doi.org/10.1037/0022-3514.65.2.293.

Stephen, I. D., & Sulikowski, D. (2019). Tinbergen's four questions. In T. Shackelford & V. Weekes-Shackelford (Eds.), *Encyclopedia of evolutionary psychological science*. Cham: Springer. https://doi.org/10.1007/978-3-319-16999-6_1347-.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie, 20*(4), 410–433.

Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 1871–1971). Chicago: Aldine.

Ueda, R., Ashida, H., Yanagisawa, K., & Abe, N. (2017). The neural basis of individual differences in mate poaching. *Social Neuroscience, 12*(4), 391–399. https://doi.org/10.1080/17470919.2016.1182065.

Uller, T., & Johansson, L. C. (2003). Human mate and the wedding ring effect. Are married men more attractive? *Human Nature, 14*(3), 267–276. https://doi.org/10.1007/s12110-003-1006-0.

Wilson, M. I., & Daly, M. (1996). Male sexual proprietariness and violence against wives. *Current Directions in Psychological Science, 5*(1), 2–7. https://doi.org/10.1111/1467-8721.ep10772668.

Yamakawa, Y., Kanai, R., Matsumura, M., & Naito, E. (2009). Social distance evaluation in human parietal cortex. *PLoS One, 4*(2), e4360. https://doi.org/10.1371/journal.pone.0004360.

2.2.3 Potential behavioral indicator of availability: Back arching

As discussed in the previous sub-section, the word *available* can include already-mated or single individuals who might be open to new relationships. In this sub-section, I studied the potential behavioral indicator of *availability* of women, irrespective of their relationship status. Ancestral men had the adaptive problem of finding sexually receptive women to engage in short-term sexual affairs (Buss & Schmitt, 1993). Female sexual receptivity, which indicates readiness for copulation, is signaled through the lordosis reflex, among a number of mammals such as lemurs (Drea et al., 2020) and marmosets (Moe et al., 2016), and rats (Kudwa et al., 2010). Lordosis reflex, which is thought to be regulated by hormones (e.g., Tennent et al., 1980; Ågmo & Ellingsen, 2003), can be defined as back arching of the spine and seemed to be lost starting with macaques. In other words, bonobos and humans are thought to lose that reflex (Wunsch, 2017), see Figure 2.2.1)). In general, among apes, hormones do not seem to have that much ruling effect on

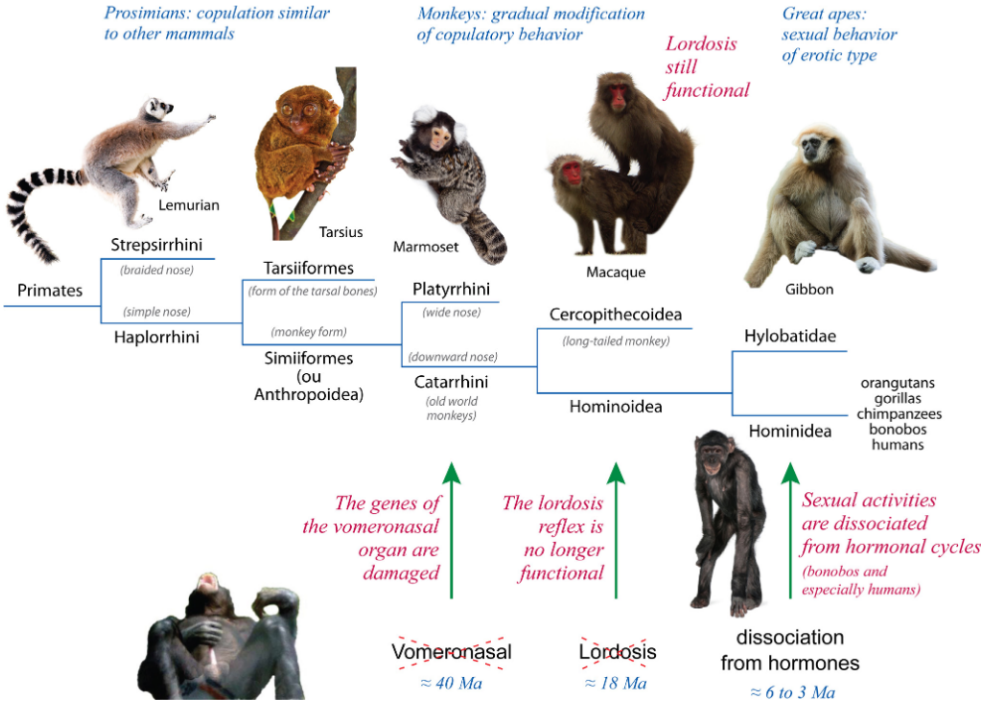


Figure 2.2.1: Lordosis reflex among primates. Image taken from Wunsch (2017).

sexual behavior. Instead, sexual receptivity can be signaled through various facial expressions and vocalizations (Dixson et al., 1998). Research concerning lordosis behavior among humans is scarce. A dissertation by Senveli (2017), however, to the best of my knowledge, is the first to suggest that lordosis behavior (i.e., back arching) might signal proceptivity. Senveli (2017) found that as the soicosexuality of women increased, so did the range of their back arching behavior in the presence of an attractive male conferederate. A study published a year after, Pazhoohi et al. (2018), stated to investigate back arching, however, they used static 3D stimuli and referred to them as "arching the back (lumbar curvature)". In other words, a morphological cue (lumbar curvature) in a standing neutral position seemed to be mixed with a behavioral cue (back arching) (Ranson et al., 2023). In short, the literature in this area is limited and in an attempt to fill that gap, Semchenko et al. (2022) conducted studies where the lordosis movement effect on males' perception of female attractiveness is investigated. With the Lordosis Detection Hypothesis, we hypothesized that men would find lordosis behavior more attractive in the short-term uncommitted mating context than in the long-term committed mating context. The reasoning behind this prediction was that in non-human mammalians lordosis behavior is a reflex signaling sexual receptivity. In both studies, we found that men found lordosis behavior more attractive in the short-term mating context just as we predicted. Therefore, it may be the case that men perceive female lordosis behavior as an indication of proceptivity. In other words, men might have developed a psychological adaptation (i.e., perceiving back arching as a signal for proceptivity) which help them to identify sexually available mates (Semchenko et al., 2022). Further studies are needed to understand whether back arching behavior indicates proceptivity. Culture might be another relevant input for future studies investigating what back arching indicates. For example, twerking dance moves resemble lordosis movement, but those moves do not necessarily mean proceptivity. In fact, Kitata (2020) reports that twerking is oversexualised by Westerners but in Kenya, it is a way of festive celebration which includes sexual expression but not an invitation to sex. Therefore, these studies should be replicated in different cultures in order to have a more comprehensive view of lordosis movement (Semchenko et al., 2022).

2.2.4 Exploratory analyses – socio-sexual orientation as input

Socio-sexual orientation can be defined as the overall tendency towards having uncommitted sex (Penke & Asendorpf, 2008). As far as I know, there are not many studies investigating the role of socio-sexuality on how men perceive female movement (e.g., dancing). The one study which I identified was conducted by Röder et al. (2015) and they found that men's sociosexual orientation did not have a significant effect on male perception of female dances (women danced as they would in a dance club) in terms of promiscuity. Because lordosis movement might be interpreted as proceptivity and we found that to be independent of men's socio-sexual orientation, our findings and their findings seem to be in line with one another. However, further studies are needed to have a clearer overview of the effect of male socio-sexual orientation on the perception of female movements and whether socio-sexual orientation interacts with the mating context or not.

2.3 The problem of identifying mates exhibiting specific fitness-related cues

Adaptive problems that ancestral men and women faced might have varied based on the mating context (Buss & Schmitt, 1993). However, the problem of finding healthy and fertile women for men exists in both mating contexts (Buss & Schmitt, 1993) as reproduction is the key in both contexts. Therefore, the male mating mind might have evolved to identify fit women through visual cues for both mating contexts. Visual cues such as lumbar curvature can indicate the potential for both survival and reproductive success. Lumbar curvature potentially protects against various medical problems such as back injuries, low back pain, and fatigue, particularly during pregnancy as it might balance the forward-shifted center of mass by moving some of the mass to the back (Whitcome et al., 2007). In a very simplified reasoning, a mother without back injuries can forage and survive better, hence the importance of lumbar curvature. Furthermore, for this cue, the effect of mating context has not been studied before.

2.3.1 Lumbar curvature

Lumbar curvature is an anatomical feature unique to homo sapiens among the living primates, lumbar curvature. The human lumbar spine includes five vertebrae (L1 to L5) between the thoracic region and sacrum (see Figure 2.3.1). Each vertebra is wider and sturdier than the next (e.g., L5 is wider than L1). They are positioned in a way that creates an external lumbar curvature. Lumbar curvature is also known as lumbar lordosis and it comes with bipedal locomotion (e.g., Harcourt-Smith, 2010) along with other morphological requirements such as an increase in hindlimb and buttock mass. Lumbar curvature helps with balance as the center of mass shifts in an upright position (Jaanusson, 1991). Relatedly, an experiment with juvenile Japanese macaques trained for bipedalism showed that they developed a curvature in the lumbar region while the free living ones did not (Preuschoft et al., 1988). As hominin evolution and bipedalism progressed, lumbar curvature seemed to increase. In non-human hominids, the angle was around $20 - 25°$, while it is roughly around 50° in humans (Been et al., 2014).

Is lumbar curvature sexually dimorphic?

Multiple studies showed that lumbar curvature is more pronounced in women than it is in men (e.g., Fernand & Fox, 1985; Norton et al., 2004; Hay et al., 2015) and studies so far did not show any significant racial difference in lumbar curvature (e.g., Fernand & Fox, 1985; Arima et al., 2018). One of the reasons

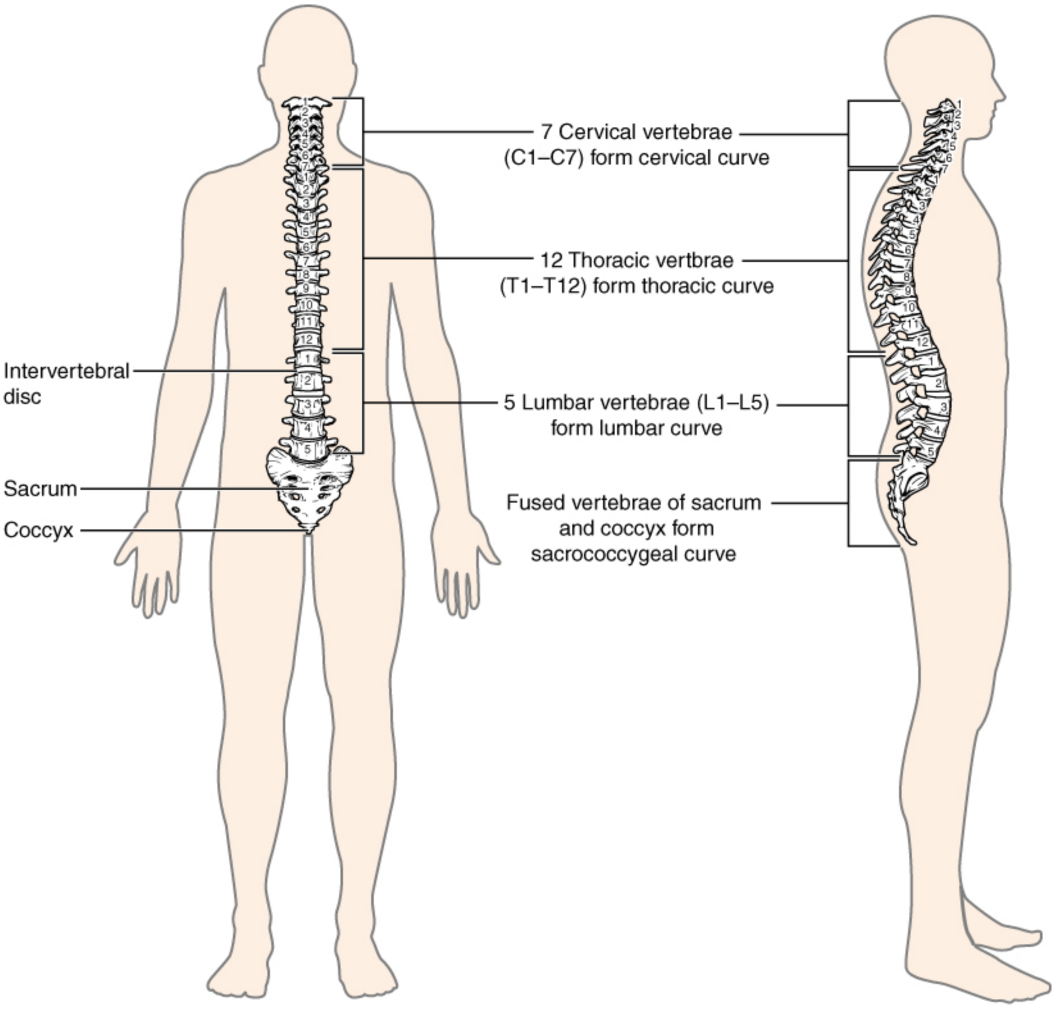


Figure 2.3.1: Illustration of human vertebra. College (2013). *CC Attribution 3.0 Unported*

for lumbar curvature to be sexually dimorphic might be the increased abdominal mass during pregnancy, shifting the center of mass forward (see Figure 2.3.2). If the center of mass is not balanced through bone structure, then hip torque might be increased by almost 800% potentially causing lower back pain and fatigue (Whitcome et al., 2007). Lower back pain and fatigue in return could negatively affect both the foraging abilities of the mother and her ability to escape from predators (Whitcome et al., 2007). The safest curvature angle against medical problems was reported as approximately 45.5° by Fernand & Fox (1985). Relatedly, Norton et al. (2004) reported that the average curvature of women who have no low back pain was 45.6°. Therefore, the optimum angle, which is potentially crucial to balance the center of a mass shift back to the hip, seemed to be

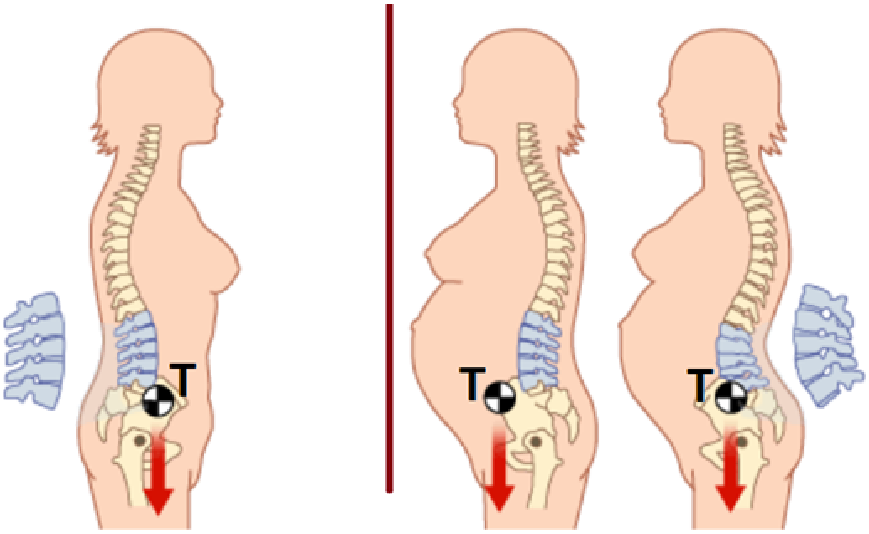


Figure 2.3.2: The illustration of human female center of mass change during pregnancy, taken from Frydrýšek (2016). *CC Attribution-Share Alike 4.0 International* Note: Only half of the original image is used as the other half contained the center of mass change of an ape during pregnancy.

around 45.5°. Deviation from the optimum angle is associated with either hyper- or hypolordosis. Both hyper and hypolordosis are linked with medical problems such as hyperlordosis with low-back pain, (Oakley et al., 2019) and hypolordosis with paraspinal muscle spasms, (Gilbert et al., 2009).

Psychological adaptations about lumbar curvature

Because lumbar curvature is a sexually dimorphic feature, one could articulate that it is not only influenced by natural selection by preventing medical problems for mothers but it might also be affected by intersexual selection. Men choosing women having an optimum lumbar curvature for increased reproductive success would be a reasonable prediction to make. However, to the best of my knowledge, there are only a few studies conducted to investigate the evolved perceptions of female lumbar curvature (e.g., Lewis et al., 2015, 2017b; Pazhoohi et al., 2018) and none tested whether these perceptions are sensitive to the mating context. In an attempt to fill the gap in that area, Semchenko et al. (2022) tested the effect of varying lumbar curvature angles in different mating contexts. Because of the fetal load during pregnancy, selection might favor the optimum angle for both the survival of the mother and the offspring (Whitcome et al., 2007). It would be advantageous for men to be more attracted to women who have near optimum lumbar curvature angle (Lewis et al., 2015). In support of this prediction, Lewis et al. (2015) found that men perceived women whose lordotic angle was closer to optimum as more attractive. However, Lewis et al. (2015) did not test whether mating context would affect that attractiveness perception or not. Theoretical reasoning directs us to think that preference towards the optimum lumbar curvature angle should not be sensitive to the mating context because for both mating contexts there is a possibility of having an offspring (e.g., Buss & Schmitt, 2019) and mothers' survival and ability to care is important for the offspring. To test these theoretical predictions via replicable experiments, we (Semchenko et al., 2022) conducted two studies, the second study replicating the first one with an independent sample. In both studies, we repeatedly showed that mating context did not have a significant effect on male perception of female attractiveness tested via stimuli varying in lumbar curvature angle (Semchenko et al., 2022). Therefore, our findings are consistent with the proposed male psychological adaptation of showing preference towards a women with optimum lumbar curvature angle and that preference is independent of the mating contexts. (Semchenko et al., 2022).

2.3.2 Exploratory analyses – socio-sexual orientation as an input

Socio-sexuality is also one of the inputs that can potentially affect how our psychological adaptations might have evolved. For example, men who scored high on socio-sexuality indicates a stronger preference towards women who has larger breast (Zelazniewicz & Pawlowski, 2011) and lower waist-to-hip ratio (Price et al., 2013) compared to men who scored lower on socio-sexuality. However, those studies did not separate mating contexts in their questions. In our study, we openly direct the participants to think in the committed and uncommitted mating contexts. If male participants are successful in shifting mating context when evaluating female attractiveness, then I would not expect to see the effect of socio-sexual orientation. The results indicated that context-independent effect of lumbar curvature was also independent of men's socio-sexual orientation (Semchenko et al., 2022). Future studies are needed to establish the reason why for this independence.

2.3.3 Semchenko et al., 2022

The author, who is the corresponding author of the article, contributed to data collection, significantly contributed to manuscript preparation, and processed, analyzed and visualized all data.

Empirical Research Paper

Personality and Social
Psychology Bulletin
1–13

DOI: 10.1177/01461672221115218
journals.sagepub.com/home/pspb
SAGE

Lordosis in Humans

Ayten Yesim Semchenko[1], Zeynep Senveli[2], Mitchell R. L. Forrest[3], Jonathon Flores[4], Vojtěch Fiala[1], Laith Al-Shawaf[5], David M. Buss[6], and David M. G. Lewis[3]

Abstract

Despite progress in attractiveness research, we have yet to identify many fitness-relevant cues in the human phenotype or humans' psychology for responding to them. Here, we test hypotheses about psychological systems that may have evolved to process distinct cues in the female lumbar region. The Fetal Load Hypothesis proposes a male preference for a morphological cue: lumbar curvature. The Lordosis Detection Hypothesis posits context-dependent male attraction to a movement: lordosis behavior. In two studies (Study 1 *N*: 102, Study 2 *N*: 231), we presented men with animated female characters that varied in their lumbar curvature and back arching (i.e., lordosis behavior). Irrespective of mating context, men's attraction increased as lumbar curvature approached the hypothesized optimum. By contrast, men experienced greater attraction to lordosis behavior in short-term than long-term mating contexts. These findings support both the Lordosis Detection and Fetal Load Hypotheses. Discussion focuses on the meaning of human lordosis and the importance of dynamic stimuli in attractiveness research.

Keywords

human mating, lordosis, lumbar curvature, attractiveness, mate preferences

Received December 30, 2020; revision accepted June 16, 2022

Natural selection should have shaped information-processing systems in sexually reproducing organisms to attend to fitness-relevant phenotypic cues in potential mates, and to regulate mating attraction in response to these cues. Abundant evidence across a wide variety of non-human taxa supports this hypothesis (e.g., Birkhead & Fletcher, 1995; Norris, 1993; Petrie, 1994; Weiss et al., 2011). In humans, this overarching hypothesis has resulted in the discovery of a variety of *evolved standards of attractiveness*: fitness-relevant phenotypic characteristics that humans systematically find attractive. For example, in women, a small waist coupled with a larger gluteofemoral region is a cue to nulligravidity that is linked to higher stores of docosahexaenoic acid, a limiting factor in infant brain development (see Lassek & Gaulin, 2019). In adaptive alignment with this, men are most attracted to a waist-to-hip ratio associated with nubility, nulliparity, and high levels of this key fatty acid (Lassek & Gaulin, 2019). Research also suggests that an individual's facial bilateral symmetry (Thornhill & Gangestad, 1999), clear skin (Fink & Penton-Voak, 2002), and straight and white teeth (Buss, 2006) are indicators of positive reproductive outcomes of mating with that individual. Evidence suggests that humans have mate preferences for all these features (see Buss, 2006; Fink & Penton-Voak, 2002; Thornhill & Gangestad, 1999; see also Lewis et al., in press, for review).

Despite the empirical contributions that an evolutionary approach has made toward our understanding of human standards of attractiveness, the complete suite of fitness-relevant cues present in the human phenotype remains largely unmapped, as does humans' psychology for responding to these cues. Our current understanding of these cues and our responses to them is largely limited to the face (e.g., Buss, 2006; Fink & Penton-Voak, 2002 ; Thornhill & Gangestad, 1999); women's waist and thighs (i.e., waist-to-hip ratio, see Lassek & Gaulin, 2019), men's muscularity (Frederick & Haselton, 2007), and composite or overall bodily indices that do not refer to a specific component of the morphological phenotype (e.g., symmetry, see Gangestad & Thornhill, 1998; Parsons, 1990). Furthermore, evolutionary research on attractiveness has been almost completely limited to static morphological cues. This nearly exclusive focus on static morphology neglects the fact that movements and other dynamic behaviors can convey important fitness-related information. Even more importantly, some of this information may be communicated

---

[1] Charles University, Prague, Czechia
[2] Boston University, MA, USA
[3] Discipline of Psychology, Murdoch University and Centre for Healthy Ageing, Health Futures Institute, Murdoch University
[4] Houston Baptist University, TX, USA
[5] University of Colorado—Colorado Springs, USA
[6] The University of Texas at Austin, USA

Corresponding Author:
Ayten Yesim Semchenko, Faculty of Science, Charles University, Prague, Czech Republic.
Email: aytenyesim@protonmail.com

exclusively through behavior. Selection should therefore have shaped psychological adaptations to attend to these behaviors.

Here, we (a) focused on a largely unmapped domain of the human phenotype—the female lumbar region, (b) identified both behavioral and morphological cues hypothesized to predict fitness-relevant outcomes, and (c) tested a priori hypotheses about the psychological systems that may have evolved to process these cues.

Lordosis Behavior

A combination of phylogenetic considerations and theoretical reasons suggests that women's behavioral phenotype in their lumbar region may contain at least one reproduction-related cue. Lordosis behavior[1] (Kuehn & Beach, 1963)—a contraction of the spinal muscles that results in an arching of the lower back—is a cue to receptivity among females of diverse mammalian taxa (Ågmo & Ellingsen, 2003; Beach, 1976; Flanagan-Cato, 2011; Gordon et al., 1977; Nance & Myatt, 1987; Owen et al., 2016; Pfaff & Sakuma, 1979; Pfaus et al., 2003; Rodriguez-Sierra et al., 1975). Historically, lordosis behavior has been regarded as a "reflex" (e.g., Pfaff & Sakuma, 1979) governed by hormones, pheromones, and the vomeronasal organ (Haga et al., 2010). In humans, the vomeronasal organ is vestigial (Zhang & Webb, 2003); hormones, while important, do not directly dictate sexual behavior; and there is a great deal of conscious regulation of mating behavior (Wunsch, 2017). Due to these differences between humans and non-primate mammalian species in which lordosis behavior has been observed, some research has suggested that lordosis may have been lost in the evolution of human sexual behavior (see Wunsch, 2017, for review).

However, there are both theoretical and empirical reasons to believe that lordosis behavior might exist in humans in a modified form that is not an obligate reflex, but rather a facultative behavior that can be selectively deployed. If lordosis was originally a cue to female sexual receptivity among our mammalian ancestors, then selection should have favored male psychological adaptations to experience mating attraction in response to this behavior. Such male responses would have created the selective conditions for the evolution of female adaptations to selectively engage in lordosis behavior to modulate male mating interest. Behavioral patterns observed in non-primate mammals provide evidence consistent with this proposed sequential evolution: (a) lordosis behavior among females as an indicator of sexual receptivity → (b) male adaptations to experience mating attraction in response to this behavior → (c) facultative female adaptations to modulate male mating interest by selectively engaging in lordosis. Indeed, in some non-primate mammals, lordosis behavior both is a cue to *receptivity* (i.e., a response to a male's attempt to initiate mating behavior) *and* can be used facultatively as a signal of *proceptivity* (i.e., a behavior initiated by a female to evoke male interest, Beach et al., 1976). For example, in some rodents, when females are attracted to a male who has not approached them, they reposition themselves in closer proximity to the male and then engage in lordosis behavior (Beach et al., 1976). Lordosis behavior has also been observed as a proceptive signal in primates (e.g., macaques, Hanby, 1976). The existence of lordosis behavior as a proceptive signal among these primates is particularly important, because, like humans, they exhibit a relative attenuation of the olfactory circuits and a reduced association between hormones and sexual activity (Wunsch, 2017). Collectively, these findings suggest that although lordosis might have initially evolved as a hormonally governed reflex, subsequent selection pressures may have shaped female adaptations to selectively use it as a proceptive signal. If so, this suggests the hypothesis that selection shaped male psychological mechanisms to attend to this behavior. We refer to this as the Lordosis Detection Hypothesis.

Lumbar Curvature

The lordosis detection hypothesis articulates one reason that selection should have favored male psychological adaptations to attend to women's lumbar region: to detect the behavioral cue of lordosis. However, women's lumbar region may also contain fitness-relevant *morphological* cues.

Wedging in women's lumbar vertebrae is critical for solving the adaptive problem of a forward-shifting center-of-mass during pregnancy. If ancestral women lacked the vertebral wedging necessary to shift their gravid center-of-mass back over the hips, they would have experienced as much as an 800% increase in hip torque during pregnancy (Whitcome et al., 2007). This torque on the hips subjects a woman's lower back musculature (e.g., erector spinae) to sustained contraction, which would have resulted in muscular fatigue, increased her susceptibility to debilitating back injury, and significantly impaired her ability to forage (see Whitcome et al., 2007). This would have risked malnutrition for the woman, her developing fetus, her other dependent offspring, and her mate. By contrast, ancestral women with sufficient vertebral wedging to shift the gravid center-of-mass back over the hips would have been significantly less likely to incur these fitness costs (Whitcome et al., 2007).

These fitness differences between women as a function of their vertebral wedging would have created selection pressures for the evolution of male psychological adaptations to attend to cues to this wedging. Men who preferentially mated with women capable of re-centering the gravid center-of-mass would have derived several fitness benefits. This would have included having a mate who was less susceptible to spinal injury during pregnancy, could forage more effectively and longer into pregnancy, and could sustain multiple pregnancies with reduced likelihood of injury. This means that a woman's lumbar vertebral wedging would have affected her fitness, the fitness of her offspring, and the fitness of her mate. These direct and indirect effects on her mate's fitness would have created selection pressures for the evolution of a male mate preference for, and attraction to, specific angles of lumbar curvature—clinically operationalized as the angle formed between the buttocks and the thoracic spine while in a neutral posture—because this is an externally observable, reliable cue to wedging in the lumbar vertebrae (e.g., see George et al., 2003).

Selection should have shaped a male preference for a "Goldilocks" or "sweet spot" degree of lumbar curvature. Both insufficient vertebral wedging and excessive vertebral wedging would have posed fitness problems. Whereas insufficient vertebral wedging (hypolordosis) would have been associated with the inability to shift the gravid center-of-mass back over the hips, excessive vertebral wedging (hyperlordosis) would have increased shearing forces on the spine, which can lead to debilitating injury such as herniated intervertebral disks (see Whitcome et al., 2007; White & Punjabi, 1990). Selection therefore should have favored a male preference for an angle of lumbar curvature that minimizes the net fitness threats posed by both hypolordosis and hyperlordosis. This intermediate angle would cue the ability to shift the gravid center-of-mass back over the hips without excessive spinal shearing, thereby avoiding the harmful outcomes associated with both hypo- and hyperlordosis. This leads to the hypothesis of a male preference for, and attraction to, an angle of lumbar curvature that is maximally distant from the countervailing fitness threats of hypolordosis and hyperlordosis,[2] which medical orthopedic literature indicates is approximately 45.5° (see Fernand & Fox, 1985). We refer to this hypothesis—that men have a mate preference for an angle of lumbar curvature of approximately 45.5°—as the Fetal Load Hypothesis (see Lewis et al., 2015; Lewis, Russell, et al., 2017).

Discriminating Between the Lordosis Detection and Fetal Load Hypotheses

The Lordosis Detection Hypothesis and Fetal Load Hypothesis might seem to be in competition with one another. Each articulates a rationale for why selection should have shaped psychological mechanisms in men's minds to attend to women's lumbar region. However, there is a crucial distinction: between behavioral cues and morphological cues. This distinction reveals that these two hypotheses are not in competition with one another but rather are complementary; they propose distinct, non-mutually exclusive features in male mating cognition.

The Lordosis Detection Hypothesis posits a mate preference for a dynamic, movement-based cue (back-arching behavior), whereas the Fetal Load Hypothesis proposes a preference for a morphological cue (a woman's lumbar curvature while in a neutral posture). *Both* hypotheses may be correct. If the Lordosis Detection Hypothesis is correct, then we should expect men to be attuned to the *movement* of increased back arching. And if the Fetal Load Hypothesis is correct, then we should expect men to be attracted to specific angles of lumbar curvature when women are in a neutral posture. Together, the Lordosis Detection Hypothesis and Fetal Load Hypothesis suggest that men's mating cognition might attend to *both* lordosis behavior and lumbar curvature.

Another way in which the hypotheses can be differentiated is by the emphasis they place on mating context. The Lordosis Detection Hypothesis proposes that mechanisms for responding to lordosis behavior should be sensitive to mating context: Because it is more pressing to identify cues to proceptivity in short-term mating contexts than long-term contexts, the Lordosis Detection Hypothesis suggests that men's attraction to back-arching behavior should be stronger in short-term than long-term contexts. By contrast, the Fetal Load Hypothesis does not predict context-dependent effects. To the extent that a central evolutionary function of both uncommitted and committed mating was to produce offspring, we should expect men to be attracted to cues to a woman's ability to successfully gestate in both short-term and long-term mating contexts.

Study 1: Testing the Fetal Load and Lordosis Detection Hypotheses

To test the Lordosis Detection Hypothesis and the Fetal Load Hypothesis, we used human modeling software to generate animated female characters that varied on two dimensions: their (a) neutral lumbar curvature and (b) degrees of back arching (i.e., lordosis behavior). This enabled us to concurrently test for independent effects of these two distinct cues, and thereby test the distinct predictions generated from the Fetal Load Hypothesis and Lordosis Detection Hypotheses.

Method

Ethics statement. This study was approved by the Charles University Human Research Ethics Committee (Approval number: 2018/008).

Participants. One hundred two heterosexual male participants (M_{age} = 28.36 years, SD_{age} = 11.43 years, age range = 18–68 years) completed the study. Participants were from Australia (62%), the United States (16%), the United Kingdom (9%), Canada (4%), and India (2%), as well as New Zealand, South Africa, Zimbabwe, China, Malaysia, UAE, Mexico, and Switzerland (all 1%). Participants were recruited through the Social Psychology Network, the subject pool at Murdoch University, personal contact from the researchers, on-campus advertising at Murdoch University, and snowball sampling. Student participants recruited via the Murdoch University subject pool received partial course credit for their participation.

Materials and procedure. As part of a larger study on attraction and mating, participants viewed the digital animated characters and completed the measures described below via

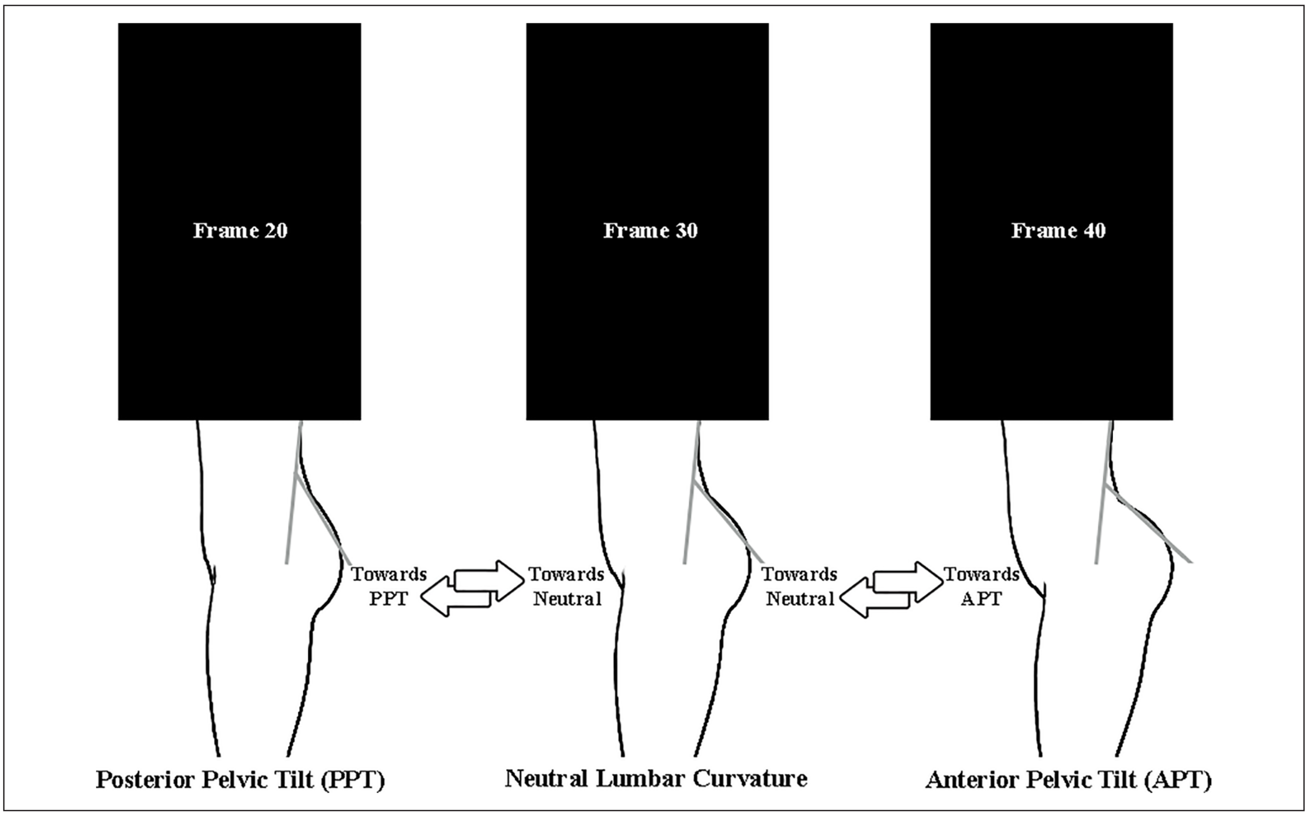


Figure 1. Static contour depiction of a dynamic study stimulus. Each stimulus was a video of an animated character moving between posterior and anterior pelvic tilt (i.e., engaging in back-arching behavior), passing through their neutral lumbar curvature. Some stimuli shared the exact same range of back-arching behavior (i.e., the range between posterior and anterior pelvic tilt) but differed in their neutral lumbar curvature; these stimuli enabled us to isolate the effect of lumbar curvature on perceived attractiveness. Other stimuli had identical angles of neutral lumbar curvature but differed in their back-arching behavior; these stimuli enabled us to isolate the effect of back-arching behavior on perceived attractiveness. *(CC-By-Attribution 4.0 International).*

an online survey hosted on the Qualtrics survey software platform.

Stimuli. We generated 17 animated virtual characters using a professional software tool for creating models of human figures and rendering animated digital content. The animated characters were displayed to participants in side profile and varied on two dimensions: their angle of neutral lumbar curvature (LC) and the degree of lower back arching that they exhibited in the animation (arching) (Figure 1; study stimuli publicly available at https://osf.io/sfcv6/?view_only=edb1bba510df41d69cbed69a0b3fa964). So that the stimuli were representative of the naturally occurring distributions of these variables, the characters ranged in neutral lumbar curvature from 29° to 66° (see Fernand & Fox, 1985) and in arching of the lower back from 8° to 28° (see Whitcome et al., 2007) (see Table S1 in the Supplemental Material for full details).

Attractiveness ratings. Each participant viewed and rated all characters. The characters were presented one by one, in random order, with order randomized anew for each participant. The participant was asked to rate each depicted female character's attractiveness (a) as a short-term mate and (b) as a long-term mate on a response scale ranging from 0 (*extremely unattractive*) to 10 (*extremely attractive*).

Results

Because each participant rated the attractiveness of all stimuli across both mating contexts, we fit study data to linear mixed-effect models that nested attractiveness ratings within each participant and incorporated a random intercept for each participant; this controlled for between-participant differences in baseline perceptions of attractiveness and enabled us to more powerfully isolate the effects of lumbar curvature and lordosis behavior on attractiveness. All analyses were conducted using the Statsmodels package (version 0.11.0; Seabold & Perktold, 2010) in Python (version 3.7.6; Van Rossum & Drake, 2009). Study data and analysis code are publicly available at https://osf.io/sfcv6/?view_only=edb1bba510df41d69cbed69a0b3fa964.

Distinct preferences for lumbar curvature and back arching? To tease apart the independent effects of neutral lumbar curvature and dynamic back arching and thereby disentangle the Fetal Load Hypothesis and the Lordosis Detection Hypothesis, we fit all study data to a linear mixed-effect model in which lumbar curvature[3] and back arching were simultaneously entered as fixed effect predictors of attractiveness ratings. We also incorporated the interactions (a) between mating context and lumbar curvature and (b) between mating context and back arching to test whether any effects of lumbar curvature or back arching were dependent on mating context.

If the Fetal Load Hypothesis is correct, then men should be most attracted to an angle of lumbar curvature that reflects the proposed biomechanical optimum for successful gestation: men's perceptions of women's attractiveness should increase as women's lumbar curvature approaches 45.5° (Prediction 1). Moreover, the Fetal Load Hypothesis suggests that this relationship between lumbar curvature and attractiveness should *not* be moderated by mating context (Prediction 2).

If the Lordosis Detection Hypothesis is correct, then men should be attracted to increased back arching (Prediction 3), but this effect should be more pronounced in short-term than in long-term mating contexts (Prediction 4).

Results aligned precisely with all four predictions. As predicted by the Fetal Load Hypothesis, men's attraction increased as the female characters' lumbar curvature approached the proposed biomechanical optimum, $b = -.051$, $SE = .007$, $p < .001$, 95% confidence interval [CI] [−.065, −.037], $\beta = -.14$, and this effect did *not* vary across mating contexts: there was no interaction between lumbar curvature and mating context, $b = -.011$, $SE = .010$, $p = .278$, 95% CI [−.030, .009], $\beta = -.02$ (Figure 2, top panel).

By contrast—and in precise alignment with the Lordosis Detection Hypothesis—the effect of back arching on attractiveness *was* context-dependent; back arching interacted with mating context to predict perceptions of attractiveness, $b = -.020$, $SE = .007$, $p = .006$, 95% CI [−.035, −.006], $\beta = -.04$. We therefore conducted subsequent analyses to identify the distinct effects of back arching in short-term and long-term contexts. The Lordosis Detection Hypothesis suggested that back arching should have a positive effect in short-term contexts and that this effect should be stronger than in long-term contexts.

This is exactly what we observed. Back arching positively influenced perceptions of attractiveness in short-term mating contexts, $b = .038$, $SE = .005$, $p < .001$, 95% CI [.028, .049], $\beta = .14$. In long-term mating, back arching was also positively associated with attractiveness, $b = .018$, $SE = .005$, $p < .001$, 95% CI [.008, .028], $\beta = .07$, but, as indicated by the significant interaction between mating context and back arching, the effect of back arching was stronger in context of short-term mating (Figure 3, top panel).

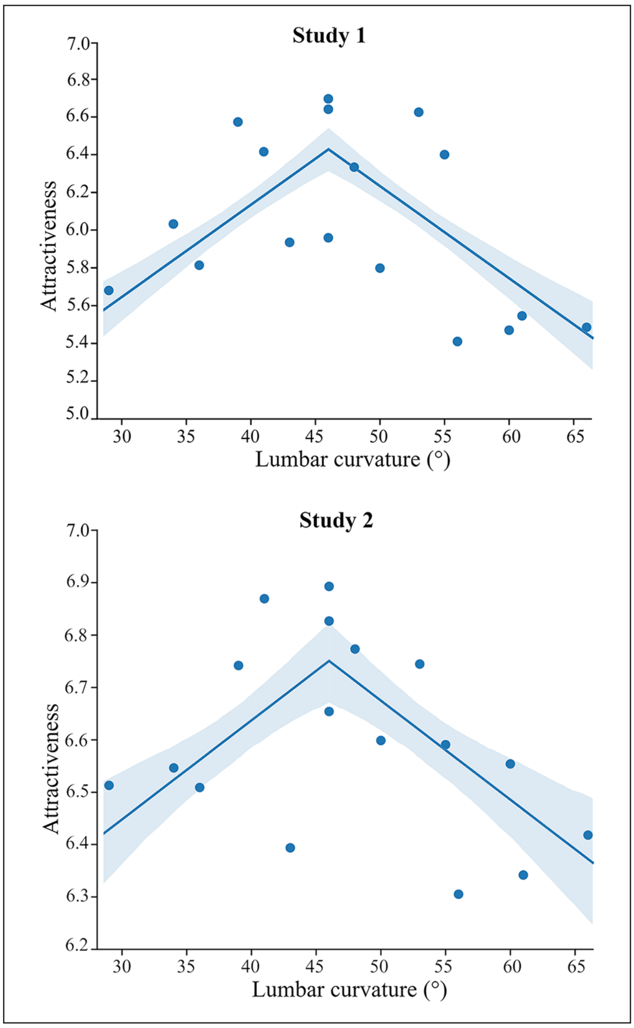


Figure 2. The relationship between lumbar curvature and attractiveness.

Note. The top panel displays the results from Study 1. The bottom panel displays the results from Study 2. Dots represent mean attractiveness ratings for each study stimulus. The regression line predicting these attractiveness ratings from the stimuli's lumbar curvature illustrates that attractiveness increased as lumbar curvature approached the proposed biomechanical optimum. Note that because the relationship between lumbar curvature and attractiveness was independent of mating context, each dot represents the average of the stimulus's short-term and long-term attractiveness ratings. Shaded region = 95% CI. (*CC-By-Attribution 4.0 International*)

Study 2: Replication and Extension

Given the reproducibility crisis in psychology (Open Science Collaboration, 2015) and the fact that Study 1 is the first to report the above findings, we conducted a second study with an independent sample to replicate these findings. In addition, we incorporated individuals' sociosexual orientation into study analyses. This enabled us to determine whether an orientation toward casual sexual relations moderated the observed effects.

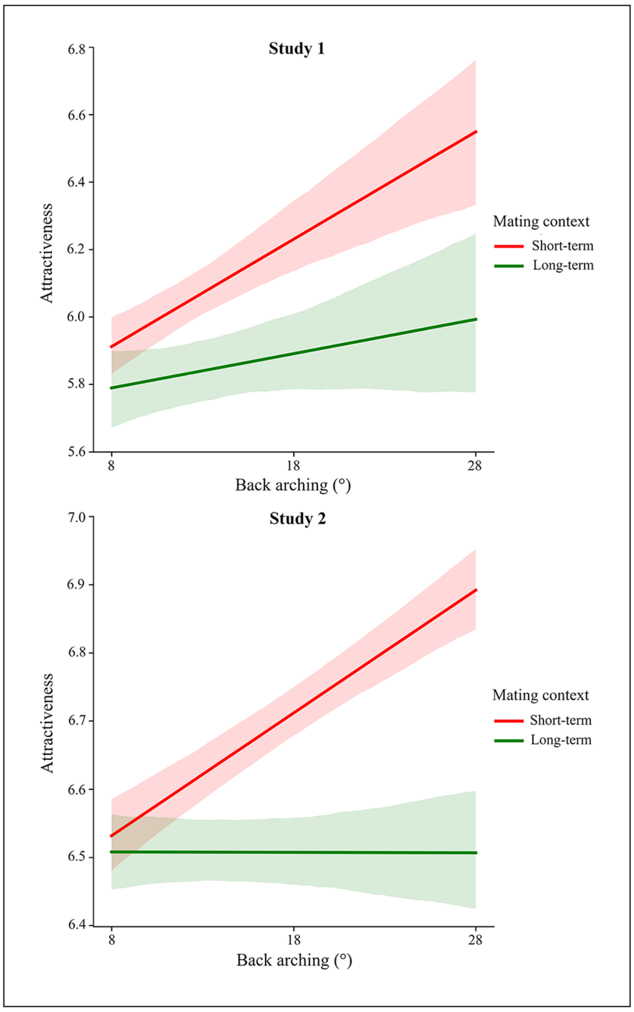


Figure 3. The mating context-dependent relationship between lordosis behavior and attractiveness.

Note. Consistent with the Lordosis Detection Hypothesis, men were more attracted to female back-arching behavior in short-term than long-term mating contexts in Study 1 (top panel), and in Study 2 (bottom panel) men were attracted to back-arching behavior in short-term, but not long-term, mating contexts. Shaded regions around regression lines = ±1 *SE*. (*CC-By-Attribution 4.0 International*)

Method

Ethics statement. The data for the replication study were collected under the same approved protocol as Study 1 and under protocol 21/09 approved by the Institutional Review Board of Charles University.

Participants. Two hundred thirty-one heterosexual male participants (M_{age} = 30.21 years, SD_{age} = 9.89 years, age range = 18–72 years) completed the study. Participants were from the United States (45%), India (21%), Australia (17%), Czech Republic (7%), Brazil (2%), and the United Kingdom (2%), as well as Vietnam, Sweden, China, Georgia, Zimbabwe, Kenya, Philippines, Japan, Italy, Poland, and Thailand (each <1%). Participants were recruited through the Social Psychology Network, MTurk, Facebook, the subject pool at Murdoch University, and a database of individuals who agreed to be contacted to participate in research studies. Student participants recruited via the Murdoch University subject pool received partial course credit for their participation.

Materials and procedure

Stimuli. The same digital animated characters used in Study 1 were used in Study 2.

Attractiveness ratings. As in Study 1, each participant viewed all characters one by one, in random order, and rated each character's attractiveness as a short-term mate and as a long-term mate on a scale from 0 (*extremely unattractive*) to 10 (*extremely attractive*).

Sociosexual orientation. We assessed participants' orientation toward casual sexual relations using the Sociosexual Orientation Inventory–Revised (SOI-R, Penke & Asendorpf, 2008), which measures a person's history of engaging in, attitudes about, and desire for uncommitted sex. The SOI-R consists of nine items such as "With how many different partners have you had sexual intercourse on one and only one occasion?," "Sex without love is OK.," and "How often do you experience sexual arousal when you are in contact with someone you are not in a committed romantic relationship with?" All items are scored on a nine-point scale and composited to form a single global SOI-R score. Higher scores correspond to a more unrestricted orientation (i.e., orientation toward casual sex).

Results

Replication analyses. First, to test the Study 1 findings for replication, we fit the Study 2 data to the exact same statistical models as those conducted in Study 1. Without exception, the four key findings replicated. In support of Prediction 1, men's perceptions of the female characters' attractiveness increased as the characters' lumbar curvature approached the proposed biomechanical optimum, $b = -.018$, $SE = .004$, $p < .001$, 95% CI [−.026, −.009], $\beta = -.05$, and, in support of Prediction 2, this effect did not depend on mating context: There was no interaction between lumbar curvature and mating context in predicting perceptions of attractiveness, $b = -.009$, $SE = .006$, $p = .153$, 95% CI [−.022, .003], $\beta = -.01$ (Figure 2, bottom panel). These findings replicated the key results in support of the Fetal Load Hypothesis.

In contrast to the context-*independent* effects of lumbar curvature predicted by the Fetal Load Hypothesis, the Lordosis Detection Hypothesis predicts context-*dependent* effects: It predicts that back arching will positively influence perceptions of attractiveness more in short-term than long-term mating contexts. Consistent with this hypothesis, the effect of back arching on men's perceptions of the female characters' attractiveness differed between short-term and long-term mating contexts, as indicated by the significant interaction between mating context and back arching in predicting perceptions of attractiveness, $b = -.017$, $SE = .005$, $p < .001$, 95% CI [−.026, −.008], $\beta = -.03$. We therefore conducted subsequent analyses to examine the effect of back arching on perceptions of attractiveness in short-term and long-term contexts separately. In alignment with the Lordosis Detection Hypothesis, and as in Study 1, back arching positively influenced men's perceptions of the female characters' attractiveness as a short-term mate, $b = .020$, $SE = .003$, $p < .001$, 95% CI [.014, .026], $\beta = .08$. By contrast, back arching did *not* positively influence men's perceptions of the female characters' attractiveness as a long-term mate, $b = .004$, $SE = .003$, $p = .246$, 95% CI [−.003, .010], $\beta = .01$ (Figure 3, bottom panel).

Extension: Men's sociosexual orientation. To test whether men's sociosexual orientation (i.e., orientation toward uncommitted sexual relations) moderated the effects of lumbar curvature and back arching, we conducted additional analyses that incorporated men's SOI-R scores. Specifically, we ran the same model as in Study 1 and the Study 2 replication analyses, but added two interactions: (a) between back arching, mating context, and men's SOI-R scores; and (b) between lumbar curvature, men's SOI-R scores, and mating context. The first interaction term enabled us to determine whether the context-dependent effect of back arching obtained among both sociosexually restricted and unrestricted men. The second interaction term enabled us to determine whether the effect of lumbar curvature varied as a function of men's sociosexual orientation, in interaction with mating context.

We did not have a priori predictions about these interactions. This is because one can reason about the possible interactions between mating context and sociosexual orientation in several different ways. One body of literature emphasizes that psychological adaptations are generally species- or sex-typical (e.g., see Tooby & Cosmides, 1990). This "universal" perspective would seem to suggest that, given the appropriate contextual inputs, most men could engage in either committed or uncommitted mating (e.g., Lewis et al., 2015; see also Al-Shawaf et al., 2018). On this view, we might not expect the effects of lumbar curvature and back arching to vary as a function of men's SOI-R scores; we might observe effects of context but not sociosexual orientation. A different perspective emphasizes sociosexual orientation as a stable individual difference variable (see Penke & Asendorpf, 2008; Simpson & Gangestad, 1991; see also Al-Shawaf, Lewis, Alley, & Buss, 2015; Al-Shawaf, Lewis, & Buss, 2015; Lewis, Al-Shawaf, et al., 2012). On this view, we might expect restricted and unrestricted men to respond differently to the cues of back arching and lumbar curvature. Currently, there are insufficient empirical data to adjudicate between these distinct views.[4] Consequently, we considered analyses involving sociosexual orientation to be exploratory.

We used a backward stepwise approach (removal criterion: $p > .05$) in which we began with a model incorporating the two, three-way interactions described above, along with all lower-order constituent terms. This resulted in a sequence of analyses that examined both three-way interactions, all two-way interactions, and the fixed effect (i.e., the "main effect") of sociosexual orientation. All analysis code is publicly available at https://osf.io/sfcv6/?view_only=edb1bba510df41d69cbed69a0b3fa964. Neither of the three-way interactions were significant (both *p*s > .39). This indicated, for example, that the context-dependent effect of back arching did not depend on men's sociosexual orientation. The fixed effect of lumbar curvature and the two-way interaction between back arching and mating context remained statistically significant in the final model; that is, the context-dependent effect of back arching and the context-independent effect of lumbar curvature were not moderated by men's SOI-R scores and were robust to their inclusion in study analyses.

The only significant terms involving men's sociosexual orientation that emerged in the final model were the fixed (i.e., "main") effect of men's SOI-R scores, $b = .528$, $SE = .063$, $p < .001$, 95% CI [.406, .651], $\beta = .38$—which indicated that unrestricted men perceived the female characters to be more attractive, on average, than did restricted men—and the interaction between men's SOI-R scores and back arching, $b = -.003$, $SE = .001$, $p = .023$, 95% CI [−.006, .000], $\beta = -.02$. To examine the interaction between men's SOI-R scores and back arching, we conducted simple slopes analyses. The interaction reflected that, averaged across mating contexts, the coefficient for back arching was larger for restricted men ($M - 1SD_{\mathrm{SOI}}$: $b = .017$, $SE = .003$, $p < .001$) than for unrestricted men ($M + 1SD_{\mathrm{SOI}}$: $b = .006$, $SE = .003$, $p = .07$). Ultimately, however, the effects observed in Study 1 and in the Study 2 replication analyses emerged among *both* restricted and unrestricted men: restricted and unrestricted men alike were attracted to back arching in short-term mating contexts ($M + 1SD_{\mathrm{SOI}}$: $b = .013$, $SE = .004$, $p < .001$; $M - 1SD_{\mathrm{SOI}}$: $b = .027$, $SE = .004$, $p < .001$) but not long-term mating contexts ($M + 1SD_{\mathrm{SOI}}$: $b = .000$, $SE = .004$, $p = .912$; $M - 1SD_{\mathrm{SOI}}$: $b = .007$, $SE = .005$, $p = .136$).

General Discussion

The current studies report and replicate several previously unknown findings. First, these studies are the first to demonstrate *independent* effects of the dynamic cue of back arching and the morphological cue of lumbar curvature. These findings support both the Fetal Load Hypothesis and the Lordosis Detection Hypothesis.

Second, these studies are the first to test whether mating context moderates the effects of lumbar curvature and back arching on perceptions of attractiveness. Consistent with the Fetal Load Hypothesis, we found that the effects of lumbar curvature were independent of mating context: men were attracted to the proposed biomechanically optimal angle of lumbar curvature regardless of mating context. By contrast, and consistent with the Lordosis Detection Hypothesis, the effects of back-arching behavior depended on mating context: Men were more attracted to back arching in short-term than long-term mating contexts. The two studies found nearly identical results, highlighting their replicability, which we discuss in greater detail below.

Mating Context and Sociosexual Orientation

Men's sociosexual orientation did not moderate any of the key effects observed in Study 1 or the Study 2 replication analyses. For example, restricted and unrestricted men alike were attracted to back arching in short-term but not long-term mating contexts. This may be most consistent with the "universal" perspective described above: Men may be able to shift into either a short-term or long-term mating mindset in alignment with the present mating context, regardless of their sociosexual orientation. The fact that sociosexual orientation exerted relatively little influence *when mating context was incorporated into study design* raises several important questions for future research.

First, if any given individual is capable of engaging in either committed or uncommitted mating in alignment with the present mating context (e.g., see Lewis et al., 2015), then by what processes do individual differences in sociosexuality predict important mating-related outcomes? We suspect that a key to the answer lies in differences in the *selection, evocation*, and *manipulation* (Buss, 1987) of mating environments by restricted and unrestricted individuals. Unrestricted individuals may preferentially select social contexts that facilitate short-term mating. They may also evoke different responses from others in the social environment (e.g., see Plomin et al., 1977; Scarr & McCartney, 1983). For example, because sociosexuality is positively associated with physical attractiveness (e.g., Al-Shawaf, Lewis, & Buss, 2015) and people value physical attractiveness in a potential mate (e.g., see Buss, 1989)—especially when seeking a short-term mate (e.g., Li & Kenrick, 2006)—sociosexually unrestricted individuals, more so than restricted individuals, may evoke an environment in which others are interested in them as short-term partners. Finally, unrestricted individuals may be more likely than restricted individuals to manipulate the mating environment so that it opens up opportunities for uncommitted sexual relations (e.g., see Lewis, Easton, et al., 2012).

In the current research, we had all men evaluate the study stimuli in both short-term and long-term mating contexts. This design inherently controls for any processes by which restricted and unrestricted men might find themselves in different mating contexts. This design—namely, making the mating context explicit—may reduce variability in participants' interpretation of context, which has several advantages. For example, if research instructs participants to consider their "ideal mate" without specifying the mating context (i.e., short-term vs. long-term), participants may think about their preferred context: Restricted individuals may consider their ideal *long-term* mate, whereas unrestricted individuals may consider their ideal *short-term* mate. If so, it would not be clear whether any differences between restricted and unrestricted participants' preferences should be attributed to differences in sociosexual orientation or differences in mating context.

A related advantage of specifying mating context is that it enables clearer tests of the overarching hypothesis of universal psychological adaptations (e.g., Tooby & Cosmides, 1990). A core hypothesized feature of universal evolved psychological mechanisms is that they are sensitive to contextual inputs and change their outputs (e.g., mate preferences) as a function of context (DeKay & Buss, 1992; see also Al-Shawaf et al., 2019, 2021; Goetz et al., 2012; Lewis, 2015; Lewis, Al-Shawaf, et al., 2017; Lewis & Buss, 2022; Lewis et al., 2021; Lukaszewski et al., 2020). On this view, we should expect to observe variability in people's preferences if they interpret ambiguous contextual information differently. Conversely, when mating context is not left open to interpretation (e.g., it is not so ambiguous that restricted and unrestricted participants can interpret it in line with their preferred mating context), we might expect to observe more similar psychological responses between restricted and unrestricted individuals. This appears to be consistent with what we observed in the current study.

The current finding—that sociosexual orientation exerted relatively little influence when mating context was explicitly incorporated into study design—together with the fact that sociosexual orientation does predict mating-related outcomes in the real world (e.g., see Simpson & Gangestad, 1991), suggests to us that intrinsic links between sociosexuality and social processes, such as the differential selection, evocation, and manipulation of mating environments by restricted and unrestricted individuals, may be key to understanding when individual differences in sociosexuality are (not) likely to predict important mating outcomes.

We also note that it may be prudent to treat the results involving sociosexual orientation more tentatively than the core results (i.e., the context-independent effect of lumbar curvature and the context-dependent effect of back arching). With respect to the effects of lumbar curvature and back arching, Study 1 effectively served as a preregistration for Study 2; in the Study 2 replication analyses, we ran the exact same statistical models as in Study 1, and these confirmatory analyses in Study 2 reproduced, without exception, all key findings involving lumbar curvature and back arching. However, because Study 2 was the first involving analyses that incorporated men's sociosexual orientation, Study 1 did not serve the same preregistration function for these analyses, and we cannot directly address the reproducibility of the results involving men's sociosexual orientation.

Under any condition, more research is needed in this area, as there is limited work concurrently investigating the effects of mating context and sociosexual orientation. Research on mate preferences has tended to focus on either the effects of mating context *or* sociosexual orientation, but not both, and not the interaction between them. Ultimately, more empirical data are needed to better resolve the relationship between mating context and sociosexual orientation, as well as their interaction.

Display of Gluteofemoral Fat Reserves: An Alternative Explanation?

In the current studies, we generated a priori predictions based on the Lordosis Detection Hypothesis and found evidence consistent with those predictions. The broad observation of male attraction to female back-arching behavior, however, is also consistent with another hypothesis: The Gluteofemoral Fat Display Hypothesis. Here, we describe this hypothesis—but also illustrate why it cannot account for study findings.

A possible alternative function of back-arching behavior could be to display gluteofemoral fat reserves; evidence suggests that men are attracted to such reserves because they are important to infant brain development (see Lassek & Gaulin, 2019). However, this hypothesis does not generate a key prediction about the context-dependent effects of back-arching behavior that (1) the Lordosis Detection Hypothesis *does* generate and (2) was supported in both the original study and the replication study. Specifically, a central prediction of the Lordosis Detection Hypothesis is that back arching will be more attractive *in short-term mating contexts* than in long-term mating contexts. The Gluteofemoral Fat Display Hypothesis does not generate this prediction. Rather, the Gluteofemoral Fat Display Hypothesis appears to either predict a context-independent effect—gluteofemoral fat reserves should be perceived as attractive in both short-term and long-term mates—or a context-dependent effect *in the opposite direction*: Because gluteofemoral fat reserves are a cue to parity and future reproductive potential—which are more important in the context of long-term mating—the Gluteofemoral Fat Display Hypothesis might predict that displaying these reserves should increase women's attractiveness *more in the context of long-term mating*. Either way, the Gluteofemoral Fat Display Hypothesis does not generate the prediction that back arching should increase attraction more in short-term than long-term contexts.

This means that tests of the context-dependent effect of lordosis behavior are a clear adjudicator between the Lordosis Detection Hypothesis and the Gluteofemoral Fat Display Hypothesis. In both the original study and the replication study, we found that back-arching behavior increased women's attractiveness more in the context of short-term than long-term mating. These findings are precisely those expected under the Lordosis Detection Hypothesis, and, at a minimum, cannot be readily accounted for by the Gluteofemoral Fat Display Hypothesis (and may directly contradict it).

The Operationalization of the "Optimum" Lumbar Curvature

We operationalized the Fetal Load Hypothesis by predicting that men will be most attracted to a lumbar curvature angle of 45.5°. This operationalization is likely to be imperfect (e.g., it rests on the assumption that the fitness costs of hypolordosis and hyperlordosis are approximately equal), but it has several key advantages relative to alternatives.

First, we arrived at this operationalization a priori rather than post hoc. After we generated the Fetal Load Hypothesis, we operationalized the optimum by using a two-step approach of first identifying, in the medical orthopedic literature, the values associated with the medical problems of hypolordosis and hyperlordosis, and then computing the value that is maximally distant from those countervailing adaptive problems. This process highlights another advantage of this operationalization: It is based on clearly outlined adaptive problems—We operationalized the optimum lumbar curvature as the point maximally distant from the medical problems of hypolordosis and hyperlordosis.

An alternative way to operationalize the Fetal Load Hypothesis would be to simply predict a quadratic (i.e., inverted U) relationship between lumbar curvature and attractiveness. However, there are two problems with this. First, it would be easy—*too* easy—to find support for this general prediction: the observation of *any* quadratic relationship would support it. This would not be scientifically prudent, as it could lead to inferring support for the Fetal Load Hypothesis if the inflection point of the curve was at 39°, 57°, or *any other value*. That is too many degrees of inferential freedom and represents a much less rigorous test of the hypothesis than the approach we used of operationalizing the hypothesized optimum in advance and testing men's preferences against this pre-specified value.

A second problem with this generic quadratic approach is that it has an element of circularity. The Fetal Load Hypothesis generates that prediction that the (a) values that men prefer will align with (b) a fitness optimum. To test that hypothesis, the *values that men prefer* cannot feed into the operationalization of *the optimum*; the optimum must be operationalized independently of any known preferred values. Otherwise, the logic becomes circular: If the hypothesis is that men's preferred values will correspond to the optimum, and then the operationalization of the optimum is based on the values preferred by men, the argument is little more than a tautology.

In sum, despite whatever limitations the 45.5° operationalization might have, it has several key advantages. The quadratic approach is potentially circular in logic and offers too many researcher degrees of freedom with respect to inferring support for the hypothesis. By contrast, the 45.5° operationalization reflects an a priori derivation of optimum and is based on values identified in advance as being linked to specific adaptive problems.

Dynamic Stimuli

The current studies point to the importance of moving beyond static stimuli in evolutionary research on attractiveness. The exclusive use of static stimuli neglects the fact that selection could have shaped mate preferences for *movements* that convey important fitness-related information. Using dynamic stimuli enables researchers to (a) test for these movement-based preferences; (b) prevent the misattribution of preferences for dynamic cues as preferences for static cues, and vice versa; and (c) test the possibility that selection shaped preferences for both static and dynamic cues in the same feature or region of the phenotype. Without stimuli that are designed to test hypotheses about both classes of phenotypic cues, certain discoveries will remain inaccessible. In the studies reported here, we identified distinct predictions generated by the Fetal Load Hypothesis and the Lordosis Detection Hypothesis, designed stimuli to test these predictions, and discovered previously unknown features of mating cognition.

Limitations and Future Directions

Despite the contributions of the studies reported here, the current research represents only an initial foray into lordosis in humans. The current studies focused on psychological adaptations to attend to the back-arching movement, but do not directly demonstrate lordosis behavior. An important task for future work will be to more clearly establish the existence of human lordosis behavior.

For now, we note that there are convergent lines of evidence suggesting that lordosis behavior likely does exist in humans—or, at the very minimum, that the assumption that it does *not* exist should be carefully reconsidered. The first line of evidence comes from vernacular dance, a "form of nonverbal communication" (Pérez, 2016, p. 16). One such vernacular dance that has recently entered common vocabulary is twerking, which refers to a "a sexually provocative dance or dance move involving thrusting movements of the bottom and hips" (Oxford University Press, n.d.). Formally, the "thrusting movements" refer to the anterior-posterior tilting of the pelvis—a defining feature of lordosis behavior. Although "twerking" might be new as a household term, its etymology dates back more than 200 years and the behavior is far from new—it was documented across diverse cultures long before it became a social media phenomenon. Indeed, the lordotic movement "unite[s] a dizzying array" (Pérez, 2016, p. 22) of dances from myriad cultures across geographic regions, religious backgrounds, biological ecologies, linguistic groups, and cultural values, attitudes, morals, and rituals (see Figure S1 in the Supplemental Material for a cross-cultural sampling of dances from Africa, Asia, Europe, Oceania, and North and South America that incorporate the lordotic movement).

A second line of evidence that points toward the existence of human lordosis behavior comes from unpublished work by Senveli (2017). Senveli took two photographs of women—one while a female research assistant was in the room with the woman, and another after a professional male model entered. A comparison of the women's photographs before and after the arrival of the male model indicated that, on average, women adjusted their posture to have a more acute angle between the thoracic spine and sacrum—that is, they engaged in back arching—when the model entered the room.

The evidence remains preliminary, but, taken together, men's attraction to the lordotic movement observed in the current study, Senveli's (2017) tentative experimental results, and the omnipresence of the lordotic movement in dances from distant and independent cultures (see Figure S1 in the Supplemental Material) suggest that, at a minimum, researchers should reconsider the assertion that lordosis behavior does not exist in humans.

We encourage future research to more firmly establish the existence of human lordosis behavior and to identify what cultural inputs during ontogeny influence the development of lordosis behavior and the meaning assigned to it, what cultural values influence perceptions and moral judgments of it, what norms regulate the contexts in which the lordotic movement is condoned or deemed taboo, and what shared and distinct meanings it has across cultures. The current manuscript has focused on one potential communicative function of human lordosis behavior, but a key goal of future research should be to identify other meanings, symbols, or signals (not necessarily related to proceptivity) that human lordosis behavior might be used to communicate.

Toward the goal of mapping the semantics of this behavior in different contexts and cultures, ethnographic accounts may be useful in demonstrating the existence of human lordosis behavior while simultaneously illuminating the diverse meanings that the behavior may have. For example, in some cultures, the lordotic movement may be embedded in specific forms of dance, and engaging in those dances may be a cultural ritual. Under such cultural conditions, the meaning of lordosis behavior could range from merely fulfilling one's cultural duties without any romantic or sexual intent to actively signaling sexual interest. Brazil's Candomblé religion illustrates this well. In Candomblé, the lordotic movement appears among the nonverbal courtship signals of the gods. The orixá (deity) Oyá de esteira, whose name refers to a bedroll that she carries with her for the purposes of opportunistic mating (Pérez, 2016), "performs the 'plate-breaking' dance: hands on hips, buttocks prominently extended" (Gleason, 1992, p. 290). In Candomblé, dance is a religious obligation (Pérez, 2016). Consequently, when a Candomblé practitioner performs the plate-breaking dance, which captures the "libidinal heat" of this "erotically charged" deity through the lordotic movement (Cartwright, 2013, p. 165), this movement may have multiple possible meanings and may induce culturally specific responses. This is just one example of the many ways in which the intent of the individual engaging in the lordotic movement as well as the perceived meaning of the behavior may vary as a function of cultural context and other situational variables.

An important avenue for future research will be to identify the distinct meanings of lordosis behavior across cultures, between individuals within a given culture, and within individuals across different situations. Although some women in some contexts might use the lordotic movement to signal mating interest, it would be logically unsound to infer that the lordotic movement always signals mating interest. Drawing conclusions about all instances from some instances is always unwarranted, and the inference "If a woman is engaging in lordosis behavior, it means that she is sexually interested" would be entirely unjustified. In other words, and for the avoidance of doubt, the notion that the lordotic movement might be used by some women in some contexts as a signal of proceptivity in no way suggests that a given woman exhibiting back-arching behavior in a particular circumstance is inviting a sexual advance. We caution against such strong and unjustified inferences; there are myriad reasons unrelated to mating why women might engage in the lordotic movement. The current studies report data consistent with the hypothesis that signaling proceptivity could be one of the reasons that a woman might engage in the lordotic movement, but future work is needed to further test this hypothesis, to more firmly establish the existence of human lordosis behavior, and to identify the many distinct meanings and functions this behavior could have in humans.

Conclusion

The current studies provide evidence of several previously undocumented features of men's mating psychology: Men's minds (a) track both the morphological cue of women's lumbar curvature *and* the dynamic cue of lordosis behavior, and (b) regulate mating attraction in response to these cues differentially as a function of mating context—in precise adaptive alignment with the context-dependent relevance of the cues. These findings, all predicted a priori on the basis of evolutionary reasoning, underscore the value of an evolutionary approach for making new predictions and discoveries about human mating psychology.

We hope that the current work also contributes to important directions for future research. In particular, we hope that the current studies inspire renewed focus on an understudied class of cues in the human phenotype: dynamic cues. Little work has been dedicated to charting these important components of the human phenotype or the psychological systems that attend to them. We hope that the current study makes a modest contribution toward the goal of mapping these cues and the cognitive systems that may have evolved to process them.

We also hope that the current studies motivate research investigating the interactions between humans' universal evolved psychological mechanisms and the specific cultural inputs to which people are exposed during their development and lifespan. Ultimately, such an integrated approach will be necessary for understanding the meaning and perception of human behavior, including similarities and differences in these meanings and perceptions across people, contexts, and cultures.

Authors' Note

A.Y.S. contributed to data collection and manuscript preparation, and prepared, analyzed, and visualized all data. Z.S. contributed to project conceptualization and manuscript drafting. J.F. contributed to study design, generated the study materials, and assisted with manuscript preparation. D.M.G.L. elaborated the hypotheses, designed the studies, and wrote the manuscript. L.A-S., M.R.L.F, and D.M.B. contributed to manuscript revising and editing. V.F. contributed to data collection and manuscript reviewing.

Declaration of Conflicting Interests

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

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This research was supported in part by grant 1742218 from Charles University Grant Agency (GAUK) to A. Y. Semchenko.

ORCID iDs

Vojtěch Fiala https://orcid.org/0000-0002-0148-5092
David M. G. Lewis https://orcid.org/0000-0002-8267-5727

Supplemental Material

Supplemental material is available online with this article.

Notes

1. Two disparate bodies of literature use the term "lordosis" in different ways. In the medical orthopedic literature, the term refers to the angle formed between the buttocks and thoracic spine while the individual is in a static posture. In the ethological literature, it refers to the dynamic *behavior* of contracting muscles in the lower spine (e.g., longissimus) such that the lower back becomes more concave. We disambiguate these concepts by referring to the static cue as *lumbar curvature* and the dynamic cue as *lordosis behavior*.
2. We note that this working operationalization assumes that the fitness costs of hypolordosis and hyperlordosis are equal. The precise fitness costs of these two adaptive problems are not known, but this operationalization is reasonable to the extent that they are similar.
3. More precisely, the variable that was entered was the *deviation* of the female characters' lumbar curvature from 45.5°; the fetal load hypothesis specifies that these deviations from the proposed

biomechanical optimum should be the construct of interest, not lumbar curvature per se (see Prediction 1).

4. We note that these distinct perspectives are not incompatible with one another. For example, there are multiple pathways by which universal psychological adaptations can produce stable individual differences (e.g., Tooby & Cosmides, 1990; see also Lewis et al., 2018, 2020).

References

Ågmo, A., & Ellingsen, E. (2003). Relevance of non-human animal studies to the understanding of human sexuality. *Scandinavian Journal of Psychology*, *44*(3), 293–301.

Al-Shawaf, L., Lewis, D. M. G., Alley, T. R., & Buss, D. M. (2015). Mating strategy, disgust, and food neophobia. *Appetite*, *85*, 30–35.

Al-Shawaf, L., Lewis, D. M. G., Barbaro, N., & Wehbe, Y. S. (2021). The products of evolution: Conceptual distinctions, evidentiary criteria, and empirical examples. In T. K. Shackelford (Ed.), *SAGE handbook of evolutionary psychology* (pp. 70–95). SAGE.

Al-Shawaf, L., Lewis, D. M. G., & Buss, D. M. (2015). Disgust and mating strategy. *Evolution and Human Behavior*, *36*(3), 199–205.

Al-Shawaf, L., Lewis, D. M. G., Ghossainy, M. E., & Buss, D. M. (2018). Experimentally inducing disgust reduces desire for short-term mating. *Evolutionary Psychological Science*, *5*, 267–275.

Al-Shawaf, L., Lewis, D. M. G., Wehbe, Y., & Buss, D. M. (2019). Context, environment, and learning in evolutionary psychology. In T. K. Shackelford & V. A. Weekes-Shackelford (Eds.), *Encyclopedia of evolutionary psychological science*. Springer.

Beach, F. A. (1976). Sexual attractivity, proceptivity, and receptivity in female mammals. *Hormones and Behavior*, *7*(1), 105–138.

Beach, F. A., Stern, B., Carmichael, M., & Ranson, E. (1976). Comparisons of sexual receptivity and proceptivity in female hamsters. *Behavioral Biology*, *18*(4), 473–487.

Birkhead, T. R., & Fletcher, F. (1995). Male phenotype and ejaculate quality in the zebra finch *Taeniopygia guttata. Proceedings of the Royal Society B*, *262*, 329–334.

Buss, D. M. (1987). Selection, evocation, and manipulation. *Journal of Personality and Social Psychology*, *53*(6), 1214–1221.

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, *12*(1), 1–49.

Buss, D. M. (2006). Strategies of human mating. *Psychological Topics*, *15*(2), 239–260.

Buss, D. M. (2021). *When men behave badly: The hidden roots of sexual deception, harassment, and assault*. Little Brown.

Cartwright, K. (2013). *Sacral grooves, limbo gateways: Travels in deep southern time, circum-Caribbean space, Afro-creole authority*. University of Georgia Press.

DeKay, W. T., & Buss, D. M. (1992). Human nature, individual differences, and the importance of context: Perspectives from evolutionary psychology. *Current Directions in Psychological Science*, *1*(6), 184–189.

Fernand, R., & Fox, D. E. (1985). Evaluation of lumbar lordosis: A prospective and retrospective study. *Spine*, *10*, 799–803.

Fink, B., & Penton-Voak, I. (2002). Evolutionary psychology of facial attractiveness. *Current Directions in Psychological Science*, *11*(5).

Flanagan-Cato, L. M. (2011). Sex differences in the neural circuit that mediates female sexual receptivity. *Frontiers in Neuroendocrinology*, *32*(2), 124–136.

Frederick, D. A., & Haselton, M. G. (2007). Why is muscularity sex? Tests of the fitness indicator hypothesis. *Personality and Social Psychology Bulletin*, *33*(8), 167–183.

Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings of the Royal Society B*, *265*, 927–933.

George, S. Z., Hicks, G. E., Nevitt, M. A., Cauley, J. A., & Vogt, M. T. (2003). The relationship between lumbar lordosis and radiologic variables and lumbar lordosis and clinical variables in elderly, African-American women. *Journal of Spinal Disorders and Techniques*, *16*, 200–206.

Gleason, J. (1992). *Oya: In praise of an African goddess*. Harper Collins.

Goetz, C. D., Easton, J. A., Lewis, D. M., & Buss, D. M. (2012). Sexual exploitability: Observable cues and their link to sexual attraction. *Evolution and Human Behavior*, *33*(4), 417–426.

Gordon, J. H., Nance, D. M., Wallis, C. J., & Gorski, R. A. (1977). Effects of estrogen on dopamine turnover, glutamic acid decarboxylase activity and lordosis behavior in septal lesioned female rats. *Brain Research Bulletin*, *2*(5), 341–346.

Haga, S., Hattori, T., Sato, T., Sato, K., Matsuda, S., Kobayakawa, R., & Touhara, K. (2010). The male mouse pheromone ESP1 enhances female sexual receptive behaviour through a specific vomeronasal receptor. *Nature*, *466*(7302), 118–122.

Hanby, J. P. (1976). Sociosexual development in primates. In P. Bateson (Ed.), *Perspectives in Ethology* (Vol. 2, pp. 1–67). Springer.

Haselton, M. G. (2003). The sexual overperception bias: Evidence of a systematic bias in men from a survey of naturally occurring events. *Journal of Research in Personality*, *37*, 34–47.

Haselton, M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology*, *78*(1), 81–91.

Kuehn, R. E., & Beach, F. A. (1963). Quantitative measurement of sexual receptivity in female rats 1. *Behaviour*, *21*(3–4), 282–299.

Lassek, W. D., & Gaulin, S. J. (2019). Evidence supporting nubility and reproductive value as the key to human female physical attractiveness. *Evolution and Human Behavior*, *40*(5), 408–419.

Lewis, D. M. G. (2015). Evolved individual differences: Advancing a condition-dependent model of personality. *Personality and Individual Differences*, *84*, 63–72.

Lewis, D. M. G., Al-Shawaf, L., & Buss, D. M. (2020). Evolutionary personality psychology. In P. Corr & G. Matthews (Eds.), *The Cambridge handbook of personality psychology* (2nd ed., pp. 223–234). Cambridge University Press.

Lewis, D. M. G., Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (2012). Friends with benefits II: Mating activation in opposite-sex friendships as a function of sociosexual orientation and relationship status. *Personality and Individual Differences*, *53*, 622–628.

Lewis, D. M. G., Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (2017). Evolutionary psychology: A how-to guide. *American Psychologist*, *72*(4), 353–373.

Lewis, D. M. G., Al-Shawaf, L., Janiak, M., & Akunebu, S. (2018). Integrating molecular genetics and evolutionary psychology: Sexual jealousy and the androgen receptor (AR) gene. *Personality and Individual Differences*, *120*, 276–282.

Lewis, D. M. G., Al-Shawaf, L., Thompson, M. B., & Buss, D. M. (2021). Evolved psychological mechanisms. In T. K. Shackelford (Ed.), *The SAGE handbook of evolutionary psychology* (pp. 96–119). SAGE.

Lewis, D. M. G., Al-Shawaf, L., & Yilmaz, C. (2015). The openness-calibration hypothesis. *Personality and Individual Differences*, *81*, 53–60.

Lewis, D. M. G., & Buss, D. M. (2022). Appearance enhancement: A cue-based approach. *Archives of Sexual Behavior*, *51*, 73–77.

Lewis, D. M. G., Easton, J. A., Goetz, C. D., & Buss, D. M. (2012). Exploitative male mating strategies: Personality, mating orientation, and relationship status. *Personality and Individual Differences*, *52*, 139–143.

Lewis, D. M. G., Evans, K. C., & Al-Shawaf, L. (in press). The logic of physical attractiveness: What people find attractive, when, and why. In D. M. Buss (Ed.), *Handbook of human mating*. Oxford University Press.

Lewis, D. M. G., Russell, E. M., Al-Shawaf, L., & Buss, D. M. (2015). Lumbar curvature: A previously undiscovered standard of attractiveness. *Evolution and Human Behavior*, *36*(5), 345–350.

Lewis, D. M. G., Russell, E. M., Al-Shawaf, L., Ta, V., Senveli, Z., Ickes, W., & Buss, D. M. (2017). Why women wear high heels: Evolution, lumbar curvature, and attractiveness. *Frontiers in Psychology*, *8*, Article 1875.

Li, N. P., & Kenrick, D. T. (2006). Sex similarities and differences in preferences for short-term mates: What, whether, and why. *Journal of Personality and Social Psychology*, *90*(3), 468–489.

Lukaszewski, A. W., Lewis, D. M. G., Durkee, P. K., Sell, A. N., Sznycer, D., & Buss, D. M. (2020). An adaptationist framework for personality science. *European Journal of Personality*, *34*, 1151–1174.

Nance, D. M., & Myatt, G. A. (1987). Female sexual behavior in the golden hamster following kainic acid lesions in the lateral septal area. *Brain Research Bulletin*, *19*(6), 751–754.

Norris, K. (1993). Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature*, *362*, 537–539.

Open Science Collaboration. (2015). Estimating the reproducibility of psychological science. *Science*, *349*(6251): aac4716.

Owen, M. A., Swaisgood, R. R., Zhou, X., & Blumstein, D. T. (2016). Signalling behaviour is influenced by transient social context in a spontaneously ovulating mammal. *Animal Behaviour*, *111*, 157–165.

Oxford University Press. (n.d.). Twerk. In *Oxford English dictionary*. Oxford University Press. https://www.oed.com/view/Entry/35043440?rskey=yJSpEq&result=1#eid

Parsons, P. A. (1990). Fluctuating asymmetry: An epigenetic measure of stress. *Biological Reviews*, *65*(2), 131–145.

Penke, L., & Asendorpf, J. B. (2008). Beyond global sociosexual orientations: A more differentiated look at sociosexuality and its effects on courtship and romantic relationships. *Journal of Personality and Social Psychology*, *95*(6), 1113–1135.

Pérez, E. (2016). The ontology of twerk: From "sexy" Black movement style to Afro-Diasporic sacred dance. *African and Black Diaspora*, *9*(1), 16–31.

Perilloux, C., Easton, J. A., & Buss, D. M. (2012). The misperception of sexual interest. *Psychological Science*, *23*, 146–151.

Petrie, M. (1994). Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, *371*, 598–599.

Pfaff, D. W., & Sakuma, Y. (1979). Facilitation of the lordosis reflex of female rats from the ventromedial nucleus of the hypothalamus. *Journal of Physiology*, *288*(1), 189–202.

Pfaus, J. G., Kippin, T. E., & Coria-Avila, G. (2003). What can animal models tell us about human sexual response? *Annual Review of Sex Research*, *14*(1), 1–63.

Plomin, R., DeFries, J. C., & Loehlin, J. C. (1977). Genotype-environment interaction and correlation in the analysis of human behavior. *Psychological Bulletin*, *84*(2), 309–322.

Rodriguez-Sierra, J. F., Crowley, W. R., & Komisaruk, B. R. (1975). Vaginal stimulation in rats induces prolonged lordosis responsiveness and sexual receptivity. *Journal of Comparative and Physiological Psychology*, *89*(1), 79–85.

Scarr, S., & McCartney, K. (1983). How people make their own environments: A theory of genotype → environment effects. *Child Development*, *54*(2), 424–435.

Seabold, S., & Perktold, J. (2010). Statsmodels: Econometric and statistical modeling with python. In *Proceedings of the 9th Python in science conference* (pp. 57–61). https://conference.scipy.org/proceedings/scipy2010/pdfs/seabold.pdf

Senveli, Z. (2017). *Behavioral display of lumbar curvature in response to the opposite sex*. http://repository.bilkent.edu.tr/handle/11693/33362

Simpson, J. A., & Gangestad, S. W. (1991). Individual differences in sociosexuality: Evidence for convergent and discriminant validity. *Journal of Personality and Social Psychology*, *60*(6), 870–883.

Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Science*, *3*(12), 452–460.

Tooby, J., & Cosmides, L. (1990). On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation. *Journal of Personality*, *58*, 17–67.

Van Rossum, G., & Drake, F. L. (2009). *Python 3 reference manual*. CreateSpace.

Weiss, S. L., Kennedy, E. A., Safran, R. J., & McGraw, K. J. (2011). Pterin-based ornamental coloration predicts yolk antioxidant levels in female striped plateau lizards (*Sceloporus virgatus*). *Journal of Animal Ecology*, *80*, 519–527.

Whitcome, K. K., Shapiro, L. J., & Lieberman, D. E. (2007). Fetal load and the evolution of lumbar lordosis in bipedal hominins. *Nature*, *450*, 1075–1078.

White, A. A., & Punjabi, M. M. (1990). *Clinical biomechanics of the spine*. Lippincott.

Wunsch, S. (2017). Phylogenesis of mammal sexuality: Analysis of the evolution of proximal factors. *Sexologies*, *26*(1), e1–e10.

Zhang, J., & Webb, D. M. (2003). Evolutionary deterioration of the vomeronasal pheromone transduction pathway in catarrhine primates. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(14), 8337–8341.

Supplemental Material

Table S1

Lumbar curvature and back arching values for each study stimulus

Stimulus	Lumbar curvature (°)	Back arching (°)
1	29	8
2	34	18
3	39	28
4	36	8
5	41	18
6	46	28
7	43	8
8	46	18
9	53	28
10	46	8
11	48	18
12	60	28
13	50	8
14	55	18
15	66	28
16	56	8
17	61	18

Figure S1

Figure S1. A cross-cultural sampling of vernacular dances from around the globe that involve the lordotic movement: Bamboula (Uruguay), Batuque (Brazil), Bèlè (Martinique), Candombe (Uruguay), Chica (Uruguay), Columbia (Cuba), Cueca Negra (Bolivia), Danças de umbigada (Brazil), Guaguancó (Cuba), Jwé Dansé (St. Lucia), Kalenda (Uruguay), Köçek (Turkey), Kuduro (Angola), Kupurlika (Macedonia), Kwassa Kwassa (Congo, Zimbabwe), Lundu (Brazil), Makossa (Cameroon), M'alayah (Oman, Saudi Arabia, United Arab Emirates), Mapouka (Côte d’Ivoire), Milonga (Argentina), Niiko (Somalia), ‘ōte‘a (Tahiti), Roman Havasi (Turkey), Sabra (Senegal), Samba de roba (Brazil), Semba (Bolivia), Twerking (USA), Ventilateur (Senegal), Yambú (Cuba), Zemba (Bolivia), Zingué (Cameroon). (*CC-By-Attribution 4.0 International*)

2.4 The problem of identifying (right) ways for appearance-enhancement

The Theory of Mind, an attribute to others' mental states and anticipation of their perceptions/behaviors (Premack & Woodruff, 1978), is one of our cognitive abilities (e.g., Liszkowski, 2013; Melhart et al., 2020) which can be very adaptive in the mating area. If people can guess what their potential mate would find attractive, then they can use it to enhance their physical attractiveness through the manipulation of physical cues (Lewis & Buss, 2022). This can prove to be advantageous for both intrasexual (i.e., through gaining an advantage among the same sex) and intersexual selection (i.e., the higher likelihood of mating). For example, if ancestral women understand what men find attractive, that can give them a strategic advantage for the challenge of acquiring a mate. As mentioned, one way of utilizing this ability to understand what men want is physical enhancement. One such enhancement can be achieved by women through wearing high heels. Before we move further with this prediction, I would like to emphasize that I present physical enhancement only as one potential explanation for wearing high heels. There might be other reasons for this behavior, for instance, women might wear high heels in order to increase their social status (Wade et al., 2022) as height is associated with dominance in relationships (Stulp et al., 2015). However, in an attempt to keep the dissertation concise, I will focus on the physical enhancement explanation for wearing high heels. Even though most studies show that wearing high heels is potentially health hazardous (Barnish et al., 2018, for a review), associated with problems such as hallux valgus (e.g., Nguyen et al., 2010; Barnish & Barnish, 2016) and musculoskeletal pain (e.g., Barnish & Barnish, 2016), some women still wear them. One possible reason why women still wear high heels might be to increase their attractiveness as multiple studies show that high heels increase women's attractiveness (Prokop, 2020). The exact mechanism of how heels increase attractiveness, whether through bringing the lumbar curvature closer to an optimum angle of 45.5° (Lewis et al., 2017b) or through manipulating the perception of the leg length (Prokop, 2020), or a combination of both or other possible mechanisms such as increased muscular tone or enhanced protrusion of breasts (Lewis et al., 2017b) is for further studies to address. However, taken altogether, the current attractiveness literature suggests that 1) high heels may make women more attractive and 2) women may be aware that men find them more attractive, and 3) despite the potential health problems it can cause, some women wear high heels. Even though we have an inner mechanism for ascribing what others might find attractive and we may enhance our attractiveness based on those cues, whether we do so or not is largely an untapped area in the current literature. Most studies focus on what the participants themselves would find attractive (e.g., Nash et al., 2006; Comfort et al., 2021; He et al., 2021) rather than what they think the opposite sex might find attractive. Wagstaff et al. (2015)'s study is one of these rare studies investigating the latter and they tested the effect of the mating context on the preference to reveal either the body or the face part of the sealed image of the opposite sex through the binary forced-choice task. They found that women correctly anticipated that men would prefer to see body over face for the short-term context while for the long-term context that difference disappeared. This study suggests that women can successfully ascribe males' state of mind and they successfully recognize the effect of mating context. More studies are needed to both replicate these findings and to test the areas where women can correctly predict what men find attractive. Hoping to contribute in this area, we extended our lumbar curvature and back arching studies, and we had female participants rated the same stimuli as in Semchenko et al. (2022) in terms of how they (women) think men would rate them. We, Ranson et al. (2023), found that women are aware of male preferences for the optimum angle of lumbar curvature and they also correctly predicted the insignificance of the mating context. Concerning lordosis movement, the findings in Semchenko et al. (2022) in Study 1 (N = 108) indicated that the effect of lordosis movement was stronger in the short-term context than in the long-term context. In the replication study with a larger study sample (N = 231), the effect of lordosis movement was also context-dependent and it was significant only in the short-term mating context, just as women predicted in Ranson et al. (2023). Women's ability to recognize male preference for the optimum angle of the morphological cue (lumbar curvature) can be a psychological adaptation giving them an advantage in identifying the right ways of appearance enhancement. For example, women might wear high heels and modify how their lumbar curvature angle appears, which in turn might increase their attractiveness (Lewis et al., 2017a). However, I would like to note that it would also be useful for rival assessment, giving them an advantage in intra-sexual competition. Regarding women's ability to correctly identify male's context-dependent preference of back arching, it could be useful for women to utilize that awareness depending on the type of relationship that they are interested in. In a similar fashion with the correct identification of the preferred lumbar curvature angle, it could also help women in rival assessment. Future studies can address how women utilize their awareness of what men find attractive. But overall, our study (Ranson et al., 2023) suggests that women might have psychological adaptations (i.e., correctly identifying what men find attractive), potentially giving them an advantage in both appearance-enhancement and in competition with other women (i.e., intra-sexual competition).

2.4.1 Ranson et al., 2023

The author, who is the corresponding author, significantly contributed to investigation, and she reviewed and edited the manuscript. She also conducted the analysis for Study 2 and visualized Study 2 data.

Personality and Individual Differences 204 (2023) 112004

Contents lists available at ScienceDirect

Personality and Individual Differences

journal homepage: www.elsevier.com/locate/paid

Lordosis in humans: women's accurate perceptions of men's context-dependent preferences

Jessica Ranson[a], Orion Read[a], Ayten Yesim Semchenko[b,*], Zeynep Senveli[c], Mitchell R.L. Forrest[d], Jonathon Flores[e], Vojtěch Fiala[b], Laith Al-Shawaf[f], David M.G. Lewis[a,g]

[a] Discipline of Psychology, Murdoch University, Australia
[b] Faculty of Science, Charles University, Czechia
[c] Department of Anthropology, Boston University, United States of America
[d] Discipline of Exercise Science, Murdoch University, Australia
[e] College of Education and Behavior Sciences, Houston Christian University, United States of America
[f] Psychology Department, University of Colorado Colorado Springs, United States of America
[g] Centre for Healthy Ageing, Health Futures Institute, Murdoch University, Australia

ARTICLE INFO

Keywords:
Human mating
Lordosis
Lumbar curvature
Attractiveness
Mate preferences
Nonverbal courtship behavior
Dynamic stimuli
Context effects

ABSTRACT

Semchenko and colleagues (in press) recently disentangled two evolutionary hypotheses and demonstrated that heterosexual men have mate preferences for both the morphological cue of women's lumbar curvature and the behavioral cue of back arching: Men are attracted to an intermediate degree of lumbar curvature in both short-term and long-term mating contexts, and, independent of this preference, are attracted to lordosis behavior in short-term, but not long-term, mating contexts. No research to date has investigated whether men are aware of these preferences. There are a priori reasons to expect this to be the case: An awareness of these preferences could functionally guide both appearance-enhancement and intrasexual competition strategies. Here, we tested whether women have accurate perceptions of men's preferences in the lumbar region. Across two studies ($Ns = 177, 293$), we found that women's perceptions align precisely with men's preferences: Women perceive men to be attracted to cues to lordosis behavior in short-term but not long-term contexts, and to be attracted to an intermediate angle of lumbar curvature independent of mating context. We hope these findings, which document previously unknown features of women's mating psychology, inspire investigations into how women might adaptively use their accurate perceptions of men's mate preferences.

1. Introduction

Recent research (Semchenko et al., in press) disentangled two evolutionary hypotheses about male mate preferences for fitness-relevant cues in the female lumbar region. The first hypothesis is what we refer to as the *lumbar curvature hypothesis*: Because a woman's neutral angle of lumbar curvature is an externally observable cue to lumbar vertebral wedging—which would have been critical for the solving the adaptive problem of a forward-shifted center-of-mass during pregnancy—selection should have favored a male preference for specific angles of lumbar curvature in women (Lewis et al., 2015). According to this hypothesis, because both too little and too much vertebral wedging would have carried fitness costs, selection should have favored a male preference for an intermediate angle of lumbar curvature. Consistent with this hypothesis, Lewis et al. (2015) found that men's attraction to women increased as the women's lumbar curvature approached an angle maximally distant from the two fitness problems of hypo- and hyperlordosis.

The second hypothesis, proposed by Senveli (2017) and by Pazhoohi et al. (2018), is what we refer to as the *lordosis behavior hypothesis*: Back-arching behavior, which is a signal of proceptivity in some mammalian species, might cue proceptivity in humans as well. If so, then selection could have favored psychological adaptations in men to attend and be attracted to lordosis behavior in women.

Although Pazhoohi et al.'s (2018) reasoning is largely sound, their presentation of the lordosis behavior hypothesis and how it relates to the lumbar curvature hypothesis is not as precise as it could be. First, the two hypotheses are conceptually distinct, and are in fact hypotheses

---

* Corresponding author at: Faculty of Science, Charles University, Prague, Czech Republic.
E-mail address: aytenyesim@protonmail.com (A.Y. Semchenko).

https://doi.org/10.1016/j.paid.2022.112004
Received 10 August 2022; Received in revised form 10 November 2022; Accepted 16 November 2022
Available online 26 December 2022

about entirely different cues. The lordosis behavior hypothesis is about the behavioral cue of back arching, whereas the lumbar curvature hypothesis is about a morphological cue. However, Pazhoohi et al.' (2018) paper does not make it abundantly clear that these are two distinct cues (to take just one example, the title of the paper – "Arching the Back (Lumbar Curvature)," explicitly conflates the two cues). Second, because women's lumbar curvature and back-arching behavior are two distinct cues, evidence that men are attracted to one cue does not count as evidence that they are *not* attracted to the other cue as well. The two hypotheses propose effects of entirely different cues, one behavioral and one morphological. In short, the lumbar curvature hypothesis and the lordosis behavior hypothesis are distinct hypotheses, and they are complementary, not competing.

Semchenko et al. (in press) discussed these issues and conducted the first studies concurrently testing both hypotheses. They found support for *both* the lumbar curvature hypothesis and the lordosis behavior hypothesis.

One of Semchenko and colleagues' key contributions was a consideration of mating context, which was missing from Lewis et al. (2015) and Pazhoohi et al. (2018) (see Al-Shawaf et al., 2019; DeKay & Buss, 1992; Lewis, Al-Shawaf, et al., 2017; Schmitt & Buss, 1996, for discussions of the importance of context in human mating psychology). The lumbar curvature hypothesis does not appear to readily generate predictions that are dependent on mating context, whereas by contrast mating context is central to the lordosis behavior hypothesis. Because a woman's immediate sexual proceptivity is directly relevant to short-term mating but not to long-term mating, identifying cues to proceptivity is a more pressing adaptive problem in short-term than long-term mating contexts. If the lordosis behavior hypothesis is correct, then we might expect men to be more attracted to cues to back-arching behavior in short-term than long-term contexts. Semchenko et al. (in press) were the first to specify and test this prediction, and found that indeed, heterosexual men were more attracted to cues to female lordotic behavior in short-term than long-term mating contexts.

Semchenko and colleagues' recent research helps to disentangle distinct evolutionary hypotheses that may have been inaccurately characterized as being competing, rather than complementary, hypotheses. However, all work to date, including that of Semchenko and colleagues, has been focused on men's psychology.

1.1. *Women's perceptions of men's mate preferences*

The current research sought to investigate women's perceptions of these male mate preferences. To our knowledge, no research has investigated whether women are aware of male mate preferences for lumbar curvature and back arching, including the context-dependence of men's attraction to back arching. These investigations into women's psychology would be of interest even if they were only exploratory, but there are a priori reasons to expect women to be aware of men's mate preferences. First, an awareness of the features (i.e., cues) to which members of the opposite sex attend during mate selection may be used to guide physical appearance-enhancement strategies and courtship behavior (e.g., see Davis & Arnocky, 2022; Lewis & Buss, 2022). Second, such an awareness may also adaptively steer women's attention toward those intrasexual rivals who pose the greatest mating competition (e.g., see Buss, 1988; Fink et al., 2014; Pazda et al., 2014). Consistent with these ideas, Wagstaff et al. (2015) found that women are accurate in their perception of how men differentially allocate attention to distinct cues in short-term versus long-term mating contexts.

1.2. *Predictions*

If selection shaped women's psychology to accurately perceive men's mate preferences, then we should expect to make the following observations.

1.2.1. *Long-term mating contexts*

Consistent with the idea that displays of proceptivity may be perceived as indicative of promiscuity and an increased likelihood of unfaithfulness, which tend to decrease a potential mate's desirability as a long-term partner (see Goetz et al., 2012; see also Oliver & Sedikides, 1992; Schmitt & Buss, 1996), Semchenko et al. (in press) did not find reliable evidence of a male mate preference for lordosis behavior in long-term mating contexts. We therefore might not expect women to perceive men to be attracted to lordosis behavior in long-term mating contexts.

By contrast, an intermediate angle of neutral lumbar curvature (operationalized as approximately 45.5° based on medical orthopedic literature; see Semchenko et al., in press, for discussion of this operationalization) is hypothesized to cue the ability to sustain multiple healthy pregnancies without suffering incapacitating back injury—an important outcome in the context of long-term mating. Consistent with this, Semchenko et al. (in press) found that men were attracted to this intermediate angle of neutral lumbar curvature in long-term contexts. Based on this, we might expect women to perceive men to be attracted to this angle when assessing a potential long-term mate.

This combination – a lack of attraction to lordosis behavior in long-term contexts combined with a preference for specific angles of lumbar curvature – leads to the prediction that in long-term mating contexts specifically, women will perceive men to prefer an angle of lumbar curvature of approximately 45.5°. This would align with men's actual preferences as observed in Lewis et al. (2015) and Semchenko et al. (in press).

1.2.2. *Short-term mating contexts*

In short-term mating contexts, on the other hand, identifying cues to proceptivity is a more pressing adaptive problem. Consistent with this, men are reliably attracted to cues to anterior pelvic tilt (i.e., lordosis behavior) in short-term contexts (Semchenko et al., in press). Based on this, we might expect women to report that men are attracted to a more acute angle between the mid-back and buttocks in short-term contexts compared to long-term contexts.

2. Study 1

To test these predictions, we presented women with a sequence of female stimuli exhibiting progressively more acute angles between the thoracic spine and sacrum (see Fig. 1), and asked them to indicate which stimulus they believe men are most attracted to in (1) short-term and (2) long-term mating contexts.

2.1. *Method*

2.1.1. *Ethics statement*

This study was approved by the Murdoch University Human Research Ethics Committee (approval number: 2017/184).

2.1.2. *Participants*

One hundred seventy-seven women (age range: 18–64[1]) were recruited to participate through social media (e.g., Facebook), the subject pool at Murdoch University, the Social Psychology Network, and snowball sampling. Participants recruited through the Murdoch University subject pool received partial course credit for their participation.

2.1.3. *Materials and procedure*

As part of a larger study on women's mating psychology, participants viewed the sequence of female stimuli and completed the measures

---

[1] Age was reported in ranges: 67% of participants were between 18 and 24 years of age, 12% were 25–34, 6% were 35–44, 6% were 45–54, 1% was 55–64, and 9% did not report their age.

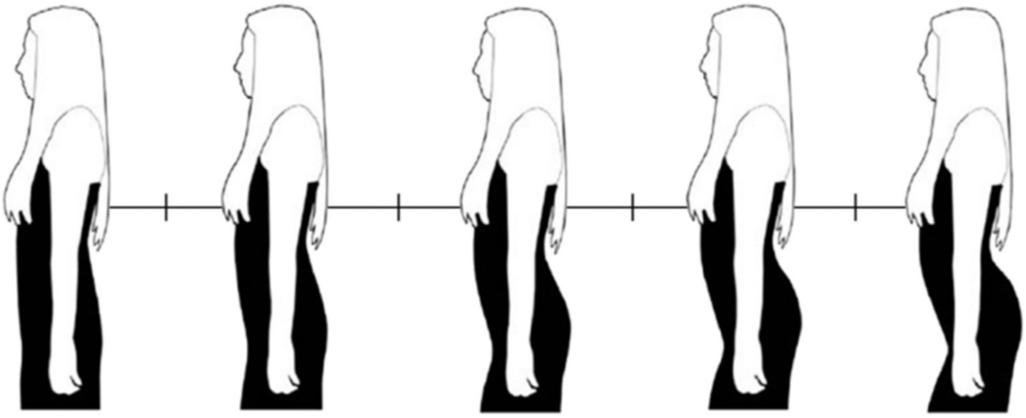


Fig. 1. Back arching silhouettes scale. (CC-By-Attribution 4.0 International.)

described below via an online survey hosted on Qualtrics.

2.1.3.1. Back arching silhouettes scale. To assess women's perceptions of men's preferences, we generated a scale that displayed a female silhouette that exhibited progressively more acute angles between mid-back and buttocks across five sequential morphs (Fig. 1). The morphs ranged in this angle from 26° to 61°—values that fall within the naturally occurring range of the angle formed between thoracic spine and sacrum (see Fernand & Fox, 1985). Because this angle can vary continuously, we added midpoints between the silhouettes to create a nine-point scale. This enabled us to capture participants' responses with greater precision; the survey instructed participants to select the midpoint between adjacent silhouettes when they felt that the most appropriate response fell between two of the silhouettes. Participants viewed this scale and were asked to indicate which woman (i.e., morph) men would find most attractive as a (1) long-term mate and (2) short-term mate. To prevent the left-hand selection bias observed previously in ascending-order figure-scales (see Doll et al., 2004; Nicholls et al., 2006), we set up the online survey to randomly assign each participant to view the scale with the concavity of the lower back increasing from left to right, or from right to left.

2.2. Results

To test study predictions, we conducted statistical analyses in JASP (version 0.11.1). To test the prediction that women's perceptions of men's long-term mate preferences would align with 45.5° – a preference predicted a priori and then found by Lewis et al. (2015) and subsequently replicated by Semchenko et al. (in press) – we conducted a single-sample t-test comparing women's perceptions of men's preferences against a test value of 45.5°. The results of this analysis suggested that women have accurate perceptions of men's mate preferences for lumbar curvature in long-term mating contexts: Women's perceptions of the angle of lumbar curvature to which men are most attracted in a long-term mate ($M = 44.43$, $SD = 8.90$) did not differ from 45.5°, $t(175) = -1.60$, $p = .112$, $d = -0.121$, 95% CI: [43.11, 45.74].

To test the prediction that, in short-term mating contexts, women would perceive men to be attracted to cues suggestive of a woman having arched her back – consistent with Semchenko et al.'s (in press) recent demonstration that heterosexual men are attracted to such cues specifically in short-term contexts – we conducted a repeated-measures t-test: We compared (1) the angle women perceive men to be most attracted to in long-term contexts with (2) the angle women perceive men to be most attracted to in short-term contexts. In support of this prediction, women perceived men to be attracted to *a more acute angle in short-term mating contexts* ($M = 49.27$, $SD = 11.25$) compared to long-term mating contexts, $M_D = 4.84$, $SE_D = 0.82$, $t(175) = -5.93$, $p < .001$, $d = 0.45$, 95% CI: [3.23, 6.46].

2.3. Discussion

The Study 1 data provide preliminary evidence consistent with the ideas that women have accurate perceptions of men's mate preferences, including a preference for lumbar curvature (as in Lewis et al., 2015) and a preference for cues to back-arching behavior (as in Pazhoohi et al., 2018), with the latter being specific to short-term mating (see Semchenko et al., in press).

However, Study 1's design, materials, and analyses all have limitations. The study design asked participants to select, for each mating context, a single morph that they perceived men to be most attracted to in that mating context. This design was reasonably well-suited for identifying mating context-based shifts. However, this design left us with a weak test of the prediction that, in long-term mating contexts, women perceive men to prefer a lumbar curvature angle of 45.5°, in alignment with men's observed preferences (e.g., Lewis et al., 2015; Semchenko et al., in press). That is, in the context of Study 1 design, this prediction specified a null effect: It predicted that there would be no difference between 45.5° and the angle women perceive men to be most attracted to in long-term contexts. This is what we observed, suggesting preliminary support for this prediction, but null results are not the strongest criteria for inferring such support.

Another limitation was that the study stimuli were static. This followed precedent in the literature, including both Lewis et al. (2015) and Pazhoohi et al. (2018). Such static stimuli might be appropriate for testing hypotheses about morphological cues, as in Lewis et al.'s (2015) research. However, given that the lordosis behavior hypothesis is specifically and explicitly about a *movement*-based cue, static stimuli are not ideal for testing this hypothesis. Static stimuli may only be valid for testing the lordosis behavior hypothesis to the extent that study participants reliably *infer movement* from them. One possible solution to this problem could be to ask participants whether they think that the stimulus displayed is in a natural (i.e., neutral) posture or has actively arched their back. However, we think that there is a far better solution: dynamic stimuli.

3. Study 2

In Study 2, we used dynamic stimuli and had participants rate these stimuli individually on continuous scales. This combination of materials and design offered several key methodological improvements.

First, and perhaps most importantly, the use of dynamic stimuli enabled us to better disentangle the cue of neutral lumbar curvature (morphology) from the cue of back-arching *movement* (behavior). Static stimuli communicate information about static cues (e.g., morphology) or require the participant to infer movement – inferences that researchers cannot be certain about. By contrast, dynamic stimuli more readily communicate information about both morphology and behavior: Dynamic stimuli can be constructed to vary in their underlying morphological characteristics *and* their behavior (i.e., movement).

Second, the use of continuous ratings of individual stimuli enabled a much stronger test of the prediction that women perceive men to be attracted to an angle of lumbar curvature of approximately 45.5°, in line with the male preference proposed a priori and reported by Lewis et al. (2015) and replicated by Semchenko et al. (in press). As noted above, the Study 1 task of having women select a single morph resulted in this prediction specifying a null effect. By contrast, having participants rate each stimulus individually on a continuous scale in Study 2 enabled us to more directly test whether women perceive men's attraction to increase as women's lumbar curvature approaches the proposed optimum. In other words, deviations from 45.5° should be associated with decreased perceptions of attractiveness—a prediction that Study 1 was not capable of directly testing.

More importantly, because the Study 2 stimuli disentangled the cue of neutral lumbar curvature (morphological cue) from the lordotic movement (behavioral cue), we were able to pull these two preferences apart and test the prediction that women will perceive men to be attracted to a neutral underlying lumbar curvature angle of 45.5° in *both* short-term and long-term contexts—in line with men's context-*independent* preferences for female lumbar curvature demonstrated by Semchenko et al. (in press).

Finally, Study 1 findings suggested that women perceive men to be attracted to greater back arching in short-term than long-term mating contexts. However, this does not directly address how women perceive men to respond to lordosis behavior in each mating context independently. That is, the Study 1 finding that women perceive men to be attracted to a more acute angle in short-term *relative* to long-term mating contexts is theoretically consistent with five different possibilities: women perceiving men to (1) be attracted to lordosis behavior in long-term mating contexts and even more attracted to it in short-term contexts, (2) be attracted to lordosis behavior in short-term contexts but have a neutral response to it in long-term contexts, (3) be attracted to lordosis behavior in short-term contexts and find it unattractive in long-term contexts, (4) have a neutral response to it in short-term contexts and find it unattractive in long-term contexts, or even (5) find it unattractive in short-term contexts and even more unattractive in long-term contexts. The use of continuous ratings in Study 2 enabled us to disambiguate between these five possibilities. This was important because the best evidence currently available suggests that possibility 2 most accurately characterizes men's preferences: Men are reliably attracted to lordosis behavior in short-term contexts but have either a less positive or a neutral response to it in long-term contexts (Semchenko et al., in press). Study 2 enabled us to determine whether women's perceptions of men's attraction (or lack thereof) to lordosis behavior align with these observed, context-dependent male preferences.

3.1. *Method*

We generated animated female characters that varied in their neutral lumbar curvature and degrees of back arching (i.e., lordosis behavior) (see Fig. 2), and had participants rate each character's attractiveness to men as a potential short-term mate and as a potential long-term mate. This enabled us to (1) disentangle the cues of lumbar curvature and the movement of back arching, (2) test the prediction that women perceive men to have context-*independent* preferences for lumbar curvature, and (3) test the prediction that women perceive men to be attracted to the lordotic movement in a context-*dependent* manner.

3.1.1. *Ethics statement*

This study was approved by the Murdoch University Human Research Ethics Committee (approval number: 2018/008) and the Institutional Review Board of Charles University (protocol number 21/09).

3.1.2. *Participants*

Two hundred ninety-three heterosexual female participants (M_{age} = 27.93 years, SD_{age} = 10.53 years, age range = 18–67 years) completed the study. Participants were from Australia (42 %), the United States (25 %), Czech Republic (8 %), India (6 %), the UK (3 %), South Africa (3 %), Brazil (2 %), Malaysia (2 %), China (1 %), Canada (1 %), Zimbabwe (1 %), as well as Kenya, Slovakia, Portugal, Germany, Vietnam, Philippines, Mauritius, Trinidad and Tobago, Japan, New Zealand, Kyrgyzstan, Georgia, and Colombia (each <1 %). Participants were recruited through the Social Psychology Network, MTurk, Facebook, the subject pool at Murdoch University, and a database of individuals who agreed to be contacted to participate in research studies. Student participants recruited via the Murdoch University subject pool received partial course credit for their participation.

3.1.3. *Materials and procedure*

As part of a larger study on attraction and mating, participants viewed the animated characters and completed the measures described below via an online survey hosted on the Qualtrics survey software platform.

3.1.3.1. Stimuli. We presented participants with 17 animated virtual characters that varied on two dimensions: (1) their neutral standing lumbar curvature and (2) the back arching that they exhibited in the animation (see Fig. 2). So that the characters accurately represented the distributions of these variables in natural human populations, we created stimuli whose neutral lumbar curvature ranged from 29° to 66° (see Fernand & Fox, 1985) and whose arching of the lower back ranged from 8° to 28° (see Whitcome et al., 2007).

3.1.3.2. Attractiveness ratings. Each participant viewed and rated all study stimuli. Each stimulus was presented individually, with order of presentation randomized for each participant. The participant rated how attractive (0 = Extremely Unattractive, 10 = Extremely Attractive) they thought men would find each woman as a short-term mate and as a long-term mate.

3.2. *Results*

Because study design involved the combination of repeated measures (i.e., attractiveness ratings) and continuous predictor variables (e.g., lumbar curvature), we fit the study data to linear mixed-effect models using the Statsmodels package (version 0.11.0; Seabold & Perktold, 2010) in Python (version 3.8.11; Van Rossum & Drake, 2009). These models nested attractiveness ratings within participants and incorporated a random intercept for each participant to control for between-participant differences in baseline perceptions of attractiveness.

3.2.1. *Effects of both lumbar curvature and lordosis behavior?*

To test for independent effects of lumbar curvature and the back-arching movement, we fit study data to a model in which lumbar curvature[2] and back arching were concurrently entered as predictors of perceived attractiveness. The model also included the interaction between lumbar curvature and mating context, and the interaction between mating context and back arching; these interactions enabled us to test whether, as predicted, women perceived men to have a context-*independent* preference for lumbar curvature and a context-*dependent* preference for back arching.

Results unambiguously supported all study predictions. Women

---

[2] More precisely, the variable entered was the deviation of the stimulus's lumbar curvature from 45.5°, as deviations from this value are the central construct of interest.

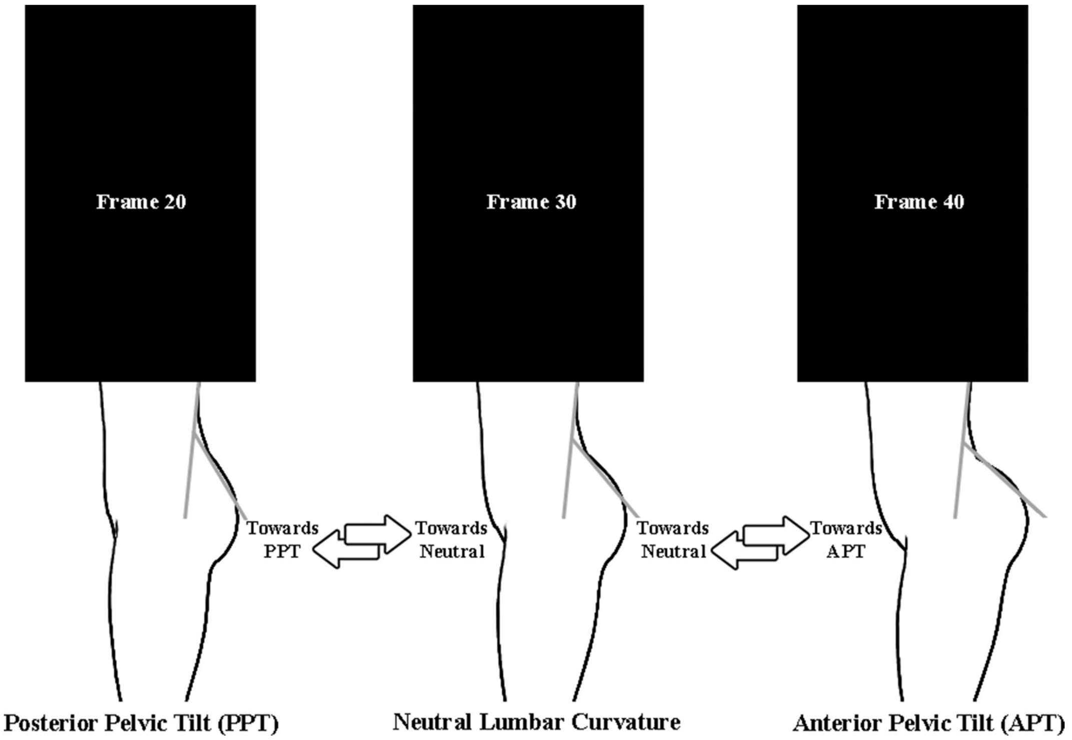


Fig. 2. Static contour depiction of a dynamic study stimulus. Each stimulus was a video of an animated character moving between posterior and anterior pelvic tilt (i.e., engaging in back-arching behavior), passing through their neutral lumbar curvature. Some stimuli shared the exact same range of back-arching behavior (i.e., the range between posterior and anterior pelvic tilt) but differed in their neutral lumbar curvature; these stimuli enabled us to isolate the effect of lumbar curvature on perceived attractiveness. Other stimuli had identical angles of neutral lumbar curvature but differed in their back-arching behavior; these stimuli enabled us to isolate the effect of back-arching behavior on perceived attractiveness. (CC-By-Attribution 4.0 International.)

perceived that men are more attracted to women whose lumbar curvature approaches 45.5°, consistent with the male preference hypothesized and found by Lewis et al. (2015), as well as reproduced by Semchenko et al. (in press); deviations from this value were associated with decreased perceptions of attractiveness, $b = -0.022$, $SE = 0.004$, $p < .001$, 95% CI: [−0.030, −0.015] (Fig. 3). As predicted, this effect was independent of mating context; the effect of neutral lumbar curvature did not differ between long-term and short-term mating contexts, lumbar curvature × mating context $b = -0.007$, $SE = 0.006$, $p = .234$, 95% CI: [−0.018, 0.004].

By contrast, and as predicted, the effect of back arching *did* depend on mating context; there was a significant interaction between back arching and mating context, $b = -0.038$, $SE = 0.004$, $p < .001$, 95% CI: [−0.046, −0.029]. This interaction indicated that the back-arching movement affected perceptions of attractiveness differently in short-term and long-term contexts. We therefore conducted tests of the effect of back arching in short-term and long-term contexts separately. These analyses revealed that, consistent with the lordosis behavior hypothesis, back arching increased perceptions of short-term attractiveness, $b = 0.043$, $SE = 0.003$, $p < .001$, 95% CI: [0.037, 0.048], but not long-term attractiveness, $b = 0.005$, $SE = 0.003$, $p = .055$, 95% CI: [−0.000, 0.010] (Fig. 4).

3.3. Discussion

Study 2 made methodological improvements and resolved several issues that were not adequately addressed by Study 1. First, Study 2 offered a stronger test of the prediction that women will perceive men to prefer an angle of lumbar curvature of approximately 45.5° in long-term mating contexts. The “support” for this prediction in Study 1 was rather weak, as it came in the form of a null effect: Women's perceptions of the angle of lumbar curvature to which men are most attracted in long-term mating contexts was not significantly different from 45.5°. Study 2 tested and demonstrated this effect much more clearly: Study 2 participants perceived men's attraction to women to decrease as the women's lumbar curvature deviated from this angle (see Fig. 3).

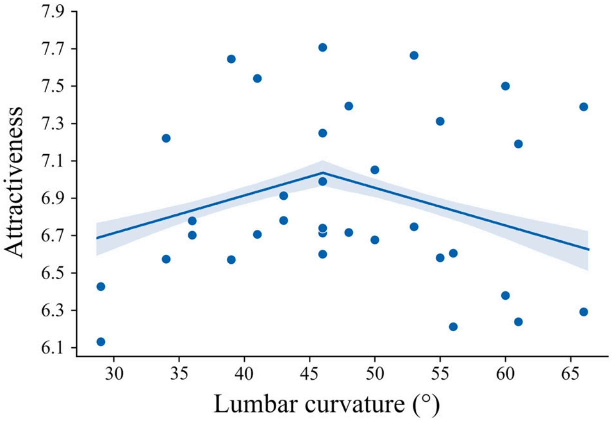


Fig. 3. The relationship between lumbar curvature and perceived attractiveness. Dots represent mean attractiveness ratings for each stimulus. The regression line predicting these ratings from the stimuli's lumbar curvature illustrates that perceived attractiveness increased as the characters' lumbar curvature approached 45.5°. Note. Because the relationship between attractiveness and lumbar curvature was independent of mating context, the mean short-term and long-term attractiveness ratings are both shown in blue. Shaded region = 95% CI. (CC-By-Attribution 4.0 International.) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Moreover, because the Study 2 stimuli disentangled the cue of neutral lumbar curvature from the lordotic movement, we were able to

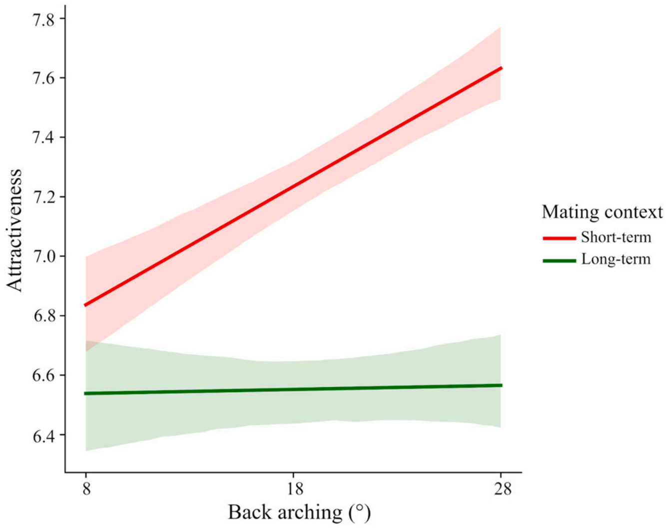


Fig. 4. The context-dependent effect of the back-arching movement on perceptions of attractiveness. Women perceived men to be attracted to back-arching behavior in short-term but not long-term mating contexts. Note. Shaded regions around regression lines = 95% CI. (CC-By-Attribution 4.0 International.)

test whether women perceive men to be attracted to a neutral underlying angle of lumbar curvature of approximately 45.5° in short-term as well as long-term contexts. Consistent with men's recently documented, context-independent preference (Semchenko et al., in press), women's perceptions of the angle of lumbar curvature that men are attracted to did *not* vary across mating contexts.

Finally, the Study 1 data were consistent with the idea that women perceive men to be more attracted to lordosis behavior in short-term than long-term mating contexts. However, the context-based difference observed in Study 1 was consistent with five distinct possibilities (see above). The Study 2 data enabled us to better determine how women perceive men to respond to back-arching behavior in each mating context separately. In alignment with men's context-dependent attraction to lordosis behavior (Semchenko et al., in press), women perceived men to be attracted to the lordotic movement in short-term but not long-term mating contexts.

4. General discussion

The current studies sought to test women's perceptions of men's mate preferences in the female lumbar region. Investigating this aspect of women's psychology would be informative even if this research were entirely exploratory, but there were theoretically principled reasons to believe that selection should have favored mechanisms in women's minds to attend to men's mate preferences. Namely, an awareness of these preferences could be used to guide physical appearance-enhancement tactics and courtship behavior (see Davis & Arnocky, 2022; Lewis & Buss, 2022), as well as to adaptively allocate attention to those intrasexual rivals likely to pose the greatest competition for mates.

Across two studies involving independent samples and different methods, we found evidence that women accurately perceive that (1) men have mate preferences for both lumbar curvature and back-arching behavior; (2) men's mate preference for lumbar curvature is independent of mating context; and (3) men's attraction to back-arching behavior is context-dependent (greater in short term than long term mating contexts). These findings document previously unknown features of women's mating psychology and help to further disentangle two evolutionary hypotheses whose relationship is most appropriately characterized not as conflicting, but rather as conceptually distinct and potentially complementary.

4.1. *Future directions*

We hope these findings inspire new research investigating how women use these accurate perceptions. One possibility is that women might engage in strategic appearance-enhancement tactics: specific behaviors that manipulate the visual cues to which men are attracted (see Davis & Arnocky, 2022; Lewis & Buss, 2022). For example, women might engage in lordosis behavior to modulate male mating interest in accordance with their own mating desires. Further research is needed in this area and many questions remain unanswered. We hope to see future research that more firmly establishes the existence of lordosis behavior in humans, identifies the specific contexts (e.g., the presence of an attractive potential mate) and individual differences (e.g., an unrestricted sociosexual orientation) that predict its use, and identifies the distinct communicative functions and meanings it may have within and across cultures.

4.1.1. *High heels*

One appearance-enhancement tactic that may be related to lordosis is the use of high-heeled shoes, which cause the angle formed between the mid-back and buttocks to become more acute. However, it is currently unclear whether high heels' documented effect on perceptions of women's attractiveness is best accounted for by the lordosis behavior hypothesis or the lumbar curvature hypothesis. Existing evidence suggests that high heels (1) increase perceptions of women's attractiveness on average, (2) cause the angle between the mid-back and buttocks to become more acute, *and* (3) shift the majority of women's lumbar curvature closer to rather than away from the optimal value proposed by Lewis et al. (2015); these three effects were reported by Lewis, Russell, et al. (2017) and independently replicated by Meskó et al. (2021). What is unclear is what explains the increases in attractiveness: the angle between the mid-back and buttocks becoming more acute, in line with the lordosis behavior hypothesis; the shifts toward or away from the optimum angle proposed by the lumbar curvature hypothesis; or a third factor yet to be identified.

One reason that the case of high heels is complicated is that they cause an initial dynamic change (i.e., they change the angle formed between women's mid-back and buttocks) but then result in a static stimulus; the angle does not continue to change once the heels have been put on. This makes it difficult to know how observers interpret the angle or why they are attracted to it: Are they responding to what they perceive to be the woman's natural angle of lumbar curvature, or to the perception that she has arched her back to signal proceptivity, or both? This uncertainty, both from the participant's and the researcher's standpoint, is a critical problem with static stimuli that we highlighted in the Study 1 Discussion.

4.1.2. *Dynamic stimuli*

Static stimuli have strong precedence in attractiveness research, and, until now, have had a monopoly on research investigating attractiveness-relevant cues in the female lumbar region. We hope that the numerous limitations of Study 1 that were tied to the use of static stimuli, juxtaposed with the advantages offered by dynamic stimuli in Study 2, underscore the value of dynamic stimuli for future research on mate preferences. This conclusion becomes even clearer when we consider the core evolutionary function of mate preferences: They motivate people to seek mates who exhibit specific fitness-relevant cues. Because *movements* can cue important fitness-relevant information, it would be extremely surprising if selection did not shape psychological adaptations to attend to dynamic cues in potential mates. Dynamic stimuli are thus essential for testing hypotheses about mate preferences for movement-based cues (such as the lordosis behavior hypothesis), for preventing the misinterpretation of preferences for static cues as preferences for dynamic cues (or vice versa), and for concurrently testing hypotheses about both dynamic and static cues in the same region of the body (as in Study 2 here). We therefore hope to see increased use of dynamic stimuli in research on human mate preferences.

5. Conclusion

Here, we discovered that women accurately perceive men to have a context-independent preference for specific angles of lumbar curvature and a context-dependent attraction to the lordotic movement. We hope these findings motivate several new research directions. First, future research is needed to understand the specific ways in which women might adaptively use their awareness of these mate preferences. Second, future research should more firmly establish the existence of human lordosis behavior, identify the specific contexts that increase the likelihood that it will be deployed, and explore the distinct communicative and non-communicate functions it may have in humans. Finally, and more broadly, we hope the current studies motivate attractiveness researchers to direct greater attention – both theoretical and empirical – to dynamic cues. These cues almost certainly communicate important information relevant to fitness, but remain largely understudied. In the case of the lumbar curvature and lordosis behavior hypotheses, the distinction between dynamic and static cues turns out to be indispensable for disentangling these two different evolutionary hypotheses and avoiding their conflation, accurately conceptualizing the relationship between them, and clarifying how previous research findings might be best interpreted.

CRediT authorship contribution statement

Jessica Ranson: Conceptualization, Methodology, Investigation, Writing – original draft. **Orion Read:** Conceptualization, Methodology, Investigation, Writing – original draft. **Ayten Yesim Semchenko:** Investigation, Data curation, Formal analysis, Visualization, Writing – review & editing. **Zeynep Senveli:** Conceptualization, Writing – original draft. **Mitchell R.L. Forrest:** Conceptualization, Writing – review & editing. **Jonathon Flores:** Conceptualization, Methodology, Visualization. **Vojtěch Fiala:** Investigation, Writing – review & editing. **Laith Al-Shawaf:** Conceptualization, Writing – original draft, Writing – review & editing. **David M.G. Lewis:** Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Writing – review & editing.

Declaration of competing interest

None.

Data availability

Data will be made available on request.

Acknowledgement

This research was supported in part by grant #1742218 from Charles University Grant Agency (GAUK) to A. Y. Semchenko.

References

Al-Shawaf, L., Lewis, D. M. G., Wehbe, Y., & Buss, D. M. (2019). Context, environment, and learning in evolutionary psychology. In T. K. Shackelford, & V. A. Weekes-Shackelford (Eds.), *Encyclopedia of evolutionary psychological science*. Springer.

Buss, D. M. (1988). The evolution of human intrasexual competition: Tactics of mate attraction. *Journal of Personality and Social Psychology, 54*(4), 616–628.

Davis, A. C., & Arnocky, S. (2022). An evolutionary perspective on appearance enhancement behavior. *Archives of Sexual Behavior, 51*(1), 3–37.

DeKay, W. T., & Buss, D. M. (1992). Human nature, individual differences, and the importance of context: Perspectives from evolutionary psychology. *Current Directions in Psychological Science, 1*(6), 184–189.

Doll, M., Ball, G. G., & Willows, N. D. (2004). Rating of figures used for body image assessment varies depending on the method of figure presentation. *International Journal of Eating Disorders, 35*(1), 109–114.

Fernand, R., & Fox, D. E. (1985). Evaluation of lumbar lordosis: A prospective and retrospective study. *Spine, 10*, 799–803.

Fink, B., Klappauf, D., Brewer, G., & Shackelford, T. K. (2014). Female physical characteristics and intra-sexual competition in women. *Personality and Individual Differences, 58*, 138–141.

Goetz, C. D., Easton, J. A., Lewis, D. M., & Buss, D. M. (2012). Sexual exploitability: Observable cues and their link to sexual attraction. *Evolution and Human Behavior, 33*(4), 417–426.

Lewis, D. M. G., & Buss, D. M. (2022). Appearance enhancement: A cue-based approach. *Archives of Sexual Behavior, 51*, 73–77.

Lewis, D. M. G., Russell, E. M., Al-Shawaf, L., & Buss, D. M. (2015). Lumbar curvature: A previously undiscovered standard of attractiveness. *Evolution and Human Behavior, 36*(5), 345–350.

Lewis, D. M. G., Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. M. (2017). Evolutionary psychology: A how-to guide. *American Psychologist, 72*(4), 353–373.

Lewis, D., Russell, E. M., Al-Shawaf, L., Ta, V., Senveli, Z., Ickes, W., & Buss, D. M. (2017). Why women wear high heels: Evolution, lumbar curvature, and attractiveness. *Frontiers in Psychology, 8*, 1875.

Meskó, N., Őry, F., Csányi, E., Juhász, L., Szilágyi, G., Lubics, O., Putz, Á., & Láng, A. (2021). Women walk in high heels: Lumbar curvature, dynamic motion stimuli and attractiveness. *International Journal of Environmental Research and Public Health, 18*(1), 299.

Nicholls, M. E. R., Orr, C. A., Okubo, M., & Loftus, A. (2006). Satisfaction guaranteed: The effect of spatial biases on responses to Likert scales. *Psychological Science, 17*(12), 1027–1028.

Oliver, M. B., & Sedikides, C. (1992). Effects of sexual permissiveness on desirability of partner as a function of low and high commitment to relationship. *Social Psychology Quarterly, 55*(3), 321–333.

Pazda, A. D., Prokop, P., & Elliot, A. J. (2014). Red and romantic rivalry: Viewing another woman in red increases perceptions of sexual receptivity, derogation, and intentions to mate-guard. *Personality and Social Psychology Bulletin, 40*(10), 1260–1269.

Pazhoohi, F., Doyle, J. F., Macedo, A. F., & Arantes, J. (2018). Arching the back (lumbar curvature) as a female sexual proceptivity signal: An eye-tracking study. *Evolutionary Psychological Science, 4*(2), 158–165.

Schmitt, D. P., & Buss, D. M. (1996). Strategic self-promotion and competitor derogation: Sex and context effects on the perceived effectiveness of mate attraction tactics. *Journal of Personality and Social Psychology, 70*(6), 1185–1204.

Seabold, S., & Perktold, J. (2010). Statsmodels: Econometric and statistical modeling with python. In *Proceedings of the 9th Python in Science Conference* (pp. 57–61).

Semchenko, A.Y., Senveli, Z., Flores, J., Forrest, M.R.L., Fiala, V., Al-Shawaf, L., Buss, D. M., & Lewis, D.M.G. (in press). Lordosis in humans. Personality and Social Psychology Bulletin. (in press). Personality and Social Psychology Bulletin.

Senveli, Z. (2017). Behavioral Display of Lumbar Curvature in Response to the Opposite Sex (Order No. 29046987). [Master's thesis, Bilkent University]. ProQuest Dissertations & Theses Global.

Van Rossum, G., & Drake, F. L. (2009). *Python 3 reference manual*. Scotts Valley, CA: CreateSpace.

Wagstaff, D., Sulikowski, D., & Burke, D. (2015). Sex-differences in preference for looking at the face or body in short-term and long-term mating contexts. *Evolution, Mind and Behaviour, 13*, 1–17.

Whitcome, K. K., Shapiro, L. J., & Lieberman, D. E. (2007). Fetal load and the evolution of lumbar lordosis in bipedal hominins. *Nature, 450*, 1075–1078.

Conclusions

Acquiring a mate is essential for reproduction, and in this dissertation, I investigated the potential psychological adaptations designed to solve some of the subproblems associated with the adaptive problem of mate acquisition. These subproblems can be listed as 1) the problem of missing opportunities to interact with a potentially suitable mate, 2) the problem of identifying mates that are available, 3) the problem of identifying mates exhibiting specific fitness-related cues, and 4) the problem of identifying (right) ways for appearance-enhancement. Concerning the first problem, throughout human history, we might have had to judge the attractiveness of the potential mate under uncertainty which may bring the problem of misjudging the potential mate's attractiveness and missing the opportunity to interact with that person. I studied how perception of attractiveness can change under uncertainty and whether that change is sex-dependent which might be the case due to the asymmetrical parental investment (Robert, 1972). I found a male overperception and female underperception bias towards opposite-sex images with incomplete information (Lewis et al., 2022). Further analyses showed that men overperceived the attractiveness of the unattractive women, while women underperceived the attractiveness of the attractive men. These findings suggest the following algorithm: 'When uncertain, always assume that the potential mate is attractive for male and unattractive for female participants', might underlie behind these biases. As discussed in Chapter 2, these perceptual biases might be psychological adaptations about physical attractiveness judgment or a byproduct of another adaptation functioning to assess non-physical features of the potential mate under uncertainty. I studied the second problem, the problem of identifying available mates, under two sub-sections: 1) I provided a succinct literature review about costs and benefits of mate poaching (Semchenko & Havlíček, 2021) because cost-benefit balance of being poached can be informative for the future studies examining the availability of already-mated individuals. 2) I investigated a potential behavioral indicator of availability of women, back arching behavior, which is rather common among female mammals to indicate sexual readiness such as Kudwa et al. (2010) with rats and Moe et al. (2016) with marmosets. I found that males might be psychologically adapted to perceive back arching as a signal of proceptivity (Semchenko et al., 2022). Concerning the third problem, by using the same stimuli in the previous study mentioned in the second problem, I studied the psychological adaptations for identifying the fitness-indicating cue, lumbar curvature (Semchenko et al., 2022). Lumbar curvature can be considered as a cue to indicate fitness because the intermediate angle (45.5°) of lumbar curvature can prevent having certain medical problems such as low-back pain (Fernand & Fox, 1985; Norton et al., 2004), which might be crucial for mother's foraging abilities and her ability to provide protection for her offspring (Wunsch, 2017). I found that men might have a psychological adaptation of preferring women with that lumbar curvature angle (45.5°) in *both* mating contexts (as reproduction is important for both mating contexts). Lastly, for the fourth problem, the problem of identifying (right) ways for appearance-enhancement, I found that women accurately predict men's preference towards the optimum lumbar curvature angle in both mating contexts and they also correctly guessed male preference of back arching behavior in the short-term uncommitted mating context (Ranson et al., 2023). Being able to predict these can be adaptive for women as it would give an advantage of correctly knowing how to enhance their appearance and even to assess potential rivals throughout our evolution.

In summary, in this dissertation, I tested the effects of theoretically-anchored inputs (e.g., lumbar curvature angle) on the predicted outputs (e.g., male perception of female attractiveness) and found evidences consistent with the proposed psychological adaptations (e.g., male preference towards an intermediate angle of lumbar curvature) designed to overcome the four stated sub-problems of mate acquisition (e.g., the problem of identifying mates exhibiting specific fitness-related cues) above.

References

Ågmo, A. & Ellingsen, E. (2003). Relevance of non-human animal studies to the understanding of human sexuality. *Scandinavian Journal of Psychology*, 44(3), 293–301.

Al-Shawaf, L., Lewis, D. M., Barbaro, N., & Wehbe, Y. S. (2021a). The products of evolution: Conceptual distinctions, evidentiary criteria, and empirical examples.

Al-Shawaf, L., Lewis, D. M. G., Barbaro, N., & Wehbe, Y. S. (2021b). : (pp. 70–95). In T. K. Shackleford (Ed.), The SAGE handbook of evolutionary psychology: Foundations of evolutionary psychology.

Anderson, K. (2006). How well does paternity confidence match actual paternity? evidence from worldwide nonpaternity rates. *Current Anthropology*, 47(3), 513–520.

Arima, H., Dimar, J. R., Glassman, S. D., Yamato, Y., Matsuyama, Y., Mac-Thiong, J.-M., Roussouly, P., Cook, B., & Carreon, L. Y. (2018). Differences in lumbar and pelvic parameters among african american, caucasian and asian populations. *European Spine Journal*, 27(12), 2990–2998.

Barnish, M., Morgan, H. M., & Barnish, J. (2018). The 2016 high heels: Health effects and psychosexual benefits (high habits) study: systematic review of reviews and additional primary studies. *BMC Public Health*, 18(1), 1–13.

Barnish, M. S. & Barnish, J. (2016). High-heeled shoes and musculoskeletal injuries: a narrative systematic review. *BMJ open*, 6(1), e010053.

Bateman, A. (1948). Intra-sexual selection in drosophila. *Heredity*, 2(3), 349–368.

Been, E., Gómez-Olivencia, A., & Kramer, P. A. (2014). Brief communication: lumbar lordosis in extinct hominins: implications of the pelvic incidence. *American Journal of Physical Anthropology*, 154(2), 307–314.

Belu, C. F. & O'Sullivan, L. F. (2019). Roving eyes: Predictors of crushes in ongoing romantic relationships and implications for relationship quality. *Journal of Relationships Research*, 10.

Blakemore, E. (2019). The chernobyl disaster: What happened, and the long-term impacts. *National Geographic.*

Bogin, B., Bragg, J., & Kuzawa, C. (2014). Humans are not cooperative breeders but practice biocultural reproduction. *Annals of Human Biology*, 41(4), 368–380.

Brandner, J. L., Brase, G. L., & Young, M. E. (2022). Size, scale, and design matter: Commentary on lewis, al-shawaf, semchenko, and evans, (2022). *Evolution and Human Behavior.*

Buracco, P. & Orizaola, G. (2022). Ionizing radiation and melanism in chornobyl tree frogs. *Evolutionary Applications.*

Buss, D. & Schmitt, D. (1993). Sexual strategies theory: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, 12, 1–49.

Buss, D. & Schmitt, D. (2019). Mate preferences and their behavioral manifestations. *Annual Review of Psychology*, 70, 77–110.

Buss, D.M. & Schmitt, D. (2017). *Sexual Strategies Theory*, (pp. 1–5). Springer International Publishing: Cham.

Buss, D. M., Haselton, M. G., Shackelford, T., Bleske, A. L., & Wakefield, J. C. (1998). Adaptations, exaptation, and spandrels. *American Psychologist*, 53(5).

Butovskaya, M., Mezentseva, A., Mabulla, A., Shackelford, T., Schaefer, K., Fink, B., & Windhager, S. (2022). Facial cues to physical strength increase attractiveness but decrease aggressiveness assessments in male maasai of northern tanzania. *Evolution and Human Behavior*, 43(2), 115–121.

Chapais, B. (2013). Monogamy, strongly bonded groups, and the evolution of human social structure. *Evolutionary Anthropology: Issues, News, and Reviews*, 22(2), 52–65.

Charlesworth, B. (2004). John maynard smith: January 6, 1920–april 19, 2004. *Genetics*, 168(3), 1105–1109.

College, O. (2013). Illustration from anatomy physiology. *Wikimedia Commons.*

Comfort, W. E., de Andrade, B. N., Wingenbach, T. S., Causeur, D., & Boggio, P. S. (2021). Implicit responses in the judgment of attractiveness in faces with differing levels of makeup. *Psychology of Aesthetics, Creativity, and the Arts.*

Cosmides, L. & Tooby, J. (1992). The adapted mind: Evolutionary psychology and the generation of culture. In *Cognitive adaptations for social exchange* (pp. 163–228). New York, NY: Oxford University Press.

Darwin, C. (1859). *The origin of species by means of natural selection*, volume 247. EA Weeks.

Darwin, C. (1871). The descent of man. *New York: D. Appleton.*

Davies, A. P. & Shackelford, T. K. (2017). Don't you wish your partner was hot like me?: The effectiveness of mate poaching across relationship types considering the relative mate-values of the poacher and the partner of the poached. *Personality and Individual Differences*, 106, 32–35.

Davies, A. P., Shackelford, T. K., & Hass, R. G. (2007). When a "poach" is not a poach: Re-defining human mate poaching and re-estimating its frequency. *Archives of Sexual Behavior*, 36(5), 702–716.

Davies, A. P., Shackelford, T. K., & Hass, R. G. (2010). Sex differences in perceptions of benefits and costs of mate poaching. *Personality and Individual Differences*, 49(5), 441–445.

Davies, A. P., Tratner, A. E., & Shackelford, T. K. (2019). Not clearly defined, not reliably measured, and not replicable: Revisiting the definition and measurement of human mate poaching. *Personality and Individual Differences*, 145, 103–105.

De La Croix, D. & Mariani, F. (2015). From polygyny to serial monogamy: a unified theory of marriage institutions. *The Review of Economic Studies*, 82(2), 565–607.

Digby, A. (1992). Victorian values and women in public and private. In *Proceedings of the British Academy*, volume 78 (pp. 195–215).

Dixson, A. F. et al. (1998). *Primate sexuality: comparative studies of the prosimians, monkeys, apes, and human beings*. Oxford University Press, USA.

Drea, C. M., Crawford, J. C., & Boulet, M. (2020). Lack of evidence for pheromones in lemurs. *Current Biology*, 30(22), R1355–R1357.

Duarte, C. M. (2014). Red ochre and shells: clues to human evolution. *Trends in ecology & evolution*, 29(10), 560–565.

Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behavior*, 70(4), 967–971.

Fenigstein, A. & Preston, M. (2007). The desired number of sexual partners as a function of gender, sexual risks, and the meaning of “ideal”. *Journal of Sex Research*, 44(1), 89–95.

Fernand, R. & Fox, D. E. (1985). Evaluation of lumbar lordosis. a prospective and retrospective study. *Spine*, 10(9), 799–803.

Frydrýšek, F. (2016). Poloha těžiště samic primátů a žen.

Gangestad, S. & Simpson, J. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, 23(4), 573–587.

Gilbert, J. W., Wheeler, G. R., Storey, B. B., Mick, G. E., Herder, S. L., Richardson, G., Wyttenbach, W. H., & Martin, J. C. (2009). Lumbar magnetic resonance imaging hypolordosis in symptomatic patients: association with paraspinal muscle spasms. *Journal of Chiropractic Medicine*, 8(3), 95–100.

Gould, S. J. & Vrba, E. S. (1982). Exaptation-a missing term in the science of form. *Paleobiology*, 8(1), 4–15.

Harcourt-Smith, W. H. (2010). The first hominins and the origins of bipedalism. *Evolution: Education and Outreach*, 3(3), 333–340.

Haselton, M. G. & Buss, D. M. (2000). Error management theory: a new perspective on biases in cross-sex mind reading. *Journal of personality and social psychology*, 78(1), 81.

Hay, O., Dar, G., Abbas, J., Stein, D., May, H., Masharawi, Y., Peled, N., & Hershkovitz, I. (2015). The lumbar lordosis in males and females, revisited. *PloS one*, 10(8), e0133685.

He, D., Workman, C. I., Kenett, Y. N., He, X., & Chatterjee, A. (2021). The effect of aging on facial attractiveness: An empirical and computational investigation. *Acta Psychologica*, 219, 103385.

Huntley, J. (2021). Australian indigenous ochres: Use, sourcing, and exchange. *The Oxford Handbook of the Archaeology of Indigenous Australia and New Guinea.*, 21.

Jaanusson, V. (1991). Morphological changes leading to hominid bipedalism. *Lethaia*, 24(4), 443–457.

Jacobs, M. (1955). Studies on territorialism and sexual selection in dragonflies. *Ecology*, 36(4), 566–586.

Jonason, P. K., Cetrulo, J. F., Madrid, J. M., & Morrison, C. (2019). Gift-giving as a courtship or mate-retention tactic?: Insights from non-human models. *Evolutionary Psychology*, 7(1).

Kardum, I., Hudek-Knezevic, J., Schmitt, D. P., & Grundler, P. (2015). Personality and mate poaching experiences. *Personality and Individual Differences*, 75, 7–12.

Karney, B. (2021). Socioeconomic status and intimate relationships. *Annual Review of Psychology*, 72, 391.

Kelly, A. J., Dubbs, S. L., Barlow, F. K., & Zietsch, B. P. (2018). Male and female nipples as a test case for the assumption that functional features vary less than nonfunctional byproducts. *Adaptive Human Behavior and Physiology*, 4, 344—-353.

Kitata, M. (2020). Sexualising the performance, objectifying the performer: The twerk dance in kenya. *Agenda*, 34(3), 11–21.

Knipper, C., Mittnik, A., Massy, K., Kociumaka, C., Kucukkalipci, I., Maus, M., Wittenborn, F., Metz, S. E., Staskiewicz, A., Krause, J., et al. (2017). Female exogamy and gene pool diversification at the transition from the final neolithic to the early bronze age in central europe. *Proceedings of the National Academy of Sciences*, 114(38), 10083–10088.

Koivisto, I. (1965). *Behavior of the Black Grouse, Lyrurus Tetrix-L.-, During the Spring Display.*

Kramer, K. (2010). Cooperative breeding and its significance to the demographic success of humans. *Annual Review of Anthropology*, 39, 417–436.

Kramer, K., Schacht, R., & Bell, A. (2017). Adult sex ratios and partner scarcity among hunter–gatherers: implications for dispersal patterns and the evolution of human sociality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1729), 20160316.

Kudwa, A., López, F., McGivern, R., & Handa, R. J. (2010). A selective androgen receptor modulator enhances male-directed sexual preference, proceptive behavior, and lordosis behavior in sexually experienced, but not sexually naive, female rats. *Endocrinology*, 151(6), 2659–2668.

Larmuseau, M., Matthijs, K., & Wenseleers, T. (2016). Cuckolded fathers rare in human populations. *Trends in Ecology Evolution*, 31(5), 327–329.

Larmuseau, M., van den Berg, P., Claerhout, S., Calafell, F., Boattini, A., Leen, G., Vandenbosch, M., Nivelle, K., Decorte, R., & Wenseleers, T. (2019). A historical-genetic reconstruction of human extra-pair paternity. *Current Biology*, 29(23), 4102–4107.e7.

Leca, J. B. (2020). Evolutionary by-products. In *Encyclopedia of Evolutionary Psychological Science*. Springer.

Lewis, D., Al-Shawaf, L., Conroy-Beam, D., Asao, K., & Buss, D. (2017a). Evolutionary psychology: A how-to guide. *American Psychologist*, 72(4), 353.

Lewis, D. M., Al-Shawaf, L., Semchenko, A. Y., & Evans, K. C. (2022). Error management theory and biased first impressions: How do people perceive potential mates under conditions of uncertainty? *Evolution and Human Behavior*, 43(2), 87–96.

Lewis, D. M. & Buss, D. M. (2022). Appearance enhancement: A cue-based approach. *Archives of Sexual Behavior*, 51(1), 73–77.

Lewis, D. M., Russell, E. M., Al-Shawaf, L., & Buss, D. M. (2015). Lumbar curvature: a previously undiscovered standard of attractiveness. *Evolution and Human Behavior*, 36(5), 345–350.

Lewis, D. M., Russell, E. M., Al-Shawaf, L., Ta, V., Senveli, Z., Ickes, W., & Buss, D. M. (2017b). Why women wear high heels: Evolution, lumbar curvature, and attractiveness. *Frontiers in Psychology*, 8, 1875.

Lewis, D. M. G., Al-Shawaf, L., Semchenko, A. Y., & Evan, K. (2023). Creative ideas, but elementary mistakes: A reply to brandner and colleagues to promote best practices in error management theory research. *Evolution and Human Behavior*.

Liszkowski, U. (2013). Using theory of mind. *Child Development Perspectives*, 7(2), 104–109.

Lloyd, E. A. (2013). Stephen j. gould and adaptation: San marco 33 years later. In *In: Danieli, G., Minelli, A., Pievani, T. (eds) Stephen J. Gould: The Scientific Legacy* (pp. 21–35). Springer.

Loyau, A. Jalme, M. & Sorci, G. (2005). Intra-and intersexual selection for multiple traits in the peacock (pavo cristatus). *Ethology*, 111(9), 810–820.

Maner, J. & Ackerman, J. (2020). Ecological sex ratios and human mating. *Trends in Cognitive Sciences*, 24(2), 98–100.

McBurney, D. H., Zapp, D. J., & Streeter, S. A. (2005). Preferred number of sexual partners: tails of distributions and tales of mating systems. *Evolution and Human Behavior*, 26(3), 271–278.

Melhart, D., Gravina, D., & Yannakakis, G. N. (2020). Moment-to-moment engagement prediction through the eyes of the observer: Pubg streaming on twitch. In *International Conference on the Foundations of Digital Games* (pp. 1–10).

Moe, Y., Kyi-Tha-Thu, C., Tanaka, T., Ito, H., Yahashi, S., Matsuda, K.-I., Kawata, M., Katsuura, G., Iwashige, F., Sakata, I., et al. (2016). A sexually dimorphic area of the dorsal hypothalamus in mice and common marmosets. *Endocrinology*, 157(12), 4817–4828.

Nash, R., Fieldman, G., Hussey, T., Lévêque, J.-L., & Pineau, P. (2006). Cosmetics: They influence more than caucasian female facial attractiveness. *Journal of applied social psychology*, 36(2), 493–504.

Nettle, D. (2002). Height and reproductive success in a cohort of british men. *Human Nature*, 13(4), 473–491.

Nguyen, U.-S., Hillstrom, H. J., Li, W., Dufour, A. B., Kiel, D. P., Procter-Gray, E., Gagnon, M. M., & Hannan, M. T. (2010). Factors associated with hallux valgus in a population-based study of older women and men: the mobilize boston study. *Osteoarthritis and cartilage*, 18(1), 41–46.

Norton, B. J., Sahrmann, S. A., & Van Dillen, L. R. (2004). Differences in measurements of lumbar curvature related to gender and low back pain. *Journal of Orthopaedic & Sports Physical Therapy*, 34(9), 524–534.

Oakley, P. A., Ehsani, N. N., & Harrison, D. E. (2019). Non-surgical reduction of lumbar hyperlordosis, forward sagittal balance and sacral tilt to relieve low back pain by chiropractic biophysics® methods: a case report. *Journal of physical therapy science*, 31(10), 860–864.

Orghian, D. & Hidalgo, C. A. (2020). Humans judge faces in incomplete photographs as physically more attractive. *Scientific Reports*, 10(1), 1–12.

Ostovich, J. & Sabini, J. (2004). How are sociosexuality, sex drive, and lifetime number of sexual partners related? *Personality and Social Psychology Bulletin*, 30(10), 1255–1266.

Ostrom, J. H. (1974). Archaeopteryx and the origin of flight. *The Quarterly Review of Biology*, 49, 27–47.

Pawlowski, B., Dunbar, R., & Lipowicz, A. (2000). Tall men have more reproductive success. *Nature*, 403(6766), 156–156.

Pazhoohi, F., Doyle, J. F., Macedo, A. F., & Arantes, J. (2018). Arching the back (lumbar curvature) as a female sexual proceptivity signal: An eye-tracking study. *Evolutionary Psychological Science*, 4(2), 158–165.

Pedersen, W., Miller, L., Putcha-Bhagavatula, A., & Yang, Y. (2002). Evolved sex differences in the number of partners desired? the long and the short of it. *Psychological Science*, 13(2), 157–161.

Penke, L. & Asendorpf, J. B. (2008). Beyond global sociosexual orientations: A more differentiated look at sociosexuality and its effects on courtship and romantic relationships. *Journal of Personality and Social Psychology*, 95(5), 1113–1135.

Poulin, M. (2007). Sex, money, and premarital partnerships in southern malawi. *Social Science Medicine*, 65(11), 2383–2393. Informed Consent in a Changing Environment.

Premack, D. & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and brain sciences*, 1(4), 515–526.

Preuschoft, H., Hayama, S., & Günther, M. (1988). Curvature of the lumbar spine as a consequence of mechanical necessities in japanese macaques trained for bipedalism. *Folia primatologica*, 50(1-2), 42–58.

Price, M. E., Pound, N., Dunn, J., Hopkins, S., & Kang, J. (2013). Body shape preferences: Associations with rater body shape and sociosexuality. *PLOSONE*.

Prokop, P. (2020). High heels enhance perceived sexual attractiveness, leg length and women's mate-guarding. *Current Psychology*, (pp. 1–11).

Ranson, J., Read, O., Semchenko, A. Y., Senveli, Z., a. F. M. R. L., Fiala, V., Al-Shawaf, L., & Lewis, D. M. G. (2023). Lordosis in humans: Mate preferences, multiple evolutionary hypotheses, and women's perceptionss. *Personality and Social Psychology Bulletin*.

Rifkin, R. F. (2015). Ethnographic insight into the prehistoric significance of red ochre. *The Digging Stick*, 32(2), 7–10.

Robert, T. (1972). Parental investment and sexual selection. *Sexual Selection & the Descent of Man, Aldine de Gruyter, New York*, (pp. 136–179).

Röder, S., Weege, B., Carbon, C.-C., Shackelford, T. K., & Fink, B. (2015). Men's perception of women's dance movements depends on mating context, but not men's sociosexual orientation. *Personality and Individual Differences*, 86, 172–175.

Roebroeks, W., Sier, M. J., Nielsen, T. K., De Loecker, D., Parés, J. M., Arps, C. E., & Mücher, H. J. (2012). Use of red ochre by early neandertals. *Proceedings of the National Academy of Sciences*, 109(6), 1889–1894.

Saad, G. & Gill, T. (2003). An evolutionary psychology perspective on gift giving among young adults. *Psychology Marketing*, 20(9), 765–784.

Scelza, B. A. (2011). Female choice and extra-pair paternity in a traditional human population. *Biology Letters*, 7(6), 889–891.

Schacht, R. & Borgerhoff Mulder, M. (2015). Sex ratio effects on reproductive strategies in humans. *Royal Society Open Science*, 2(1), 140402.

Schacht, R. & Kramer, K. (2019). Are we monogamous? a review of the evolution of pair-bonding in humans and its contemporary variation cross-culturally. *Frontiers in Ecology and Evolution*, 7, 230.

Schmitt, D. P. (2004). Patterns and universals of mate poaching across 53 nations: the effects of sex, culture, and personality on romantically attracting another person's partner. *Journal of Personality and Social Psychology*, 86(4), 560.

Schmitt, D. P. & Buss, D. M. (2001). Human mate poaching: Tactics and temptations for infiltrating existing mateships. *Journal of personality and Social Psychology*, 80(6), 894.

Sear, R. & Mace, R. (2008). Who keeps children alive? a review of the effects of kin on child survival. *Evolution and Human Behavior*, 29(1), 1–18.

Sell, A., Lukazsweski, A., & Townsley, M. (2017). Cues of upper body strength account for most of the variance in men's bodily attractiveness. *Proceedings of the Royal Society B: Biological Sciences*, 284(1869), 20171819.

Semchenko, A. Y. & Havlíček, J. (2021). Costs and benefits of mate poaching. In *Encyclopedia of Evolutionary Psychological Science* (pp. 1535–1540). Springer.

Semchenko, A. Y., Senveli, Z., Forrest, M. R. L., Flores, J., Fiala, V., Al-Shawaf, L., Buss, D. M., & Lewis, D. M. G. (In Press, 2022). Lordosis in humans. *Personality and Social Psychology Bulletin*.

Senveli, Z. (2017). Behavioral display of lumbar curvature in response to opposite sex.

Shan, W., Shenghua, J., Davis, H., Peng, K., Shao, X., Wu, Y., Liu, S., Lu, J., Yang, J., Zhang, W., et al. (2012). Mating strategies in chinese culture: Female risk avoiding vs. male risk taking. *Evolution and Human Behavior*, 33(3), 182–192.

Snyder, J., Fessler, D., Tiokhin, L., Frederick, D., Lee, S., & Navarrete, C. (2011). Trade-offs in a dangerous world: Women's fear of crime predicts preferences for aggressive and formidable mates. *Evolution and Human Behavior*, 32(2), 127–137.

Stulp, G., Buunk, A., Verhulst, S., & Pollet, T. (2013). Tall claims? sense and nonsense about the importance of height of us presidents. *The Leadership Quarterly*, 24(1), 159–171.

Stulp, G., Buunk, A. P., Verhulst, S., & Pollet, T. V. (2015). Human height is positively related to interpersonal dominance in dyadic interactions. *PloS one*, 10(2), e0117860.

Tennent, B. J., Smith, E. R., & Davidson, J. M. (1980). The effects of estrogen and progesterone on female rat proceptive behavior. *Hormones and Behavior*, 14(1), 65–75.

Thomas, A. & Balmford, A. (1995). How natural selection shapes birds' tails. *The American Naturalist*, 146(6), 848–868.

Timmermans, E. & Courtois, C. (2018). From swiping to casual sex and/or committed relationships: Exploring the experiences of tinder users. *The Information Society*, 34(2), 59–70.

Tooby, J. & Cosmides, L. (2016). The theoretical foundations of evolutionary psychology.

Touraille, P. & Gouyon, P. (2008). Why are women smaller than men. *When Anthropology Meets Evolutionary Biology. Nat Preced*, 713.

Tyson, G., Perta, V., Haddadi, H., & Seto, M. (2016). A first look at user activity on tinder. In *2016 IEEE/ACM International Conference on Advances in Social Networks Analysis and Mining (ASONAM)* (pp. 461–466).: IEEE.

Ueda, R., Ashida, H., Yanagisawa, K., & Abe, N. (2017). The neural basis of individual differences in mate poaching. *Social neuroscience*, 12(4), 391–399.

Vojt, G., Pothoulaki, M., Laidlaw, R., & Flowers, P. (2020). What do we know about types of intimate relationship and associated sexual partners-a scoping review of interdisciplinary literature.

Vorherr, H. (1974). *The breast: morphology, physiology and lactation.* Academic Press, London.

Wade, T. J., Burch, R., Fisher, M. L., & Casper, H. (2022). On a pedestal: High heels and the perceived attractiveness and evolutionary fitness of women. *Personality and Individual Differences*, 188, 111456.

Wagstaff, D. L., Sulikowski, D., & Burke, D. (2015). Sex-differences in preference for looking at the face or body in short-term and long-term mating contexts. *Evolution, Mind and Behaviour*, 13(1), 1–17.

Wallace, A. (1891). *Natural selection and tropical nature: Essays on descriptive and theoretical biology.* Macmillan and Company.

Weiling, F. (1991). Historical study: Johann gregor mendel 1822–1884. *American Journal of Medical Genetics*, 40(1), 1–25.

Wentland, J. J. & Reissing, E. (2011). Taking casual sex not too casually: Exploring definitions of casual sexual relationships. *Canadian Journal of Human Sexuality*, 20(3).

Wentland, J. J. & Reissing, E. (2014). Casual sexual relationships: Identifying definitions for one night stands, booty calls, fuck buddies, and friends with benefits. *The Canadian Journal of Human Sexuality*, 23(3), 167–177.

Whitcome, K. K., Shapiro, L. J., & Lieberman, D. E. (2007). Fetal load and the evolution of lumbar lordosis in bipedal hominins. *Nature*, 450(7172), 1075–1078.

Wunsch, S. (2017). Phylogenesis of mammal sexuality. analysis of the evolution of proximal factors. *Sexologies*, 26(1), e1–e10.

Yonemura, K., Ono, F., & Watanabe, K. (2013). Back view of beauty: A bias in attractiveness judgment. *Perception*, 42(1), 95–102.

Yorzinski, J., Patricelli, G.L. Bykau, S., & Platt, M. (2017). Selective attention in peacocks during assessment of rival males. *Journal of Experimental Biology*, 220(6), 1146–1153.

Zelazniewicz, A. M. & Pawlowski, B. (2011). Female breast size attractiveness for men as a function of sociosexual orientation (restricted vs. unrestricted). *Archives of Sexual Behavior*, 40, 1129–1135.

Zhang, Y., Malo, M. E., Tschirhart, T., Xia, Y., Wang, Z., Dadachova, E., & Sun, J. (2022). Effects of melanized bacteria and soluble melanin on the intestinal homeostasis and microbiome in vivo. *Toxics*.

Zuk, M. & Simmons, L. (2018). *Sexual selection: a very short introduction.* Oxford University Press.