Received: 23 February 2017 | Revised: 8 December 2017 | Accepted: 22 January 2018

DOI: 10.1002/jez.b.22795

COMMENTARY AND PERSPECTIVE

WILEY JEZ-B MOLECULAR AND DEVELOPMENTAL EVOLUTION

Female orgasm and the emergence of prosocial empathy: An evo-devo perspective

James Kennedy[1] | Mihaela Pavlíčev[2,3]

[1]Washington, DC

[2]Center for Prevention of Preterm Birth, Perinatal Institute, Cincinnati Children's Hospital Medical Center, Cincinnati, Ohio

[3]Department of Pediatrics, University of Cincinnati College of Medicine, Cincinnati, Ohio

Correspondence
James Kennedy.
Email: kennedy.james@zoho.com

Abstract

In human females, direct or indirect stimulation of the clitoris plays a central role in reaching orgasm. A majority of women report that penetrative coitus alone is insufficient for triggering orgasm, puzzling researchers who expect orgasm to be an outcome of procreative intercourse. In the present paper, we turn our attention to the evolutionary role that such unreliability of orgasm at coitus might have played in human evolution. We emphasize that we do not thereby attempt an explanation of its origin, but its potential evolutionary effect. The present proposal suggests that the variable female orgasm, the position of the clitoris remote from the vagina, and the mismatch of the male refractory period with the female capacity for multiple orgasms, may have contributed to the evolution of human prosocial qualities.

KEYWORDS

empathy, orgasm, prosocial, sexual selection

1 | INTRODUCTION: THE ENIGMA OF THE FEMALE ORGASM

Had evolution placed the human clitoris inside the vagina, then both parties in penetrative sexual intercourse could be rewarded with simultaneous orgasms and enhanced pair-bonding, and biologists could point to this arrangement as an excellent adaptation that motivates both sexes to engage efficiently and happily in reproductive behaviors. Instead, the orgasm-triggering human glans clitoris lies in a position where procreative intercourse does not reliably stimulate it, under a hood at the juncture of the labia as far as one and three-quarters inches (Wallen & Lloyd, 2011) beyond the anterior reach of the vagina, puzzling and frustrating scientific narrators. Further, females but not males possess the capacity for unlimited numbers of orgasms, the female genitalia are highly individualized and difficult for an unfamiliar partner to navigate, and while the vagina has evolved to be a perfect instrument for stimulation of the penis to orgasm during intercourse the reciprocal is not true. Further, evolution has given our species a timer in the form of the male refractory period, such that the male's ejaculation typically marks the end of a sexual session. Seen through the narrow (phallocentric) lens of reproduction, the arrangement is so bizarre that a number of researchers have concluded that female orgasm has no fitness-increasing function, although many other theories exist (Lloyd, 2005; Zietsch & Santtila , 2013).

The consequence of the apparent many-faceted mismatch of evolution in early humans would have been that, during a typical heterosexual encounter, the female orgasmed if the male partner intentionally stimulated the clitoris in an activity other than the procreational intercourse that was sufficient for his own orgasm. The anatomical design means that the female human's proclivity for orgasm is structurally and functionally independent of activity directly related to procreation. Clitoral stimulation does elicit vaginal lubrication, which facilitates intercourse, but female orgasm does not require penetration; in a practical sense, where the goal is her orgasm, penetration is likely irrelevant. On the other hand, female orgasm is not necessary for reproduction, or even helpful in any clearly identifiable way.

Many researchers have tried to explain why evolution would have placed the human glans clitoris in a remote location (Wallen & Lloyd, 2011), and many have wondered why females have orgasms at all (Symons, 1979, and others), as there seems to be no reproductive or adaptive reason for them (Zietsch & Santtila, 2013). Theorists have suggested that the glans clitoris is divorced from the vagina to accommodate bipedalism (Gräslund, 2004; Wolfe, 1991) or childbirth (Pavelka, 1995). In some other primates, the glans clitoris is prominent and/or nearer the vagina; the human glans clitoris is small and situated at some distance from the vagina. Given this enigmatic arrangement, the explanations for the origin and/or maintenance of the human female orgasm are divided between adaptive and by-product narratives (Lloyd, 2005; Symons, 1979), where adaptations may have to do with bonding (Eibl Eibesfeldt, 1989; Morris, 1967), endocrine responses (Huynh, et al., 2013; Motta-Mena & Puts, 2016), or managing the movement of sperm toward the ovum (discussed in Levin, 2011), and by-product theories suggest that female orgasm is a vestige (Lloyd, 2005) or an accident (Pearson, 2011). Given this

complexity, the question is often asked: is the female orgasm evolutionarily important, or even adaptive?

It is worthwhile to briefly reconsider that *adaptive* means that the trait has originated for a specific function (Gould & Vrba, 1982). This is hard to extrapolate from the trait's current role in a single species in principle because traits can change their roles during evolution, are often co-opted into new roles (exaptation), or lose their roles altogether. Some such vestiges disappear, but others may be so tightly integrated in the organism's development that they (secondarily to the original function) play a structural role and persist across generations. For these reasons, it is important to ask whether a trait is adaptive in the first place, rather than assuming that this is the case (Lloyd, 2015); and to confirm adaptation, it is not sufficient to show that a trait affects fitness in one species, or that it has been maintained in evolution, as the current role might not have been its original function (Wagner & Pavlicev, 2017). Most work on female orgasm has not focused on studying the origin, but rather on the role that the female orgasm plays in humans or in the primate lineage. And regardless of whether orgasm itself was an adaptation, it may very well have affected the direction of evolution even if not by its primary function. Traits, for whatever function they arise, generate opportunities for novel evolutionary dynamics. For example, bird feathers evolved to improve thermoregulation, yet they set the stage for flight, and as a consequence, the radiation of a highly successful group—the birds. Similarly, hormone progesterone is a landmark of pregnancy maintenance across placental mammals and has been crucial in generating a huge variety of pregnancy types, yet it did not evolve for pregnancy but predated it by millions of years. Another example is prolactin, a hormone named after its essential role in mammalian lactation, however prolactin has been present at least since the last common ancestor with the teleosts.

Here, we propose that the structure of the female external genitalia—regardless of the explanation for its origin—might in a similar way have contributed to the basis for evolution of an important and complex human interindividual trait. The present model suggests that the variability of female orgasm and genital structures may have offered an opportunity for adaptive development of prosocial empathy.

2 | PROSOCIAL EMPATHY

Prosocial empathy as discussed here is an essential feature of human social life and includes the quality sometimes called intersubjectivity or mind-reading. Related to theory of mind in psychology, this is the ability of individuals to know with some accuracy what another person is thinking and how they feel. The ability seems to function differently from ordinary objective inference from perception; intersubjectivity is a low-latency process that allows nearly instantaneous understanding of others. Although it is difficult to assess intersubjectivity in nonhuman species, there is evidence that some other species are capable of it to some degree (e.g., de Waal, 2010).

The present thesis is that the anatomical separation of orgasm from the reproductive function in humans may have led to the emergence of a new kind of prosocial empathy or intersubjectivity. The fact that coitus alone is reliably sufficient for the male's but not the female's orgasm set the stage for a selection criterion where females preferred to mate with males who had a particular kind of social insight, motivation, and self-discipline that enabled them to elicit orgasm. The preferred male would have been one showing an active interest in his partner's experience; he would have the interpersonal sensitivity to identify what "works" sexually and to adjust his behavior in response to her responding, and the motivation and self-discipline to defer his own ejaculation until she had reached orgasm. We are proposing that a cluster of empathic prosocial tendencies may have come to dominance in the human species as a consequence of this sexual selection process.

That is not to say that this is the only path leading to modern human eusociality; the ability to understand how others think and feel would have introduced advantages across the range of social behaviors that helped the species overcome several fitness challenges. In the long run, we would expect the effect of human sexual asymmetry to integrate into a comprehensive schema of human sociality, as several types of selective pressures converged to produce the modern human.

A recent approach to understanding intersubjective empathy has emerged from the discovery of mirror neurons (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992), which respond when a subject performs a behavior and also sympathetically when the subject observes another individual perform that same behavior. Iacobonni (2009) has argued that neural mirroring answers the question of how humans can have access and understanding of others' minds. According to this view, intersubjectivity or mind-reading emerges from a real-time mental simulation of the other person's behavior, with the subject literally feeling what it is like to be the other person. This simultaneous simulation can support social collaboration and interaction at a level unknown to species lacking the ability. A population of individuals sympathetically tuned to one another may produce a "shared manifold" (Gallese, 2003) comprising a communal empathic understanding of selves and others.

Mirror neuron research provoked great initial interest, which has been followed by the current phase of caution and skeptical enthusiasm as more thorough knowledge is gained about the function of these specialized neurons in humans. Whether mirror neurons are found to be the mechanism for it or not, the concept of real-time simulation of others has suggested a new way of looking at social empathy.

Citing mirror neuron research in apes and humans, de Waal (2010) emphasizes that human mind-reading abilities are continuous with those of other species. Attributing intersubjective empathy to other apes as well as humans, de Waal (2010) points to the importance of "body-mapping," of identifying one's body with another's, where an individual can feel in their own body what the other person is experiencing in theirs. In de Waal's narrative, empathy and self-awareness are linked, and are not unique to human beings; he demonstrates the existence of empathy in elephants, dolphins, and apes, and notes that among these species it is comparable to empathy in humans.

The concept of body-mapping in the intimate heterosexual scenario is a special case in the current discussion due to the fact that male and female bodies do not correspond in relevant ways. For a man to bring a woman to orgasm, he has to stimulate body parts he literally does not have (homology between penis and clitoris is not obvious); he has to

read her mind about phenomena that are not part of his own experience. Thus, the empathic sociality discussed here seems to contain an added dimension beyond straightforward one-to-one body-mapping; although the male may share the experience of the female's pleasure response, he cannot identify the physical sensations of her body with anything he has known. He does however share the evaluative and emotional aspects of sexual arousal, and can learn to enact behaviors that elicit these in his partner, responding to emotional cues rather than physical identification with the partner.

In contrast with de Waal, Hrdy (2011) considers human intersubjectivity to be discontinuous from that of other species, and suggests that the phenomenon emerged from the necessity of communal caretaking and provisioning of human infants. Hrdy (2011) notes that cooperative breeding, where infants were cared for not only by their parents but also by other group members, known as alloparents, is universal in human communities and almost unknown among other species of great apes. Human infants take longer to mature and are dependent on others longer than any other mammal; as a consequence, Hrdy argues, the task of child-care is too burdensome for a mother alone or a mother and father. Alloparenting allowed children to be dependent for a longer period of time, allowing the evolution of even larger brains and humans with modern empathic mind-reading capabilities.

The trust required for alloparenting introduces several opportunities for intersubjectivity. The infant in a cooperative breeding society would have had to understand not only its mother's mind but also the attitudes and intentions of others who helped out. The infant who could read the minds of caregivers and respond appropriately with crying, smiling and other engaging facial expressions, gurgling or other behaviors would receive the best care and feeding; Hrdy argues that cooperative breeding made human infants sensitive to the intentions of "others" as well as "mothers." Hrdy has described these choices as selection pressures that favored the "emotionally modern" ape. Further, mothers would have needed to evaluate the intentions of others before she entrusted her child to them. The result is a kind of phenomenal intersubjectivity where individuals are able to empathize with and understand the thinking of others even when they are not related to them.

The present thesis does not assert that sexual interaction offered the only path to modern human sociality. As humans diverged evolutionarily, our species changed in many ways, accelerating biological changes by setting the stage with cultural habits that altered our environmental niche even as we adapted to it. Tool-making, agriculture, language, marriage, and kinship practices—many features of early human life changed the meaning of fitness dynamically. Among these changes was a new kind of intimacy in sexual behavior, where partners learned to communicate and to understand one another in a very personal and unprecedented way.

3 | ORGASM AND THE ARRANGEMENT OF FEMALE GENITALIA

The adaptation discussed here comprises two corresponding components. For one, the female genitalia would have evolved into an arrangement with the clitoris located at some distance from the vagina, making it unlikely for the female to achieve orgasm during coitus without additional stimulation. We do not currently know what evolutionary processes underlay this anatomical change from the genitalia in which the clitoris is positioned in copulatory canal. It appears to have coincided with the evolution of spontaneous ovulation (Pavlicev and Wagner 2016). But given the evolved anatomical landscape, only some males would have had the qualities that enabled them to elicit orgasm, and we assume that there would have been selection preference for individuals with those qualities.

Wallen and Lloyd (2008) review the literature and reanalyze data regarding the distance between the clitoris and urethral meatus (CUMD), finding a strong inverse relationship between CUMD and orgasm during intercourse. Those authors suggest that CUMD is a function of prenatal androgen exposure, and conclude that women exposed to lower levels of prenatal androgens are more likely to experience orgasm during sexual intercourse.

Discussion of CUMD tends to center around the question of women experiencing, or not experiencing, orgasm during intercourse. This question is of interest within a cultural context that considers intercourse to be "real sex" and expects women to find satisfaction in that act; the present discussion does not make such an assumption, but expects human female orgasm to be more reliably elicited by attention other than unassisted penile penetration. We do not consider the requirement of an attentive, empathic, and self-disciplined partner to be a disappointment, failure, or problem, but rather is seen as an evolutionary development that led to positive adaptations of the human species.

A parallel discussion arises regarding findings that lesbians have typically higher rates of orgasm than heterosexual women. This finding seems surprising only if one regards orgasm primarily as an outcome of penetrative intercourse. The idea that a female partner is better able to simulate a body comprising the same parts as her own is not surprising in the least, and the data confirm the expectation. The finding is not inconsistent with the present proposition. Our perspective only requires the female's partner to be male as far as activities pertaining to reproduction, which is in the human a goal separate from the attainment of orgasm. As we are discussing the evolution of an adaptation, reproduction is a necessary part of it, and thus a male partner must be involved on some occasions, but he is not a requirement for orgasm and has no special qualities for eliciting it that a woman does not have.

As noted by Pavličev and Wagner (2016), the evolution of the clitoris away from the vagina, in primates and some other species, has been associated phylogenetically with the emergence of spontaneous ovulation, as contrasted with evolutionarily ancestral induced ovulation in response to environmental stimuli or copulation. In animals where ovulation is a response to copulation, the clitoris, usually positioned inside the vagina, serves as part of the system that supports fertility in the presence of a consort. In species with a spontaneous periodic ovulatory cycle the clitoris tends to be remote from the vagina, and does not function to promote ovulation; its existence may be vestigial in some species with spontaneous ovulation, though it is believed that all species of primates can respond orgasmically to clitoral stimulation. Symons (1979) has argued that female orgasm is

a potential in all female mammals. An orgasm-like response has been elicited in other primates experimentally but because of the inability to communicate it is not known if other species experience orgasm as humans do (Allen & Lemmon, 1981).

4 | FEMALE ORGASM CALLS FOR PARTNER EMPATHY, EFFORT, AND SELF-DISCIPLINE

The present perspective identifies the remote clitoris as a factor contributing to an evolutionary trend toward modern human empathic sociality. Note that the present model suggests a consequence of anatomy, perhaps also the maintenance of orgasm, but not the origins of either—the clitoris is external to the vagina in most primates and females of numerous species seem to be capable of orgasm (Dixson, 2015). Sexuality and orgasm are uniquely integrated into human social life.

The earliest hominids are believed to have originally been violent beings, but adapted in the human lineage to living more or less peacefully in groups (Gómez, Verdú, González-Megías, & Méndez, 2016). For this to happen, it was necessary to temper male aggressiveness, which is expressed in Hominids particularly in terms of territoriality and mate-guarding or control over the female mate's access to other males. For a harmonious and complex society, males needed to develop a capacity for empathy and caring, and needed to develop the self-discipline to control their violent urges.

As there does not seem to be solid evidence that the clitoris serves the orgasm reflex reliably during coitus in any primate species, it appears unlikely that its main role is directly associated with copulation. In the bonobo, where the clitoris has evolved to be prominent and easily accessible during tumescence (Dahl, 1985), it is frequently stimulated as a social gesture, often to a climax that appears to be orgasmic. The bonobo clitoris has taken on a social function independent of reproduction, especially serving the formation of alliances between females, who are able to rub their clitorises together to orgasm in the ventro-ventral position, and may do so many times a day.

The present perspective proposes that the human clitoris also has a social function, which is indirectly related to procreation; if stimulation of the clitoris by a male occurs, it typically occurs in a context also involving copulation or other sexual behaviors. Orgasm being desired by the female, and her arousal serving to set the stage for intercourse, the clitoris indirectly promotes intercourse and reproduction. If orgasm led to endocrine responses propitious for bonding (Coria-Avila, Herrera-Covarrubias, Ismail, & Pfaus, 2016; Young and Wang, 2004), then the ancestral female's orgasm would have increased her affiliation to the mate, and if the activities resulted in coitus and the male's orgasm as well, the affiliation would be reciprocal and the seeds of offspring may have been planted. Note that this type of theory can get complicated if assumptions of pair-bonding are not met, as in social animals that may take multiple partners; implications for competitiveness and genetic inheritance are varied, depending on whether one assumes polygynous or polyandrous practices, or both, to be ancestral.

5 | ADEPTNESS: A MANY-FACETED PROSOCIAL TRAIT

For early humans, female orgasm probably functioned in mate selection (Miller, 2011; Sefcek, Brumbach, Vasquez, & Miller, 2007), and the present paper elaborates further on that theme. The ability to elicit orgasm in a heterosexual situation was likely immediately rewarding for the ancestral female. It may have been a measure of the quality, a fitness indicator (Miller, 2000), of her partner in a general sense. However, note that the honest signal of fitness is not a necessary condition. It is established that the sole preference of one sex, in this case grounded on pleasure that seems to be ancestral to primate females, is a sufficient condition to impose selection on the other sex, given that the choice can be made freely (Fisher, 1915; Kirkpatrick, 1982; Lande, 1981; Prum, 2017).

The suite of aptitudes that enabled a male to elicit orgasm will be called "adeptness" in the present discussion, and male individuals capable of eliciting orgasm will be referred to as "adept males." Because of the arrangement of the vulva, reliable elicitation of female orgasm in the heterosexual context requires deliberate and knowledgeable action on the part of the partner. It is not likely to occur if he simply pursues his own pleasure and reproductive goals. And, not incidentally, the partner does not need to be male, or even animate, for that matter (Burns, 2016).

It is reasonable to suggest that early females preferred a sexual interaction that resulted in the intense subjective pleasure of orgasm, and it follows that they preferred partners who knew how to elicit the response. The remote placement of the clitoris created a kind of test or standard that could be passed only by a partner capable of empathy, intent, restraint and conscious effort. The traits in an adept male, which enabled him to elicit female orgasm were prosocial qualities of a kind that we recognize as human; these qualities were beneficial for the pair and their offspring as well as the overall social unit, and increased the probability of propagation of the couple's genetic information through succeeding generations and in relatively stable family groups.

The sexually adept male had to care enough about his female partner to perform the acts that elicited her orgasm, even while he himself was in an excited state and desired ejaculation. The proclivity to attend to the female's desire is a complex quality encompassing elements of empathy, perspective-taking, altruism, and self-discipline. The sexually adept ancestral male empathically sensed his partner's need and found ways to accommodate her, even though his own short-term motives diverged from hers. He identified the female's desire and catered to it as she wished, deferring his own immediate benefit.

Keep in mind that these qualities probably evolved before the emergence of language, and almost certainly before clothing was adopted or sexual behavior became a private activity (Gray, 2013), hidden from conspecifics. The implications are that the male had to make adjustments based on his partner's nonverbal feedback, and, like other early discoveries, knowledge of the clitoral stimulation technique would have become widely known in the social group. Males who are capable of it—which would not be everybody—could choose whether to

engage in the behavior, and females could choose partners they hoped would please them. It is significant, but beyond the scope of the present paper, that almost all human societies have developed norms of dress, modesty, and privacy that conceal information and make it more difficult for individuals to evaluate the likely sexual interest of potential mates.

The adept male needed to be capable of self-discipline under pressure, including the ability and willingness to defer his own orgasm until his partner was sated. Because of the lethargy-inducing effect of the male refractory phase, if the female was to have an orgasm it had to happen before he ejaculated; he had to attend to his partner first, before attaining his own reward. Though ejaculation does not necessarily end a session, male continuance after that point is considered heroic, or at least chivalric; his physiological response makes him tend to lose interest.

Further, a human female can have a number of orgasms in a single session, with no upper bound known, and her experience can range from a twinge of pleasure to seismic magnitude. Therefore, "her orgasm" is not like a box to check off before getting to the part where the male ejaculates. As a selection criterion, female orgasm is not binary; partners can be rated on a compound scale including dimensions of cardinality and intensity.

Male ejaculation is necessary for reproduction but is not necessary for female gratification. Though penetrative intercourse is not usually sufficient for orgasm, it is not unpleasant for the female, and following her orgasms she may be more likely to indulge her partner, resulting in his orgasm; thus there is some indirect relationship between female orgasm and reproduction. The remote position of the clitoris does not directly encourage intercourse, but it does not preclude it, either, and clitoral stimulation does serve to prepare the vagina to receive the penis—arousal and not orgasm is a precondition for coitus. Although female orgasm does not seem to affect reproduction directly in any way important enough for researchers to agree on, it occurs proximal to coitus and the male's aptitude for eliciting the female response would likely have been associated with increased opportunities for procreation.

The variation of the clitoris from one individual to another has been taken as evidence that female orgasm is not a product of selection (Symons, 1979; Wallen & Lloyd, 2008). In either case, the result of what Symons called "the astonishing sexual plasticity of the human female" was that evolution did not select a simple action pattern in the partner but rather a general attitude of innovation, attention, and adaptiveness, requiring the ancestral male to be sensitive to the female's responses to his actions, and to adjust his behavior to the landscape of her unique body and reaction. It should be stressed that the selected qualities of the adept male—empathy, discipline, and so on—would not have been tied only to sexual activities, but rather instantiated a general social orientation toward pleasing a conspecific while delaying one's own gratification. Further, although this complex of tendencies may have emerged in the asymmetry of the mating milieu, there is no reason to believe its inheritance was sex-linked.

6 | ADEPTNESS AND REPRODUCTIVE ADVANTAGE

These prosocial qualities in the adept male gave fitness advantage to both the adept male and the female who chose him as a partner. The empathic, caring, altruistic male who put his partner's needs first in the sexual microcosm was likely to be a good provider generally, keeping her and their progeny safe, even at potential cost to himself. His adaptability suggests he was able to innovate to avoid danger and deal with threats, and his orientation toward the other implies he was advantaged at forming social alliances that might benefit the pair. His disciplined capability for deferring his own gratification suggests that he could form and follow a plan for managing difficulties presented by the environment, acting with purpose rather than following his own immediate impulse.

The adept male's altruistic orientation suggests that his offspring were more likely to survive to adulthood under his attentive care, passing on his genes; in a pair-bonding culture he would take care of his family with his focus on their needs. Because he was a desirable partner and because of the bonding effects of sexual arousal and orgasm in both partners (Young and Wang, 2004), he would have been more likely to enter into a long-term relationship, with a greater number of surviving offspring than his inept peers.

Also, and perhaps paradoxically, if his aptitude became known outside the pair relationship—our nearest primate relatives have sexual relations in public, and it is likely that even relatively recent humans did, too (Gray, 2013)—he would be likely to receive invitations from other females and may have passed his heritage through multiple maternal lineages. In a social group that did not emphasize long-term bonding the adept male would have likely been a widely desired consort with a higher than average number of female partners and hence a greater genetic advantage in the next generation. To summarize, the complex trait of adeptness might have advantaged the ancestral male's genes through three causal pathways: (1) He will have had an eager partner and numerous offspring; (2) His offspring will have benefited from his altruism and discipline, with increased survival probability, and; (3) He is likely to have mated with other females who valued his adeptness.

It may seem ironic to attribute traits like empathy and self-discipline especially to males, who commit overwhelmingly more violent crimes (Lauritsen, Heimer, & Lynch, 2009), provoke and fight wars (Urdal, 2006), rape and abuse women (Tjaden & Thoennes, 2006), and do other mean and nasty things much more frequently than females. Recently, Gómez et al. (2016) analyzed lethal violence against conspecifics across many species of mammals, and concluded that humans are phylogenetically predisposed to high levels of lethal violence, which is associated with both sociality and territoriality. Their analysis of artifacts confirms that the earliest humans were about as violent as their behavioral model predicts, that is, very violent, but that levels of lethal violence have dropped as history has progressed. They attribute these changes to the modulating influence of culture. As there is obviously a nontrivial level of lethal violence even in modern culture, it is proposed that the evolutionary adaptations described here did not supplant or

eliminate aggressive tendencies, but rather enabled their moderation through concern for others and self-control.

7 | WHY ARE HUMAN MALES NOT MORE ADEPT THEN?

The stereotype of the cross-cultural sexual ineptitude of males looms as an objection to the proposition that human prosociality emerged from early males adapting their behavior to their partner's unique physiological structure and sexual response. Without any statistical analysis or data, Davenport (1977, p.149) summarized a widely held viewpoint: "In most of the societies for which there are data, it is reported that men take the initiative and, without extended foreplay, proceed vigorously toward climax without much regard for achieving synchrony with the women's orgasm. Again and again, there are reports that coitus is primarily completed in terms of the man's passions and pleasures, with scant attention paid to the woman's response. If women do experience orgasm, they do so passively." We address this apparent controversy in three points. First, we note that for the female choice to be an effective driver of male adeptness, it must be executed freely. Second, the aptitude must be strongly heritable, rather than skill itself. Third, in spite of strongly negative judgment by Davenport, men may not be as inept as they are reputed to be.

7.1 | Female choice

The model presented here is an idealized model of female choice focused on a single male trait. In order for the female choice to shape male behavior, she must be free to choose, and in fact must carry through with the decision. Female choice may be limited in two ways. One is that females are not free from other interests, which may conflict with their choice based on the male adeptness—females may have been dependent on male provisioning and such dependence may have interfered with the ability to choose, as the most adept males might not be the best in providing security, shelter, food, and so on. In other words, selection will have acted on a combination of traits, adeptness being one. A second, less straightforward but no less effective factor limiting female choice may be the direct suppression of the female entitlement to choose, which is widespread even in modern human populations. In patriarchal societies with strict marriage customs women may be promised and married young, without any choice of their own. An even more subtle type of suppression of choice that is common in the Western world is to label female anorgasmia as mental disease and hence a defect of a woman, thereby discounting her opportunity to choose, and also the ineptness of a partner.

7.2 | The heritable skills are not specific to sexual behavior

We are further suggesting that these new cognitive skills generalized outside the sexual situation, that the ability to empathize with a sexual partner will have generalized to an ability to empathize with other group members as well, to understand their intent and their needs from the distal perspective, and to defer one's own immediate urges, in a way that had not existed previously. This generalized orientation is the important thing here, not the sexual skill itself; the new vulvar arrangement selected a new kind of cognitive orientation in the male partner.

The present perspective supposes that this new kind of loving orientation amplified pair-bonding, and further that the ability to understand others' intent gave the adept male and his offspring an advantage in anticipating and affecting the actions of conspecifics. As interpersonal understanding, the adept male's orientation brings a social advantage that translates to survival and reproduction, and prevalence in subsequent populations. Females would proliferate within the security of a family bond with the new adept males, who gained the social advantage of empathy, understanding, motivation to please, and ability to delay their own gratification.

7.3 | The legend of the inept male

Perhaps Davenport's statement regarding the "scant attention paid to the woman's response," quoted above, should be read as a criticism of the paucity of data rather than an editorial on the subject of male incompetence. The paragraph immediately following the quoted one refers to his own research in "East Bay," a Melanesian island culture, where they "engage in extended foreplay that begins with caressing, advances to fondling and mouthing of breasts and body, and, as passion mounts, there is mutual masturbation" (p. 149). This does not sound like selfish male ineptitude or scant attention.

Davenport mentions that the East Bay approach is similar to the Trukese technique of "striking," which he describes in a remarkable passage. Speaking of Romonum Island, in the Truk group of Micronesia, he writes: "Lovers commonly inflict pain on one another in foreplay. Suffering pain inflicted by a sweetheart is regarded as both a test of strong affection and as sexually arousing. The most erotic form of coitus, called 'striking,' is clitoral, with insertion into the vagina just before orgasm and ejaculation (p.126)." (By this, Davenport seems to mean *male* orgasm and ejaculation.)

We find a more thorough description of Truk striking in Swartz (1958): "This involves the man manipulating his penis against the woman's genitals for the purpose of stimulating the clitoris. The penis is inserted into the vagina just before ejaculation, but informants say that sometimes it is not inserted at all (p. 478)." Swartz quotes Gladwin and Sarason (1953, p.114): "Here the objective is not merely to bring the woman to orgasm but for each to arouse in the other the greatest possible heights of passion." An account by anthropologist Beatriz Moral (2002) describes a Chuuk (Truk) legend in which "The man (Wonofaat) displays his savoir faire by his mastery of the most popular sexual practice in Chuuk: the Chuukese hammer. This practice consists or rubbing the clitoris with the tip of the penis and is considered a national treasure of which all Chukkese (women and men) are very proud." In nearby Yap, a technique called gichigich is practiced by young people before marriage: "During this encounter, the man sits with his back against the side of the hut and his legs straight out. The woman straddles him, and he inserts his penis into her vagina a little bit, and then proceeds to stimulate her for several hours while she has dozens of orgasms" (Kimmel & Holler, 2000, p.63).

These Micronesian techniques resemble practices known in Central Africa as Kunyaza , Kachabali, and other names (Bizimana, 2010; Skafte & Silberschmidt, 2014; Taylor, 1990). This body of techniques includes tapping and rubbing the external vulva with the glans penis until the woman ejaculates and orgasms (Swartz, 1958, also mentions micturition during Truk striking). This sexual tradition practiced within the regions of Burundi, Rwanda, the Eastern Democratic Republic of Congo, Western Uganda and Western Tanzania is known to science mainly because of research spurred by the HIV epidemic there; in Davenport's time there may have been no data regarding Kunyaza by any name.

Incidentally, both the Central African and Pacific populations can be described as outwardly patriarchal, with physical abuse of women not uncommon, and yet even there we find highly developed sexual practice where the male is focused on the female's pleasure, deferring his own release until she is sated. In China, a millennia-old tradition of Taoist sexual techniques emphasized the retention of semen and prolonged intercourse and is studied and practiced into the present time. "Female orgasms (khuai) strengthened man's vital powers, hence the male act was to be prolonged as much as possible so that the Yang might be nourished by as much Yin as possible" (Needham, 1956, p. 149). On the Indian subcontinent, ancient erotic art and texts such as the Kama Sutra indicate a widespread interest in diverse sexual activities, contradicting Davenport's gloomy assessment. The fifteenth century Islamic text, The Perfumed Garden of Sensual Delight, describes details of sexual interactions and skills where the female's orgasm is considered important. Though the text describes a kind of sexual ideal and not necessarily a cultural norm, a survey of sexual knowledge in a modern Islamic population of young Pakistani men (Qidwai, 2000) found that only 2.7% believed that women do not have orgasms. A majority 57.9% of men in the sample reported that they did know that women can have orgasms, whereas another 39.4% did not know if they did. Ignorance of female orgasm was common but was not the majority position.

In an authoritative study of the prevalence of female orgasm, Lloyd (2005) reviewed 32 published results and after considering particulars of measurement and definition, sampling biases, and so on, concluded that about 25% of heterosexual women always orgasm during intercourse, but as she notes, that estimate almost certainly includes instances of "assisted intercourse," where the clitoris is stimulated along with penetration. Without that, Lloyd estimates that "about 8 percent of women reliably have otherwise unassisted orgasms during penile-vaginal intercourse, while nearly all men do" (Dingfelder, 2011). In a recent study of Finnish women, Kontula and Miettinen (2016) corroborated Lloyd's estimate with a finding that 6% of women reported that they usually have an orgasm via stimulating the vagina.

Several recent studies show that modern men display some non-negligible degree of adeptness. Looking at self-report data from a broad U.S. sample, Frederick et al. (2017) found that 82% of the 24,102 heterosexual women in their sample reported orgasming half the time or more when "physically intimate" in the last month (their Figure 1). Further, 48% reported they "usually/always" receive oral sex, and 86% reported "usually/always" manual stimulation of genitals during their last sexual encounter. (Note respondents may have had some confusion about whether the question asked how often the respondent engaged in an activity or whether they engaged in it the last time they had sex.)

Similarly, Garcia et al. (2014) found that 73.4% of their sample of 1,154 heterosexual women reported experiencing orgasm in at least 50% of their sexual encounters with a familiar partner (their Table 1).

Studies reporting on the Australian Study of Health and Relationships published in 2006 (Richters, de Visser, Rissel, & Smith, 2006) and 2014 (Rissel et al., 2014), describing data collected at intervals more than a decade apart, found about the same rate of women's orgasms at their most recent encounter, 66.2% in 2001–2 and 68.9% in 2012–13. Richters, et al. (2014) concorded orgasm with activities performed and reported that 49.6% of incidents involving only penetrative sex resulted in orgasm for the female. The 2006 study reported that 73.3% of women reported manual stimulation of genitals at the most recent encounter, and 22.9% reported cunnilingus. Numbers were again comparable in 2014 with 75.7% of women reporting manual stimulation during their last encounter, and 24.3% reporting cunnilingus. This is a significant number of men showing some interest in their partners' pleasure while deferring their own climax.

The baseline case for male ineptness is an encounter where the couple has penetrative intercourse only, without stimulation of the clitoris by either partner; this is the kind of activity with "scant attention paid to the woman's response" that Davenport (1977) found in the research data available in the 1970s. In this scenario we would expect women to report single-digit measures of reliably orgasming, and they most definitely exceed that. If we take Lloyd's "reliably" to mean that women orgasm at least half the time during penile-vaginal intercourse, then the difference between 8% and approximately 75% represents the effect of partners doing more than the minimum that satisfies their own needs, as described by Davenport (1977).

Frederick (2017) and Garcia (2014) both report on lesbian orgasm rates and find that women reliably experience orgasm with another women approximately 15% more often than with men. Elliott (2015) has suggested that "It may be that lesbian women are free to explore one another's bodies without the underlying anxiety related to reaching orgasm in a 'normal' way through penetrative sex (p.67)." Other explanations are possible; the rates for women with female partners probably peg the top of the scale. With a perfectly adept partner we might expect about 90% of women to orgasm half the time or more. Male partners fall short of that mark by about 13%. We would not take this as evidence for the conclusion that "men take the initiative and, without extended foreplay, proceed vigorously toward climax without much regard for achieving synchrony with the women's orgasm (Davenport, 1977)." Qualitative anthropological reports from a nonsystematic sample of cultures do not refute Davenport's opinion, which was not backed up by any systematic empirical support. However, evidence from diverse societies including our own modern Western society does demonstrate that male interest in the female's orgasm is widespread.

Table 1 compiles some of the findings for comparison and identification of patterns. Though measures differ between studies, the trend is clear. Penetrative sex alone elicits orgasm in a small percentage of women. The opportunity to add stimulation of the clitoris increases the probability of orgasm above the 50% mark, with a solid majority

TABLE 1 Self-Reported Orgasmic Success for Women (in Percent of Participants)

Source	Unassisted vaginal penetration	Penetration unspecified		Recent rate heterosexual women	Recent rate lesbian women
		Always	Mostly		
Lloyd	8	25	>50		
Frederick				82	94
Garcia				73.4	85.6
Rissel				66.2[a]	
Richters		49.6[a]		68.9[a]	
Kontula	6	54 (clitoral and vaginal)			

Note: [1]Mostly: over 50% of time. "Unassisted penetration" estimated by Lloyd in Dingfelder (2011). "Penetration unspecified" from Lloyd (2005) review of literature, may be assisted penetration or not: "a narrow majority of women have orgasm with intercourse more than half the time." "Recent rate" presents recent sexual encounter no matter what activities, data from Frederick et al. (2017), Figure 1, and Garcia, et al. (2014), Table 1. Kontula and Miettinen (2016) data from FINSEX survey.
[a]Percent reporting orgasm in most recent encounter.

of women in the cited studies reporting attainment of orgasm in two-thirds to four-fifths of their sexual encounters, indicating that partners practiced some form of clitoral stimulation beyond penile penetration.

"Foreplay" is a term used to describe activities intended to stimulate the woman in order to arouse her and prepare her for intercourse. These activities, which are considered enlightened and considerate in Western culture, offer the opportunity for pleasure for the woman in the earlier part of a situational progression that culminates in penetration and male ejaculation. That is, the concept of foreplay assumes that male orgasm is the goal of sexual interaction, with the woman's pleasure serving instrumentally to pave the way to it. It is impossible to statistically disentangle reported behaviors that are intended to elicit the woman's orgasm from those which are intended to set the stage for penetration, but whatever the intention, oral and manual stimulation and deep kissing do tend to lead to orgasm. For example, reanalysis of Frederick, et al.'s Table 5 finds positive correlation $r = 83.2$, $P < 0.0001$, between the number of reported activities at the most recent interaction and percentage of "Usually-Always" orgasm for heterosexual women. It is possible that male partners consider the woman's orgasm to be an important part of the process, or it may be an epiphenomenon that "just happens" along the path to the male's climax. In either case, males who engage in nonpenetrative sexual behaviors, whatever their intention, are more likely to elicit orgasm in their female partners.

Thus, despite the comedians and complaints it appears justified to grant that more than a few human males, whether in tropical tribal cultures or modern industrialized society, have attained some degree of sexual adeptness. This finding is not necessary for the present proposal but should at least give pause to those who find it incredible that a few early men could have been adept at discovering and enacting the behaviors that would result in their partners' orgasm, when her clitoris was small, hooded, situated distantly from the vaginal orifice in a physiologically unique arrangement, and his own sexual interest was sustained only until his ejaculation.

8 | ADAPTIVENESS AND FERTILITY

The present argument regards the evolution of prosocial empathy partly as a consequence of the need of male partners to respond to the female sexual preference, namely find the way to solve the difficulty to elicit female orgasm. It is plausible to ask then whether this evolutionary scenario may not also lead to an association between the female orgasm and female fertility as a secondary consequence.

As follows from our scenario, the females with orgasms would be primarily the females in the relationship with the more adept partners. If the ability to elicit female orgasm provided a selective advantage to males this might at the same time also lead to higher fertility of women associated with such males, given that the relationship is maintained. The major advantage for the male thereby does not arise from more frequent reproductive sex with the same female (i.e., the relationship is not necessarily exclusive), but repeated encounters might nevertheless have built up a sense of intimacy and responsibility between the couple and protection of a caring male may secondarily increase the survival chances of the female and her offspring.

Zietsch and Santilla (2013) have tested directly, whether women who have more orgasms are more fertile, in order to infer whether female orgasm is adaptive. They found no significant correlation between orgasm rate and number of offspring, concluding that there is no strong causal relationship between orgasm and fertility.

We do not think the lack of strong correlation between orgasm and fertility contradicts our present model. It is first noteworthy that our model suggests a secondary effect on females under specific circumstances, of the selection that acts primarily on males. But above all it suggest a past process that may be hard to detect in modern populations for several reasons, one being that its dominance may be, or have become, weak, but also due to the effects of contraception, and the percentage of women that do not depend on adept male for orgasm.

9 | CONCLUSIONS

This perspective suggests an evolutionary role for female orgasm in shaping human societal traits. Importantly, this evolutionary role explicitly does not provide an explanation for the *origin* of female orgasm, but it might nevertheless have contributed the reason for female orgasm's maintenance in evolution.

Penetrative intercourse is orgasmic for men, and in an androcentric culture the female's experience may seem less important than the male's, with the result being a public understanding of sex that normalizes the act favored by males. Further, once emerging humans came to understand the role of penetration in reproduction, sexual behavior would likely have been culturally defined as activity that is "intended for" procreation, and nonreproductive behaviors that "only" elicit female orgasms could be downgraded and denigrated as nonessential or even nonsensical. These mutually reinforcing misunderstandings would have affected human history, and they certainly still affect modern history, making it, among other things, possible for modern humans to wonder why the female orgasm exists or to ignore it altogether.

The present analysis suggests an evolutionary mechanism for the development of the foundational traits that make culture and peaceful sociality possible in our species. Women, who were not sufficiently stimulated during penetrative intercourse, preferred male partners who would empathize and care enough to stimulate them during sexual interactions. Some but not all males had the ability to sense a female's need and the motivation to respond to it, delaying their own orgasm. Those adept males had a selection advantage, and the traits that supported adeptness increased in prevalence over the generations.

Over time the capacity for empathy, perspective-taking, innovation, and adaptiveness, caring, and self-discipline became dominant in the population, even if the particular knowledge and skill of orgasm elicitation specifically was lost or suppressed culturally. And it should be emphasized again that the model does not require sexual skill per se to be heritable, but rather the aptitude for attending to the partner in a more general sense, where procreational sex is only one use case.

The model proposed here is one of the evolution of a relational trait, which is dependent on the interaction and properties of both sexes, the female preference and male adeptness, rather than being attributed to a single individual (Fisher, 1915; Kirkpatrick, 1982; Lande, 1981; Prum, 2017). Physical characteristics of the female create the opportunity for success of empathic and altruistic social behavior in the male, and the aptitude for such behavior is transmitted to offspring. Relational traits often evade treatment by straightforward individual-based evolutionary models, but are crucial to the evolution of interpersonal social patterns.

In sum, the present thesis suggests that the pattern of human sexual responses created an opportunity to bias mate selection in a direction that favored genetic propagation of prosocial qualities demonstrated by an early male's ability to elicit the female's orgasm. This complex of qualities increased the probability of propagation of the adept male's genes and the fitness of the couple's offspring and further it is noted that no matter how overtly suppressed these loving qualities may be in any society they are the building-blocks of the complex human social structures we know today.

ORCID

James Kennedy http://orcid.org/0000-0002-5393-2771

REFERENCES

Allen, M. L., & Lemmon, W. B. (1981). Orgasm in female primates. *American Journal of Primatology*, *1*, 1098–2345. https://doi.org/10.1002/ajp.1350010104

Bizimana, N. (2010). Another way for lovemaking in Africa: Kunyaza, a traditional sexual technique for triggering female orgasm at heterosexual encounters. *Sexologies*, *19*(3)157–162. https://doi.org/10.1016/j.sexol.2009.12.003

Burns, J. (2016). How The 'Niche' Sex Toy Market Grew Into An Unstoppable $15B Industry. In *Forbes*, July 15, 2016. Retrieved from https://www.forbes.com/sites/janetwburns/2016/07/15/adult-expo-founders-talk-15b-sex-toy-industry-after-20-years-in-the-fray/#736315c338a1 .

Coria-Avila, G. A., Herrera-Covarrubias, D., Ismail, N., & Pfaus, J. G. (2016). The role of orgasm in the development and shaping of partner preferences. *Socioaffective Neuroscience & Psychology*, *6*, https://doi.org/10.3402/snp.v6.31815

Dahl, J. F. (1985). The External Genitalia of Female Pygmy Chimpanzees. *The Anatomical Record*, *211*, 24–28.

Davenport, W. H. (1977). Sex in cross-cultural perspective. In F. A. Beach (Ed.), *Human Sexuality in Four Perspectives* (pp. 115–163). Baltimore: Johns Hopkins University Press.

De Waal, F. (2010). *The age of empathy: Nature's lessons for a kinder society*. US: Broadway Books.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, *91*, 176–180. https://doi.org/10.1007/bf00230027

Dingfelder, S. F. (2011). Understanding orgasm. *APA Monitor*, *42*(4), 42.

Dixson, A. (2015). Primate sexuality. *The International Encyclopedia of Human Sexuality*, 861–1042. https://doi.org/10.1002/9781118896877.wbiehs375

Eibl-Eibesfeldt (1989). *Human ethology*. New York: Aldine de Gruyter. https://doi.org/10.1002/ajpa.1330820215

Elliott, & Georgina, F. (2015). Coming to understand. (Unpublished Doctoral thesis, City University London).

Fisher, R. A. (1915). The evolution of sexual preference. *The Eugenics Review*, *7*(3), 184–192.

Frederick, D. A., John, H. K., Garcia, J. R., & Lloyd, E. A. (2017). Differences in Orgasm Frequency Among Gay, Lesbian, Bisexual, and Heterosexual Men and Women in a U.S. National Sample. Archives of Sexual Behavior (Epub ahead of print). https://doi.org/10.1007/s10508-017-0939-z

Gallese, V. (2003). The roots of empathy: The shared manifold hypothesis and the neural basis of intersubjectivity. *Psychopathology*, *36*(4), 171–180. https://doi.org/10.1159/000072786

Garcia, J. R., Lloyd, E. A., Wallen, K., & Fisher, H. E. (2014). Variation in orgasm occurrence by sexual orientation in a sample of U.S. singles. *Journal of Sexual Medicine*, *11*, 2645–2652. https://doi.org/10.1111/jsm.12669

Gladwin, T., & Sarason, S. B. (1953). *Truk: Man in paradise*. Viking Fund Publication in Anthropology No. 20, New York.

Gómez, J. M., Verdú, M., González-Megías, A., & Méndez, M. (2016). The phylogenetic roots of human lethal violence. *Nature.538*, 233–237. https://doi.org/10.1038/nature19758

Gould, S. J., & Vrba, E. S. (1982). Exaptation—A missing term in the science of form." *Paleobiology*, *8*(1), 4–15. https://doi.org/10.1017/s0094837300004310

Gräslund, B. (2004). *Early humans and their world*. London: Routledge. https://doi.org/10.4324/9780203306598

Gray, P. B. (2013). Evolution and human sexuality. *American Journal of Physical Anthropology*, *57*, 94–118. https://doi.org/10.1002/ajpa.22394

Hrdy, S. B. (2011). *Mothers and others: The evolutionary origins of mutual understanding*. Cambridge, MA: Harvard University Press.

Huynh, H. K., Willemsen, A. T., & Holstege, G. (2013). Female orgasm but not male ejaculation activates the pituitary. A PET-neuro-imaging study. *Neuroimage*, *76*, 178–182. https://doi.org/10.1016/j.neuroimage.2013.03.012

Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annual Review of Psychology*, *60*(1), 653–670. https://doi.org/10.1146/annurev.psych.60.110707.163604

Kimmel, M. S., & Holler, J. Z. (2000). Spanning the world: Cross-cultural constructions of gender (Chapter 3). *The Gendered Society*. New York: Oxford University Press.

Kirkpatrick, M. (1982). Sexual selection and the evolution of female choice. *Evolution*, *82*, 1–12.

Kontula, O., & Miettinen, A. (2016). Determinants of female sexual orgasms, *Socioaffective Neuroscience & Psychology*, *6*(1), 31624, https://doi.org/10.3402/snp.v6.31624

Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the United States of America*, *78*, 3721–3725.

Lauritsen, J. L., Heimer, K., & Lynch, J. P. (2009). Trends in the gender gap in violent offending: New evidence from the National Crime Victimization Survey. *Criminology*, *47*(2), 361–399. https://doi.org/10.1111/j.1745-9125.2009.00149.x

Levin, R. J. (2011). Can the controversy about the putative role of the human female orgasm in sperm transport be settled with our current physiological knowledge of coitus?. *The Journal of Sexual Medicine*, *8*(6), 1566–1578. https://doi.org/10.1111/j.1743-6109.2010.02162.x

Lloyd, E. A. (2005). *The case of the female orgasm: Bias in the science of evolution*. Cambridge, MA: Harvard University Press.

Lloyd, E. A. (2015). Adaptationism and the logic of research questions: How to think clearly about the evolutionary causes. *Biological Theory*, *10*, 343–362. https://doi.org/10.1007/s13752-015-0214-2

Miller, G. (2000). Mental traits as fitness indicators: Expanding evolutionary psychology's adaptationism. *Annals of the New York Academy of Sciences*, *907*(1), 62–74. https://doi.org/10.1111/j.1749-6632.2000.tb06616.x

Miller, G. (2011). *The mating mind: How sexual choice shaped the evolution of human nature*. New York: Anchor Books.

Moral, B. (2002). Erotic legends and narratives In Chuuk, Micronesia. *Micronesian Journal Of The Humanities And Social Sciences*, *1*, 26–38.

Morris, D. (1967). *The naked ape: A zoologist's study of the human animal*. London: Cape.

Motta-Mena, N. V., & Puts, D. A. (2016). Endocrinology of human female sexuality, mating, and reproductive behavior, *Hormones and Behavior*, *91*, 19–35. https://doi.org/10.1016/j.yhbeh.2016.11.012

Needham, J. (1956). *Science and civilization in China (Vol. 2)*. London: Cambridge University Press.

Pavelka, M. S. M. (1995). Sexual Nature: What Can We Learn from a Cross-Species Perspective? in Sexual Nature/Sexual Culture. In P. R. Abramson & S. D. Pinkerton (Eds.), *Sexual Nature/Sexual Culture*. Chicago: University of Chicago Press.

Pavličev, M., & Wagner, G. (2016). The evolutionary origin of female orgasm. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, *326*(6), 326–337. https://doi.org/10.1002/jez.b.22690

Pearson, A. (2011). Female orgasm: Happy accident or evolved trait? *New Scientist*, *211*, 11. https://doi.org/10.1016/s0262-4079(11)62251-3

Prum, R. O. (2017). *The evolution of beauty: How Darwin's forgotten theory of mate choice shapes the natural world—and us*(1st ed.). New York: Doubleday.

Qidwai, W. (2000). Perceptions about female sexuality among young Pakistani men presenting to family physicians at a teaching hospital in Karachi. *Journal of Pakistan Medical Association*, *50*(2), 74–77.

Richters, J., de Visser, R., Rissel, C., & Smith, A. (2006). Sexual practices at last heterosexual encounter and occurrence of orgasm in a national survey. *Journal of Sex Research*, *43*(3), 217–226. https://doi.org/10.1080/00224490609552320

Rissel, C., Badcock, P. B., Smith, A. M. A., Richters, J., de Visser, R. O., Grulich, A. E., & Simpson, J. M. (2014). Heterosexual experience and recent heterosexual encounters among Australian adults: The Second Australian Study of Health and Relationships. *Sexual Health*, *11*(5), 416. https://doi.org/10.1071/sh14105

Sefcek, J. A., Brumbach, B. H., Vasquez, G., & Miller, G. F. (2007). The evolutionary psychology of human mate choice: How ecology, genes, fertility, and fashion influence mating strategies. *Journal of Psychology & Human Sexuality*, *18*(2-3), 125–182. https://doi.org/10.1300/j056v18n02_05

Skafte, I., & Silberschmidt, M. (2014). Female gratification, sexual power and safer sex: Female sexuality as an empowering resource among women in Rwanda, Culture. *Health & Sexuality: An International Journal for Research, Intervention and Care*, 16:1, 1–13, https://doi.org/10.1080/13691058.2013.815368

Swartz, M. J. (1958). Sexuality on Romonum, Truk. *American Anthropologist*, *60*, 467–486.

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

Taylor, C. C. (1990). "Condoms and Cosmology: The 'Fractal' Person and Sexual Risk in Rwanda." *Social Science & Medicine*, *31* (9): 1023–1028.

Tjaden, P. G., & Thoennes, N. (2006). *Extent, nature, and consequences of rape victimization: Findings from the National Violence Against Women Survey*. Washington, DC: US Department of Justice, Office of Justice Programs, National Institute of Justice. https://doi.org/10.1037/e513832006-001

Urdal, H. (2006). A Clash of Generations? Youth Bulges and Political Violence. *International Studies Quarterly*, *50*(3), 607–629. https://doi.org/10.1111/j.1468-2478.2006.00416.x

Wagner, G. P., & Pavlicev, M. (2017). Origin, function and effects of female orgasm: All three are different. Reply to comments by Dr. Barry Komisaruk. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*. https://doi.org/10.1002/jez.b.22737

Wallen, K., & Lloyd, E. A. (2008). Clitoral variability compared with penile variability supports nonadaptation of female orgasm. *Evolution & Development*, *10*, 1–2. https://doi.org/10.1111/j.1525-142x.2007.00207.x

Wallen, K., & Lloyd, E. A. (2011). Female sexual arousal: Genital anatomy and orgasm in intercourse. *Hormones and behavior*, *59*(5), 780–792. https://doi.org/10.1016/j.yhbeh.2010.12.004

Wolfe, L. D. (1991). Human evolution and the sexual behavior of female Primates. In J. D. Loy & C. B. Peters (Eds.), *Understanding Behavior: What Primate Studies Tell Us About Human Behavior*. Cary, NC: Oxford University Press. In c.

Young, L. J., & Wang, Z. (2004). The neurobiology of pair bonding. *Nature Neuroscience*, *7*(10), 10481054. https://doi.org/10.1038/nn1327

Zietsch, B. P., & Santtila, P. (2013). No direct relationship between human female orgasm rate and number of offspring. *Animal Behaviour*, *86*, 253–255. https://doi.org/10.1016/j.anbehav.2013.05.011

How to cite this article: Kennedy J, Pavličev M. Female orgasm and the emergence of prosocial empathy: An evo-devo perspective. *J Exp Zool (Mol Dev Evol)*. 2018;1–10. https://doi.org/10.1002/jez.b.22795