

Evolution and Human Behavior 33 (2012) 1-9

Evolution and Human Behavior

# Original Article

# Men's masculinity and attractiveness predict their female partners' reported orgasm frequency and timing

David A. Puts<sup>a,\*</sup>, Lisa L.M. Welling<sup>a</sup>, Robert P. Burriss<sup>a,1</sup>, Khytam Dawood<sup>b</sup>

<sup>a</sup>Department of Anthropology, Pennsylvania State University, University Park, PA 16802, USA

<sup>b</sup>Department of Psychology, Pennsylvania State University, University Park, PA 16802, USA

Initial receipt 25 January 2011; final revision received 10 March 2011

#### **Abstract**

It has been hypothesized that female orgasm evolved to facilitate recruitment of high-quality genes for offspring. Supporting evidence indicates that female orgasm promotes conception, although this may be mediated by the timing of female orgasm in relation to male ejaculation. This hypothesis also predicts that women will achieve orgasm more frequently when copulating with high-quality males, but limited data exist to support this prediction. We therefore explored relationships between the timing and frequency of women's orgasms and putative markers of the genetic quality of their mates, including measures of attractiveness, facial symmetry, dominance, and masculinity. We found that women reported more frequent and earlier-timed orgasms when mated to masculine and dominant men—those with high scores on a principal component characterized by high objectively-measured facial masculinity, observer-rated facial masculinity, partner-rated masculinity, and partner-rated dominance. Women reported more frequent orgasm during or after male ejaculation when mated to attractive men—those with high scores on a principal component characterized by high observer-rated and self-rated attractiveness. Putative measures of men's genetic quality did not predict their mates' orgasms from self-masturbation or from non-coital partnered sexual behavior. Overall, these results appear to support a role for female orgasm in sire choice.

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Keywords: Evolution; Female orgasm; Good genes; Mate choice

### 1. Introduction

Female orgasm may have evolved to function in sire choice by increasing the probability of fertilization from high quality males (Puts, 2006, 2007; Puts & Dawood, 2006; Smith, 1984; Thornhill, Gangestad, & Comer, 1995). Such an adaptation could be favored by selection if some ancestral females mated (1) within a single ovulatory cycle with males who varied in quality and/or (2) in different ovulatory cycles with males of varying quality, but the costs of forgoing fertilization in one cycle were sometimes offset by the benefits of reproducing with a higher quality male in a future cycle.

Consistent with the sire choice hypothesis, several lines of evidence suggest that women's orgasm promotes conception. For example, peristaltic uterine contractions

E-mail address: dap27@psu.edu (D.A. Puts).

transport sperm through the female reproductive tract in humans (Zervomanolakis et al., 2007, 2009) and nonhuman animals (Fox & Fox, 1971; Singer, 1973). These peristaltic contractions are induced both by electrical stimulation in nonhuman animals (Beyer, Anguiano, & Mena, 1961; Setekleiv, 1964) of brain regions activated during orgasm in women (Komisaruk et al., 2004) and by treatment in women with oxytocin (Wildt, Kissler, Licht, & Becker, 1998; Zervomanolakis et al., 2007, 2009), a hormone released during orgasm (Blaicher et al., 1999; Carmichael et al., 1987; Carmichael, Warburton, Dixen, & Davidson, 1994). Importantly, during the fertile phase of the ovulatory cycle, oxytocin induces the transport of a semen-like fluid into the oviduct with the dominant follicle (Wildt et al., 1998). Such directed transport should promote fertilization by bringing the sperm into proximity with the ovum and the oviductal epithelium. Contact with oviductal epithelium may prolong sperm longevity, increase the number of capacitated sperm (sperm capable of fertilizing an ovum), and lengthen the interval over which some

<sup>\*</sup> Corresponding author.

Current address: Department of Psychology, University of Stirling, UK.

sperm in an ejaculate are capacitated (Smith, 1998; Suarez, 1998, but see Levin, 2002).

Orgasm (Fox, Wolff, & Baker, 1970) and oxytocin (Wildt et al., 1998) may reverse uterine pressure from outward to inward, which may prevent sperm loss from "flowback" and aid sperm in reaching the oviducts. Indeed, Baker and Bellis (1993) found that female orgasm predicted greater sperm retention, although these results have been questioned (Lloyd, 2005, but see Puts & Dawood, 2006). Female orgasm may also allow the earlier entry of sperm into the cervix by resolving the "vaginal tenting" of sexual arousal, which elevates the cervix from the posterior vaginal wall, removing it from the semen pool (Levin, 2002). This should remove sperm from the more hostile environment of the vagina, prevent sperm loss, and help sperm reach the oviducts (Fox & Fox, 1971). Prolactin secretion during orgasm may also capacitate sperm (Meston, Levin, Sipski, Hull, & Heiman, 2004). Orgasmic vaginal contractions may excite male ejaculation (Fox & Fox, 1971; Meston et al., 2004), which could coordinate ejaculation with the various possible conception-enhancing processes associated with orgasm in women. Finally, the affective reward value of orgasm (e.g., Eschler, 2004) may motivate women to continue copulating until orgasm is achieved, or to copulate again with males with whom they experienced orgasm.

In addition, the timing of women's orgasm may influence conception. Baker and Bellis (1993) found that women's orgasms between 1 min before and 45 min after male ejaculation predicted sperm retention. Thus, orgasm either immediately before or within a long interval after ejaculation may promote conception. Alternatively, indirect evidence suggests that female orgasm specifically before male ejaculation promotes conception. Female orgasm before ejaculation is associated with greater sexual satisfaction (Darling, Davidson, & Cox, 1991), perhaps because it allows for coital and possibly vaginal orgasm, which women may find more satisfying than clitorallyinduced orgasm (Davidson & Darling, 1989). Because positive emotion may function to reinforce fitness-enhancing behavior (Plutchik, 1980), this timing effect suggests greater fitness benefits, such as elevated probability of conception, when female orgasm occurs before ejaculation. Moreover, greater sexual satisfaction is likely to stimulate greater oxytocin release (Carmichael et al., 1994), which evidence reviewed above suggests would further elevate the probability of fertilization.

If female orgasm functions in sire choice by promoting conception, then women should be likelier to experience orgasm with males whose genes would augment fitness in the women's offspring. Testing this proposition is complicated in part because evolutionary biologists have no ideal metric for genetic quality. However, several measures are commonly used.

The major histocompatibility complex (MHC) is the main genomic region mediating disease resistance, and

mating with MHC-compatible mates (those discordant at MHC loci) should produce offspring with stronger immune systems (Potts & Wakeland, 1993). Olfactory preferences for MHC-compatible mates have been observed across vertebrate taxa, including humans (reviewed in Roberts & Little, 2008, see also Chaix, Cao, & Donnelly, 2008; Lie, Rhodes, & Simmons, 2008; Roberts et al., 2005). Women reported more orgasms if their MHC genes were complementary with their partner's, but only during the fertile ovulatory cycle phase (Garver-Apgar, Gangestad, Thornhill, Miller, & Olp, 2006).

Physical attractiveness is another putative measure of genetic quality (Andersson, 1994; Gangestad & Buss, 1993; Grammer, Fink, Moller, & Thornhill, 2003). Men's attractiveness predicted their female partner's copulatory orgasm frequency, although men's partners assessed attractiveness, so orgasm may have caused women to find their partners more attractive, rather than the reverse (Shackelford et al., 2000). In another study, women's reported copulatory orgasms were marginally significantly more frequent if their mates were independently rated as being more attractive and significantly more frequent if their mates had lower bodily fluctuating asymmetry (FA, asymmetry in anatomical traits that are normally bilaterally symmetric, a putative inverse measure of genetic quality) (Thornhill et al., 1995).

Androgen-dependent, masculine traits may also indicate heritable fitness because androgens may be produced in proportion to inherited immunocompetence (Folstad & Karter, 1992) and in inverse proportion to number of harmful mutations (Zahavi & Zahavi, 1997). In addition, many masculine traits may have originated in men primarily through male dominance contests rather than female choice (Puts, 2010) but may be especially strong indicators of genetic quality. This is because traits used in contests tend to be costly to produce, constantly tested by competitors, and thus should provide accurate information about male quality to potential mates (Berglund, Bisazza, & Pilastro, 1996). However, we are aware of no study that has explored relationships between men's masculinity or dominance and orgasm in their mates.

We therefore examined relationships between putative markers of men's genetic quality: attractiveness ratings, dominance ratings, facial FA and masculinity (rated and objectively measured from facial images)—and the frequency and timing of copulatory orgasm in their female partners.

#### 2. Methods

## 2.1. Participants

Participants were drawn from a larger study of relationship formation comprising 117 heterosexual couples from a north eastern US university. Excluding couples in which at least one member opted out after participating, did not consent to being photographed or exhibited facial

injury, our sample included 110 men (mean age=20.76, S.D.=3.37, range=18-45) and 110 women (mean age=20.12, S.D.=1.92, range=18-28). One hundred and eight men identified as white, one as Filipino and one as Hispanic; 104 women identified as white, and one each identified as American Indian, Asian Indian, Hispanic and Native Hawaiian. Participants were compensated with either US \$14 or course credit.

#### 2.2. Procedures

Participants attended two laboratory sessions 1 week apart. During the first session, we photographed participants in a windowless laboratory with consistent overhead lighting, using an 8.0-megapixel Olympus E-300 digital camera with built-in flash, a focal distance of approximately 2 m and standardized white-balance. Participants removed spectacles and facial jewelry, maintained a neutral expression, ensured that their heads were not tilted and used hair bands to remove hair from forehead and ears.

During both sessions, participants completed a questionnaire at private computer workstations. They reported date of birth and relationship length to the nearest month. On 10-point scales (1=not at all, 10=very), women rated their own attractiveness and their partner's dominance and masculinity; men rated their own attractiveness, dominance and masculinity and their partner's femininity. Using items modified from Thornhill et al. (1995), we asked the percentage of time that participants experienced orgasm (a) during sex with their partner in ways other than sexual intercourse (e.g., oral sex), (b) during sexual intercourse (vaginal penetration with the penis), (c) before their partner during sexual intercourse, (d) after their partner during sexual intercourse or (e) at the same time as their partner during sexual intercourse. In addition, we asked the percentage of time that participants experienced orgasm during self-masturbation. Responses from the two sessions were averaged. Women's reports of their relationship length and orgasm frequencies are used in the present study.

## 2.3. Masculinity and symmetry measurement

Using specialist software, we produced nine sexually dimorphic measures from distances between facial landmarks and used these measures to calculate a composite index of facial masculinity (Burriss, Roberts, Welling, Puts, & Little, in press). We also assessed horizontal and vertical asymmetry following Scheib, Gangestad, and Thornhill (1999), summing these for an index of overall facial asymmetry.

## 2.4. Masculinity and attractiveness ratings

For 70 couples, both partners consented to having their photograph used in internet-based research. We rotated and scaled photographs of these participants so that pupils



Fig. 1. Example of masked facial photograph.

lay on a horizontal line, and interpupilary distance was constant across photographs. We then masked photographs to obscure hair, neck and clothing (Fig. 1). Nine women and nine men at a northwestern UK university rated the photographs for attractiveness (seven-point scale: 1=very unattractive, 7=very attractive) and masculinity (1=very feminine, 7=very masculine). We instructed judges to rate masculinity against that of other persons of the same sex. Order of stimulus presentation and the rating tasks (female attractiveness, male attractiveness, female masculinity, male masculinity) were randomized. Each face received a mean other-rated attractiveness and mean other-rated masculinity score.

#### 3. Results

Descriptive statistics are reported in Table 1.

## 3.1. Principal components analyses

We performed separate principal components analyses (PCA) on variables related to male quality, female quality and female orgasm frequency. Components with eigenvalues >1 were varimax-rotated and saved as variables. In order to identify non-overlapping components of male and female quality and female orgasm frequency and to maximize interpretability of the results, we chose varimax rotation, which produces orthogonal (uncorrelated) components and

Table 1 Descriptive statistics

	N	Mean	Range	S.D.
Relationship length (months)	110	15.4	1–106	17.4
Partner-rated male dominance	115	5.7	1.5-9.5	1.6
Partner-rated male masculinity	115	7.5	1.0-10.0	1.6
Self-rated male attractiveness	114	6.8	3.0-10.0	1.2
Self-rated male dominance	112	6.4	1.5-9.0	1.5
Self-rated male masculinity	114	7.3	2.0-10.0	1.6
Other-rated male attractiveness	71	3.2	1.1-5.3	0.9
Other-rated male masculinity	71	4.3	2.3-6.2	0.9
Male asymmetry index	110	50.5	15.2-122.2	22.3
Male masculinity index	110	2.8	-3.2 to 8.2	2.6
Partner-rated female femininity	114	7.4	3.0-10.0	1.5
Self-rated female attractiveness	115	6.7	3.0-9.5	1.1
Other-rated female attractiveness	72	3.1	1.6-5.4	0.9
Other-rated female masculinity	72	4.1	2.3-6.2	0.9
Female asymmetry index	111	47.7	11.4-107.0	19.3
Female masculinity index	111	-2.8	-9.0 to 2.1	2.6
Coital orgasm frequency (%)*	86	52.5	"5-10%" to "95-100%"	32.8
Coital orgasm frequency before ejaculation (%)*	87	41.9	"5-10%" to "90-95%"	31.8
Coital orgasm frequency during ejaculation (%)*	85	27.7	"5-10%" to "95-100%"	23.3
Coital orgasm frequency after ejaculation (%)*	85	32.9	"5-10%" to "95-100%"	26.8
Non-coital partnered orgasm frequency (%)*	92	54.5	"5-10%" to "95-100%"	32.6
Self-masturbatory orgasm frequency (%)*	64	71.9	"5-10%" to "95-100%"	35.6

<sup>\*</sup> Mean calculated on midpoints of intervals.

tends to produce either large or small loadings of each variable onto a particular factor.

For the PCA performed on male traits (Tables 2 and 3), other-rated facial masculinity, facial masculinity index, partner-rated masculinity and partner-rated dominance loaded heavily on to PC1 ("Male Masculinity"). Other-rated facial attractiveness and self-rated attractiveness loaded heavily onto PC2 ("Male Attractiveness"). Men's self-rated dominance and masculinity loaded heavily onto PC3 ("Self-Rated Male Dominance").

For the PCA of female traits (Tables 4 and 5), otherrated masculinity and masculinity index loaded heavily positively, and other-rated attractiveness rated heavily negatively onto PC1 ("Female masculinity"). Partnerrated femininity and age loaded heavily negatively and positively, respectively, onto PC2 ("Partner-rated Female Masculinity"). Self-rated attractiveness loaded heavily positively, and asymmetry index loaded heavily negatively, onto PC3 ("Self-Rated Female Attractiveness/Symmetry").

For the PCA performed on female orgasm frequencies (Tables 6 and 7), frequency of female coital orgasm before male orgasm and frequency of female orgasm during coitus loaded heavily onto PC1 ("Female Coital Orgasm Before/Total"). Frequency of female coital orgasm after male orgasm and frequency during male orgasm loaded heavily onto PC2 ("Female Coital Orgasm After/During"). Frequency of female orgasm during self-masturbation and frequency of non-coital female orgasms

Table 2 Zero-order correlations among male traits (and *N*)

	Partner-rated masculinity	Self-rated attractiveness	Self-rated dominance	Self-rated masculinity	Other-rated facial attractiveness	Other-rated facial masculinity	Facial asymmetry index	Facial masculinity index
Partner-rated dominance	.51*** (115)	.06 (112)	.18 <sup>†</sup> (110)	.26** (112)	.08 (70)	.22 (70)	.02 (110)	.13 (110)
Partner-rated masculinity		.06 (112)	.28** (110)	.47*** (112)	11 (70)	.23† (70)	.06 (110)	.29** (110)
Self-rated attractiveness			.36*** (112)	.35*** (114)	.60*** (71)	.14 (71)	.12 (110)	.08 (110)
Self-rated dominance				.57*** (112)	.15 (71)	.08 (71)	01 (108)	.02 (108)
Self-rated masculinity					.11 (71)	.13 (71)	.02 (110)	$.17^{\dagger}$ (110)
Other-rated facial attractiveness						.39*** (71)	.17 (70)	.06 (70)
Other-rated facial masculinity							05 (70)	.51*** (70)
Facial asymmetry index								.13 (110)

<sup>\*</sup>p<.05, \*\*p<.01, \*\*\*p<.001, †p<.10.

Table 3
Component loadings for PCA performed on male traits

	Component			
	Male masculinity	Male attractiveness	Self-rated male dominance	
	EV=2.5, 27.5%	EV=1.8, 19.6%	EV=1.3, 14.2%	
Partner-rated dominance	.589	195	.148	
Partner-rated masculinity	.693	336	.393	
Self-rated attractiveness	029	.781	.352	
Self-rated dominance	041	.092	.831	
Self-rated masculinity	.294	.030	.811	
Other-rated facial attractiveness	.132	.846	.112	
Other-rated facial masculinity	.739	.389	096	
Facial asymmetry index	036	.404	117	
Facial masculinity index	.728	.148	.025	

EV, eigenvalue.

Percentages refer to the amount of variance explained.

with partner loaded heavily onto PC3 ("Female Non-coital Orgasm").

### 3.2. Multiple regression

Components of male quality were entered into separate multiple regression models to predict each component of female orgasm frequency, controlling for components of female quality and relationship duration.

Male Masculinity positively (t=2.18,  $\beta$ =.36, p=.039) and Male Self-rated Dominance negatively (t=-2.34,  $\beta$ =-.39, p=.027) predicted Female Coital Orgasm Before/ Total (all other p>.10; model:  $F_{32,7}$ =2.40, R=.63, p=.050, Table 8). Male Attractiveness (t=2.96,  $\beta$ =.50, t=.007) and relationship length (t=2.56, t=.43, t=.017) significantly predicted Female Coital Orgasm After/During (all other t=2.12; model: t=3.4, t=.64, t=.048, Table 9). Female Masculinity (t=-2.92, t=-.54, t=.007) significantly negatively predicted Female Non-coital Orgasm (all other t=2.38; model: t=3.7, t=1.36, t=53, t=2.65, Table 10). Entering men's age into these analyses did not alter the results.

Table 5
Component loadings for PCA performed on female traits

	Component			
	Female masculinity	Partner-rated female masculinity	Self-rated female attractiveness/ symmetry	
	EV=2.4, 34.4%	EV=1.2, 16.6%	EV=1.1, 15.4%	
Self-rated attractiveness	.097	010	.855	
Other-rated a ttractiveness	846	.144	.200	
Other-rated masculinity	.902	.152	130	
Facial asymmetry index	.279	.117	575	
Facial masculinity index	.752	.340	.155	
Partner-rated femininity	.080	880	.086	
Age at session one	.220	.561	041	

Percentages refer to the amount of variance explained.

#### 4. Discussion

Approximately 70% of the variation among women in copulatory orgasm frequencies is due to environmental differences (Dawood, Kirk, Bailey, Andrews, & Martin, 2005; Dunn, Cherkas, & Spector, 2005), although this estimate subsumes measurement error and all nongenetic influences, including psychosocial development (Cohen & Belsky, 2008; Harris, Cherkas, Kato, Heiman, & Spector, 2008) and prenatal environment (Wallen & Lloyd, 2011). Some of the environmental contribution to between-female variability in orgasm frequency results from variation in the quality of women's sexual experience (Brody & Weiss, 2010; Puppo, 2010; Richters, Visser, Rissel, & Smith, 2006; Singh, Meyer, Zambarano, & Hurlbert, 1998; Weiss & Brody, 2009), including characteristics of their sexual partners (Garver-Apgar et al., 2006; Shackelford et al., 2000; Thornhill et al., 1995).

We found that objective measures of the quality of women's mates—men's attractiveness and masculinity—significantly predicted the women's orgasms. Men's

Table 4
Zero-order correlations among female traits (and *N*)

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	Other-rated attractiveness	Other-rater masculinity	Facial asymmetry index	Facial masculinity index	Partner-rated femininity	Age at session 1
Self-rater attractiveness	.09 (71)	07 (71)	12 (111)	07 (111)	05 (112)	.04 (115)
Other-rater attractiveness		69*** (72)	24* (70)	40*** (70)	10 (71)	18 (71)
Other-rater masculinity			.25* (70)	.68*** (70)	12 (71)	.20 (71)
Facial asymmetry Index			` '	.14 (111)	00 (111)	.07 (111)
Facial masculinity index					08 (111)	.04 (111)
Partner-rated femininity						11 (112)

 $<sup>^{\</sup>dagger}p$ <.10, \*\*p<.01, \*p<.05, \*\*\*p<.001.

Table 6
Zero-order correlations among female orgasm frequency items (and N)

	Frequency of coital orgasm before partner	Frequency of coital orgasm after partner	Frequency of simultaneous coital orgasm	Frequency of partnered non-coital orgasm	Frequency of orgasm from self-masturbation
Frequency of coital orgasm Frequency of coital orgasm before partner	.55*** (86)	.21 <sup>†</sup> (85) 20 <sup>†</sup> (85)	.56*** (85) .18 <sup>†</sup> (85)	08 (82) 06 (83)	.14 (57) .06 (58)
Frequency of coital orgasm after partner		.20 (83)	.16 (84)	.09 (81)	.17 (56)
Frequency of simultaneous coital orgasm				.05 (81)	02 (57)
Frequency of partnered non-coital orgasm					.33* (61)

<sup>\*\*</sup>p<.01, †p<.10, \*p<.05, \*\*\*p<.001.

masculinity, a putative indicator of genetic quality, positively predicted a component of women's copulatory orgasm related to overall frequency and frequency before male ejaculation. Earlier-timed orgasms suggest more intense sexual arousal and indeed are associated with greater sexual pleasure (Darling et al., 1991). This positive affect may signal the realization of fitness benefits (Plutchik, 1980). Moreover, sexual arousal and orgasm stimulate oxytocin release (Carmichael et al., 1994), which causes the directed transport of a semen-like substance into the oviduct with the dominant follicle (Wildt et al., 1998). Thus, possible conception-promoting correlates of female orgasm may be especially effective and/or likely when copulation occurs with masculine males. Interestingly, this component of female orgasm was negatively predicted by male self-rated dominance and masculinity. Because more objective measures of male dominance, masculinity and attractiveness either weakly or negatively loaded onto the self-rated dominance/masculinity component, we suspect that selfrated dominance/masculinity measured something other than genetic quality.

Table 7
Component loadings for PCA performed on female orgasm frequency items

	Component				
	Female coital orgasm before/total	Female coital orgasm after/during	Female non-coital orgasm		
	EV=1.9, 32.2%	EV=1.4, 23.4%	EV=1.1, 18.6%		
Frequency of coital orgasm Frequency of coital orgasm before partner	.809 .901	.442 182	027 036		
Frequency of coital orgasm after partner	196	.816	.169		
Frequency of simultaneous coital orgasms	.330	.724	148		
Frequency of partner orgasm, other than intercourse	263	063	.731		
Frequency of orgasm via self-masturbation	.187	.097	.848		

EV=Eigenvalue, percentages refer to the amount of variance explained.

We also found that male partners' physical attractiveness, along with relationship length, predicted a component of women's copulatory orgasm related to frequency during or after male ejaculation. Baker and Bellis (1993) found greater sperm retention associated with women's orgasms occurring between 1 min before and 45 min after male ejaculation, a window roughly corresponding to the orgasm component that we identified. Indeed, Thornhill et al. (1995) found that men's attractiveness marginally significantly predicted, and low male FA significantly predicted, the occurrence of women's orgasms during or after male ejaculation, although FA did not load heavily onto any component of male quality in the present study.

Whereas men's masculinity and attractiveness predicted the frequency and timing of women's copulatory orgasms, these components did not predict women's orgasms achieved through self-masturbation or non-coital sexual activity with a partner. This suggests that male sire quality increases female orgasm specifically during sexual behaviors that could result in conception, thus supporting the sire choice hypothesis.

## 4.1. Limitations

The present data do not address by which proximate mechanisms men's attractiveness, dominance, and masculinity may affect the timing and frequency of their partners' orgasms. Several possibilities exist, including greater psychological excitement resulting from the male's visual (e.g., Penton-Voak & Perrett, 2000), acoustic (e.g., Puts, 2005) or olfactory (e.g., Wedekind, Seebeck, Bettens, &

Table 8
Results of multiple regression predicting female coital orgasm before/total

	β	t	p
Male masculinity	.36	2.18	.039
Male attractiveness	06	34	.737
Male self-rat. dom.	39	-2.35	.027
Female masculinity	30	-1.70	.102
Part-rat. female masc.	.04	.26	.801
Self-rat. female attr./symm.	.24	1.48	.150
Relationship duration	.04	.23	.819

Table 9
Results of multiple regression predicting Female Coital Orgasm After/During

	β	t	p
Male masculinity	26	-1.57	.128
Male attractiveness	.50	2.96	.007
Male self-rat. dom.	.24	1.44	.161
Female masculinity	.06	.37	.717
Part-rat. female masc.	03	17	.863
Self-rat. female attr./symm.	03	16	.871
Relationship duration	.427	2.56	.017

Paepke, 1995) qualities; physical tactile characteristics of the male, possibly including muscularity (Frederick & Haselton, 2007), weight (Thornhill et al., 1995), and penis size (Brody & Weiss, 2010; Lever, Frederick, & Peplau, 2006; Miller, 2000); and superior sexual technique or duration (Singh et al., 1998; Weiss & Brody, 2009), perhaps resulting from the greater sexual experience of more attractive or dominant men (Hodges-Simeon, Gaulin, & Puts, 2010; Hughes & Gallup, 2003; Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Perusse, 1993; Puts, Gaulin, & Verdolini, 2006).

Similarly, our data provide little information about the specific sexual behaviors that led to women's orgasms. For example, we asked female participants about the frequencies of their orgasms from sexual intercourse, defined this as vaginal penetration with the penis, and differentiated these orgasms from those obtained in other ways such as oral sex. Some participants may have interpreted this as a distinction between orgasms from sex with versus without penilevaginal intercourse, while others may have interpreted this as whether the immediate cause of orgasm was vaginal penetration with the penis.

Finally, our data cannot definitively rule out alternative evolutionary hypotheses, such as the hypothesis that orgasm in women is a byproduct of selection for orgasm in men (Symons, 1979). The present results would seem to suggest that female orgasm has been specially designed (Williams, 1966) for extracting genetic benefits. However, it is also possible that, for example, female orgasm is a byproduct of male orgasm, and that relationships between male mate quality and the frequency and timing of female orgasm reflect byproducts of pre-copulatory female mate choice mechanisms.

#### 4.2. Summary

Although our results require replication, they are consistent with the hypothesis that female orgasm is a copulatory mate choice mechanism, perhaps for selecting high-quality genes for offspring. Future research should address the proximate mechanisms by which male mate quality influences the frequency and timing of their partners' orgasmic response. More work is also needed to clarify

Table 10
Results of multiple regression predicting Female Non-Coital Orgasm

	β	t	p
Male masculinity	01	03	.977
Male attractiveness	.10	.52	.608
Male self-rat. dom.	.03	.16	.878
Female masculinity	54	292	.007
Part-rat. female masc.	03	14	.890
Self-rat. female attr./symm.	17	88	.387
Relationship duration	12	66	.516

whether female orgasm promotes conception, and if so, the role of its timing in relation to ejaculation.

## Acknowledgments

The authors thank Jill Armington, Emily Barben, Julia Barndt, Sara Carlson, Kathryn Cheney, Samantha Melonas, Diana Rosaleyra, Charlene Scheld and Kevin Singh for help with data collection, David Perrett and Bernard Tiddeman for use of the Psychomorph program, Anthony Little for use of his internet server, and Rob Kurzban and two anonymous reviewers for constructive comments on our manuscript.

#### References

Andersson, M. (1994). Sexual selection. Princeton, NJ: Princeton University Press.Baker, R. R., & Bellis, M. A. (1993). Human sperm competition: ejaculate manipulation by female and a function for the female orgasm. Animal Behaviour. 46, 887–909.

Berglund, A., Bisazza, A., & Pilastro, A. (1996). Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, *58*, 385–399.

Beyer, C., Anguiano, G., & Mena, F. (1961). Oxytocin release by stimulation of the cingulate gyrus. American Journal of Physiology, 200, 625–627.

Blaicher, W., Gruber, D., Bieglmayer, C., Blaicher, A. M., Knogler, W., & Huber, J. C. (1999). The role of oxytocin in relation to female sexual arousal. *Gynecologic Obstetric Investigation*, 47(2), 125–126.

Brody, S., & Weiss, P. (2010). Vaginal orgasm is associated with vaginal (not clitoral) sex education, focusing mental attention on vaginal sensations, intercourse duration, and a preference for a longer penis. *Journal of Sexual Medicine*, 7, 2774–2781.

Burriss, R. P., Roberts, S. C., Welling, L. L. M., Puts, D. A., & Little, A. C. (2011). Heterosexual romantic couples mate assortatively for facial symmetry, but not masculinity. *Personality and Social Psychology Bulletin*, 37(5), 601–613.

Carmichael, M. S., Humbert, R., Dixen, J., Palmisano, G., Greenleaf, W., & Davidson, J. M. (1987). Plasma oxytocin increases in the human sexual response. *Journal of Clinical Endocrinology and Metabolism*, 64(1), 27–31.

Carmichael, M. S., Warburton, V. L., Dixen, J., & Davidson, J. M. (1994).Relationships among cardiovascular, muscular, and oxytocin responses during human sexual activity. *Archives of Sexual Behavior*, 23(1), 59–79.

Chaix, R., Cao, C., & Donnelly, P. (2008). Is mate choice in humans MHC-dependent? PLoS Genetics, 4(9), e1000184.

Cohen, D. L., & Belsky, J. (2008). Avoidant romantic attachment and female orgasm: Testing an emotion-regulation hypothesis. *Attachment* and Human Development, 10(1), 1–10.

Darling, C. A., Davidson Sr, J. K., & Cox, R. P. (1991). Female sexual response and the timing of partner orgasm. *Journal of Sex and Marital Therapy*, 17(1), 3–21.

- Davidson, J. K., & Darling, C. A. (1989). Self-perceived differences in the female orgasmic response. Family Practice Research Journal, 8(2), 75–84.
- Dawood, K., Kirk, K. M., Bailey, J. M., Andrews, P. W., & Martin, N. G. (2005). Genetic and environmental influences on the frequency of orgasm in women. *Twin Reseach and Human Genetics*, 8(1), 27–33.
- Dunn, K. M., Cherkas, L. F., & Spector, T. D. (2005). Genetic influences on variation in female orgasmic function: A twin study. *Biology Letters*, 1(3), 260–263.
- Eschler, L. (2004). Prize Essay: The physiology of the female orgasm as a proximate mechanism. Sexualities. *Evolution & Gender*, 6(2-3), 171–194.
- Folstad, I., & Karter, A. J. (1992). Parasites, bright males and the immunocompetence handicap. *The American Naturalist*, 139, 603–622.
- Fox, C. A., & Fox, B. (1971). A comparative study of coital physiology, with special reference to the sexual climax. *Journal of Reproduction and Fertility*, 24(3), 319–336.
- Fox, C. A., Wolff, H. S., & Baker, J. A. (1970). Measurement of intravaginal and intra-uterine pressures during human coitus by radiotelemetry. *Journal of Reproduction and Fertility*, 22, 243–251.
- Frederick, D. A., & Haselton, M. G. (2007). Why is muscularity sexy? Tests of the fitness indicator hypothesis. *Personality and Social Psychology Bulletin*, 33(8), 1167–1183.
- Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. Ethology and Sociobiology, 14(2), 89–96.
- Garver-Apgar, C. E., Gangestad, S. W., Thornhill, R., Miller, R. D., & Olp, J. J. (2006). Major histocompatibility complex alleles, sexual responsivity, and unfaithfulness in romantic couples. *Psychological Science*, 17(10), 830–835.
- Grammer, K., Fink, B., Moller, A. P., & Thornhill, R. (2003). Darwinian aesthetics: Sexual selection and the biology of beauty. *Biological Reviews of the Cambridge Philosophical Society*, 78(3), 385–407.
- Harris, J. M., Cherkas, L. F., Kato, B. S., Heiman, J. R., & Spector, T. D. (2008). Normal variations in personality are associated with coital orgasmic infrequency in heterosexual women: A population-based study. *Journal of Sexual Medicine*, 5(5), 1177–1183.
- Hodges-Simeon, C. R., Gaulin, S. J., & Puts, D. A. (2010). Voice correlates of mating success in men: Examining "contests" versus "mate choice" modes of sexual selection. *Archives of Sexual Behavior*.
- Hughes, S., & Gallup, G. (2003). Sex differences in morphological predictors of sexual behavior: Shoulder-to-hip and waist-to-hip ratios. *Evolution and Human Behavior*, 24, 173–178.
- Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001).
  Male facial attractiveness: Evidence of hormone-mediated adaptive design. Evolution and Human Behavior, 22, 251–267.
- Komisaruk, B. R., Whipple, B., Crawford, A., Liu, W. C., Kalnin, A., & Mosier, K. (2004). Brain activation during vaginocervical self-stimulation and orgasm in women with complete spinal cord injury: fMRI evidence of mediation by the vagus nerves. *Brain Research*, 1024(1-2), 77–88.
- Lever, J., Frederick, D. A., & Peplau, L. A. (2006). Does size matter? Men's and women's views on penis size across the lifespan. *Psychology of Men* and Masculinity, 7, 129–143.
- Levin, R. J. (2002). The physiology of sexual arousal in the human female: A recreational and procreational synthesis. Archives of Sexual Behavior, 31(5), 405–411.
- Lie, H. C., Rhodes, G., & Simmons, L. W. (2008). Genetic diversity revealed in human faces. Evolution, 62(10), 2473–2486.
- Lloyd, E. A. (2005). The case of female orgasm: Bias in the science of evolution. Cambridge, MA: Harvard University Press; 2005.
- Meston, C. M., Levin, R. J., Sipski, M. L., Hull, E. M., & Heiman, J. R. (2004). Women's orgasm. *Annual Review of Sex Research*, 15, 173–257.
- Miller, G. F. (2000). The mating mind: How sexual choice shaped the evolution of human nature. New York: Doubleday.
- Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically: Further evidence. *Evolution and Human Behavior*, 21, 39–48.

- Perusse, D. (1993). Cultural and reproductive success in industrial societies: testing the relationship at proximate and ultimate levels. *Behavioral and Brain Sciences*, 16, 267–283.
- Plutchik, R. (1980). A general psychoevolutionary theory of emotion. In Emotion: Theory, research, and experience: Vol. 1, Theories of emotion. R. Plutchik & H. Kellerman (Eds). New York: Academic Press, pp. 3–24.
- Potts, W. K., & Wakeland, E. K. (1993). Evolution of MHC genetic diversity: a tale of incest, pestilence and sexual preference. *Trends in Genetics*, 9(12), 408–412.
- Puppo, V. (2010). Embryology and anatomy of the vulva: The female orgasm and women's sexual health. European Journal of Obstetrics, Gynecology, and Reproductive Biology.
- Puts, D. A. (2005). Mating context and menstrual phase affect women's preferences for male voice pitch. *Evolution and Human Behavior*, 26, 388–397.
- Puts, D. A. (2006). And hast thou slain the Jabberwock? Response to Wallen. *Archives of Sexual Behavior*, 35(6), 637–639.
- Puts, D. A. (2007). Of bugs and boojums: Female orgasm as a facultative adaptation. *Archives of Sexual Behavior*, 36(3), 337–339.
- Puts, D. A. (2010). Beauty and the beast: Mechanisms of sexual selection in humans. Evolution and Human Behavior, 31, 157–175.
- Puts, D. A., & Dawood, K. (2006). The evolution of female orgasm: Adaptation or byproduct? Twin Research and Human Genetics, 9(3), 467–472.
- Puts, D. A., Gaulin, S. J. C., & Verdolini, K. (2006). Dominance and the evolution of sexual dimorphism in human voice pitch. *Evolution and Human Behavior*, 27, 283–296.
- Richters, J., 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.
- Roberts, S. C., & Little, A. C. (2008). Good genes, complementary genes and human mate preferences. *Genetica*, 134(1), 31–43.
- Roberts, S. C., Little, A. C., Gosling, L. M., Jones, B. C., Perrett, D, I., Carter, V., et al. (2005). MHC-assortative facial preferences in humans. *Biology Letters*, 1(4), 400–403.
- Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceeding Biological Sciences*, 266(1431), 1913–1917.
- Setekleiv, J. (1964). Uterine motility of the estrogenized rabbit. V. Response to brain stimulation. *Acta Physiologica Scandinavica*, 62, 313–322.
- Shackelford, T. K., Weekes-Shackelford, V. A., LeBlanc, G. J., Bleske, A. L., Euler, H. A., & Hoier, S. (2000). Female coital orgasm and male attractiveness. *Human Nature*, 11, 299–306.
- Singer, I. (1973). The Goal of Human Sexuality. New York: W.W. Norton.
  Singh, D., Meyer, W., Zambarano, R. J., & Hurlbert, D. F. (1998).
  Frequency and timing of coital orgasm in women desirous of becoming pregnant. Archives of Sexual Behavior, 27(1), 15–29.
- Smith, R. L. (1984). Human sperm competition. In *Sperm competition and the evolution of animal mating systems*. R. L. Smith (Ed.). London: Academic Press, pp. 601–660.
- Smith, T. T. (1998). The modulation of sperm function by the oviductal epithelium. *Biology of Reproduction*, 58(5), 1102–1104.
- Suarez, S. S. (1998). The oviductal sperm reservoir in mammals: Mechanisms of formation. *Biology of Reproduction*, 58(5), 1105–1107.
- Symons, D. (1979). The evolution of human sexuality. New York: Oxford University Press.
- Thornhill, R., Gangestad, S. W., & Comer, R. (1995). Human female orgasm and mate fluctuating asymmetry. *Animal Behavior*, 50, 1601–1615.
- Wallen, K., & Lloyd, E. A. (2011). Female sexual arousal: Genital anatomy and orgasm in intercourse. Hormones and Behavior.
- Wedekind, C., Seebeck, T., Bettens, F., & Paepke, A. J. (1995). MHC-dependent mate preferences in humans. *Proceeding of the Royal Society B: Biological Sciences*, 260(1359), 245–249.
- Weiss, P., & Brody, S. (2009). Women's partnered orgasm consistency is associated with greater duration of penile-vaginal intercourse but not of foreplay. *Journal of Sexual Medicine*, 6(1), 135–141.
- Wildt, L., Kissler, S., Licht, P., & Becker, W. (1998). Sperm transport in the human female genital tract and its modulation by oxytocin as assessed by

- hysterosalpingoscintigraphy, hysterotonography, electrohysterography and Doppler sonography. *Human Reproduction Update*, 4(5), 655–666.
- Williams, G. C. (1966). Adaptation and natural selection. Princeton, NJ: Princeton University Press.
- Zahavi, A., & Zahavi, A. (1997). *The handicap principle*. New York: Oxford University Press.
- Zervomanolakis, I., Ott, H. W., Hadziomerovic, D., Mattle, V., Seeber, B. E. & Virgolini, I., (2007). Physiology of upward transport in the human
- female genital tract. Annals of the New York Academy of Sciences, 1101, 1–20
- Zervomanolakis, I., Ott, H. W., Muller, J., Seeber, B. E., Friess, S. C., Matte, V., et al. (2009). Uterine mechanisms of ipsilateral directed spermatozoa transport: Evidence for a contribution of the utero-ovarian countercurrent system. *European Journal of Obstetrics, Gynecology, and Reproductive Biology, 144*(Suppl 1), S45–S49.