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Original Article

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

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Abstract

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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 principle 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 principle 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. © 2011 Published by Elsevier Inc.

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

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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

transport sperm through the female reproductive tract in 38 humans (Zervomanolakis et al., 2007, 2009) and nonhuman 39 animals (Fox & Fox, 1971; Singer, 1973). These peristaltic 40 contractions are induced both by electrical stimulation in 41 nonhuman animals (Beyer, Anguiano, & Mena, 1961; 42 Setekleiv, 1964) of brain regions activated during orgasm 43 in women (Komisaruk et al., 2004) and by treatment in 44 women with oxytocin (Wildt, Kissler, Licht, & Becker, 45 1998; Zervomanolakis et al., 2007, 2009), a hormone 46 released during orgasm (Blaicher et al., 1999; Carmichael 47 et al., 1987; Carmichael, Warburton, Dixen, & Davidson, 48 1994). Importantly, during the fertile phase of the 49 ovulatory cycle, oxytocin induces the transport of a 50 semen-like fluid into the oviduct with the dominant follicle 51 (Wildt et al., 1998). Such directed transport should promote 52 fertilization by bringing the sperm into proximity with the 53 ovum and the oviductal epithelium. Contact with oviductal 54 epithelium may prolong sperm longevity, increase the 55 number of capacitated sperm (sperm capable of fertilizing 56 an ovum), and lengthen the interval over which some 57

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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 114 MHC loci) should produce offspring with stronger immune 115 systems (Potts & Wakeland, 1993). Olfactory preferences 116 for MHC-compatible mates have been observed across 117 vertebrate taxa, including humans (reviewed in Roberts & 118 Little, 2008, see also Chaix, Cao, & Donnelly, 2008; Lie, 119 Rhodes, & Simmons, 2008; Roberts et al., 2005). Women 120 reported more orgasms if their MHC genes were complenentary with their partner's, but only during the fertile 122 ovulatory cycle phase (Garver-Apgar, Gangestad, Thornhill, 123 Miller, & Olp, 2006).

Physical attractiveness is another putative measure of 125 genetic quality (Andersson, 1994; Gangestad & Buss, 1993; 126 Grammer, Fink, Moller, & Thornhill, 2003). Men's 127 attractiveness predicted their female partner's copulatory 128 orgasm frequency, although men's partners assessed 129 attractiveness, so orgasm may have caused women to find 130 their partners more attractive, rather than the reverse 131 (Shackelford et al., 2000). In another study, women's 132 reported copulatory orgasms were marginally significantly 133 more frequent if their mates were independently rated as 134 being more attractive and significantly more frequent if 135 their mates had lower bodily fluctuating asymmetry (FA, 136 asymmetry in anatomical traits that are normally bilaterally 137 symmetric, a putative inverse measure of genetic quality) 138 (Thornhill et al., 1995).

Androgen-dependent, masculine traits may also indicate 140 heritable fitness because androgens may be produced in 141 proportion to inherited immunocompetence (Folstad & 142 Karter, 1992) and in inverse proportion to number of 143 harmful mutations (Zahavi & Zahavi, 1997). In addition, 144 many masculine traits may have originated in men primarily 145 through male dominance contests rather than female choice 146 (Puts, 2010) but may be especially strong indicators of 147 genetic quality. This is because traits used in contests tend to 148 be costly to produce, constantly tested by competitors, and 149 thus should provide accurate information about male quality 150 to potential mates (Berglund, Bisazza, & Pilastro, 1996). 151 However, we are aware of no study that has explored 152 relationships between men's masculinity or dominance and 153 orgasm in their mates.

We therefore examined relationships between putative 155 markers of men's genetic quality: attractiveness ratings, 156 dominance ratings, facial FA and masculinity (rated and 157 objectively measured from facial images)—and the frequen- 158 cy and timing of copulatory orgasm in their female partners. 159

2. Methods 160

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2.1. Participants

Participants were drawn from a larger study of 162 relationship formation comprising 117 heterosexual couples 163 from a north-eastern USA university. Excluding couples in 164 which at least one member opted out after participating, did 165 not consent to being photographed or exhibited facial 166

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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

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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 land-marks 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

lay on a horizontal line, and interpupilary distance was 220 constant across photographs. We then masked photographs 242 to obscure hair, neck and clothing (Fig. 1). Nine women 243 and nine men at a northwest UK university rated the 244 photographs for attractiveness (seven-point scale: 1=very 245 unattractive, 7=very attractive) and masculinity (1=very 246 feminine, 7=very masculine). We instructed judges to rate 247 masculinity against that of other persons of the same sex. 248 Order of stimulus presentation and the rating tasks (female 249 attractiveness, male attractiveness, female masculinity, 250 male masculinity) were randomized. Each face received 251 a mean other-rated attractiveness and mean other-rated 252 masculinity score.

3. Results 254

Descriptive statistics are reported in Table 1. 255

3.1. Principle components analyses

We performed separate principle components analyses 257 (PCA) on variables related to male quality, female quality 258 and female orgasm frequency. Components with eigenvalues 259 >1 were varimax-rotated and saved as variables. In order to 260 identify non-overlapping components of male and female 261 quality and female orgasm frequency and to maximize 262 interpretability of the results, we chose varimax rotation, 263 which produces orthogonal (uncorrelated) components and 264

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t1.1

t1.2

t1.26

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Table 1
Descriptive statistics

t1.3		N	Mean	Range	S.D.
t1.4	Relationship length (months)	110	15.4	1–106	17.4
t1.5	Partner-rated male dominance	115	5.7	1.5-9.5	1.6
t1.6	Partner-rated male masculinity	115	7.5	1.0-10.0	1.6
t1.7	Self-rated male attractiveness	114	6.8	3.0-10.0	1.2
t1.8	Self-rated male dominance	112	6.4	1.5-9.0	1.5
t1.9	Self-rated male masculinity	114	7.3	2.0-10.0	1.6
t1.10	Other-rated male attractiveness	71	3.2	1.1-5.3	0.9
t1.11	Other-rated male masculinity	71	4.3	2.3-6.2	0.9
t1.12	Male asymmetry index	110	50.5	15.2–122.2	22.3
t1.13	Male masculinity index	110	2.8	-3.2 to 8.2	2.6
t1.14	Partner-rated female femininity	114	7.4	3.0-10.0	1.5
t1.15	Self-rated female attractiveness	115	6.7	3.0-9.5	1.1
t1.16	Other-rated female attractiveness	72	3.1	1.6-5.4	0.9
t1.17	Other-rated female masculinity	72	4.1	2.3-6.2	0.9
t1.18	Female asymmetry index	111	47.7	11.4-107.0	19.3
t1.19	Female masculinity index	111	-2.8	-9.0 to 2.1	2.6
t1.20	Coital orgasm frequency (%)*	86	52.5	"5–10%" to "95-100%"	32.8
t1.21	Coital orgasm frequency before ejaculation (%)*	87	41.9	"5–10%" to "90–95%"	31.8
t1.22	Coital orgasm frequency during ejaculation (%)*	85	27.7	"5–10%" to "95–100%"	23.3
t1.23	Coital orgasm frequency after ejaculation (%)*	85	32.9	"5–10%" to "95–100%"	26.8
t1.24	Non-coital partnered orgasm frequency (%)*	92	54.5	"5–10%" to "95–100%"	32.6
t1.25	Self-masturbatory orgasm frequency (%)*	64	71.9	"5–10%" to "95–100%"	35.6

^{*} 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 279 positively, respectively, onto PC2 ("Partner-rated Female 280 Masculinity"). Self-rated attractiveness loaded heavily 281 positively, and asymmetry index loaded heavily negatively, 282 onto PC3 ("Self-Rated Female Attractiveness/Symmetry"). 283

For the PCA performed on female orgasm frequencies 284 (Tables 6 and 7), frequency of female coital orgasm 285 before male orgasm and frequency of female orgasm 286 during coitus loaded heavily onto PC1 ("Female Coital 287 Orgasm Before/Total"). Frequency of female coital 288 orgasm after male orgasm and frequency during male 289 orgasm loaded heavily onto PC2 ("Female Coital Orgasm 290 After/During"). Frequency of female orgasm during self- 291 masturbation and frequency of non-coital female orgasms 292

t2.1 Table 2 t2.2 Zero-order correlations among male traits (and *N*)

2.3		Partrat. masc.	Self-rat. attr.	Self-rat. dom.	Self-rat. masc.	Other-rat. fac. attr.	Other-rat. fac. masc.	Fac. asym. index	Fac. masc. index
2.4	Partrat. dom.	.51*** (115)	.06 (112)	.18 [†] (110)	.26** (112)	.08 (70)	.22 (70)	.02 (110)	.13 (110)
t2.5	Partrat. masc.		.06 (112)	.28** (110)	.47*** (112)	11 (70)	.23 [†] (70)	.06 (110)	.29** (110)
t2.6	Self-rat. attr.			.36*** (112)	.35*** (114)	.60*** (71)	.14 (71)	.12 (110)	.08 (110)
t2.7	Self-rat. dom.				.57*** (112)	.15 (71)	.08 (71)	01 (108)	.02 (108)
t2.8	Self-rat. masc.					.11 (71)	.13 (71)	.02 (110)	.17 [†] (110)
t2.9	Other-rat. fac. attr.						.39*** (71)	.17 (70)	.06 (70)
t2.10	Other-rat. fac. masc.							05 (70)	.51*** (70)
t2.11	Fac. asym. index								.13 (110)

Q5 t2.12 *p<.05.

t2.13 ** p<.01.

t2.14 *** p<.001.

t2.15 † p<.10.

t5.1

t5.2

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t3.1 t3.2	Component loadings for PCA performed on male traits						
t3.3		Component					
t3.4		Male masculinity	Male attractiveness	Self-rated male dominance			
t3.5		EV=2.5, 27.5%	EV=1.8, 19.6%	EV=1.3, 14.2%			
t3.6	Partner-rated dominance	.589	195	.148			
t3.7	Partner-rated masculinity	.693	336	.393			
t3.8	Self-rated attractiveness	029	.781	.352			
t3.9	Self-rated dominance	041	.092	.831			
t3.10	Self-rated masculinity	.294	.030	.811			
t3.11	Other-rated facial attractiveness	.132	.846	.112			
t3.12	Other-rated facial masculinity	.739	.389	096			
t3.13	Facial asymmetry index	036	.404	117			
t3.14	Facial masculinity index	.728	.148	.025			

t3.15 EV, eigenvalue.

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Table 2

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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, β =.36, p=.039) and Male Self-rated Dominance negatively (t=-2.34, β =-.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, β =.50, p=.007) and relationship length (t=2.56, β =.43, p=.017) significantly predicted Female Coital Orgasm After/During (all other p>.12; model: $F_{32,7}$ =2.43, R=.64, p=.048, Table 9). Self-Rated Male Dominance (t=-2.92, β =-.54, p=.007) significantly negatively predicted Female Non-coital Orgasm (all other p>.38; model: $F_{32,7}$ =1.36, R=.53, p=.265, 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

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t5.13

Approximately 70% of the variation among women in 333 copulatory orgasm frequencies is due to environmental 334 differences (Dawood, Kirk, Bailey, Andrews, & Martin, 335 2005; Dunn, Cherkas, & Spector, 2005), although this 336 estimate subsumes measurement error and all nongenetic 337 influences, including psychosocial development (Cohen & 338) Belsky, 2008; Harris, Cherkas, Kato, Heiman, & Spector, 339 2008) and prenatal environment (Wallen & Lloyd, 2011). 340 Some of the environmental contribution to between-female 341 variability in orgasm frequency results from variation in the 342 quality of women's sexual experience (Brody & Weiss, 343 2010; Puppo, 2010; Richters, Visser, Rissel, & Smith, 2006; 344 Singh, Meyer, Zambarano, & Hurlbert, 1998; Weiss & 345 Brody, 2009), including characteristics of their sexual 346 partners (Garver-Apgar et al., 2006; Shackelford et al., 347 2000; Thornhill et al., 1995).

We found that objective measures of the quality of 349 women's mates—men's attractiveness and masculinity— 350 significantly predicted the women's orgasms. Men's 351

t4.1 Table 4 t4.2 Zero-order correlations among female traits (and *N*)

3		Other-rat. attr.	Other-rat. masc.	Fac. asym. Index	Fac. masc. index	Partrat. fem.	Age at sess.
Self-ra	at. attr.	.09 (71)	07 (71)	12 (111)	07 (111)	05 (112)	.04 (115)
Other-	-rat. attr.		69*** (72)	24* (70)	40*** (70)	10 (71)	18 (71)
Other-	-rat. masc.			.25* (70)	.68*** (70)	12 (71)	.20 (71)
Fac. a	sym. Index				.14 (111)	00 (111)	.07 (111)
Fac. n	nasc. index					08 (111)	.04 (111)
Part1	rat. fem.						11 (112)

Q8 t4.10 [†]p<.10.

t4.11 **n<.01

t4.12 * p<.05.

t4.13 *** p<.001.

t3.16 Percentages refer to the amount of variance explained.

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t6.1 Table 6

t6.2 Zero-order correlations among female orgasm frequency items (and N)

10 t6.3		Freq. coital org. before partner	Freq. coital org. after partner	Freq. simul. coital org.	Freq. partnered non-coit. org.	Freq. org. self-mast.
t6.4	Freq. coital org.	.55*** (86)	.21 [†] (85)	.56*** (85)	08 (82)	.14 (57)
t6.5	Freq. coital org. before partner		20^{\dagger} (85)	.18 [†] (85)	06 (83)	.06 (58)
t6.6	Freq. coital org. after partner			.16 (84)	.09 (81)	.17 (56)
t6.7	Freq. simul. coital org.				.05 (81)	02 (57)
t6.8	Freq. partnered non-coit. org.					.33* (61)

Q11 t6.9 **p<.01

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t7.1

t7.2

t6.10 † p<.10.

t6.11 * p<.05.

t6.12 *** 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 roughly for refri			
t7.3		Component		
t7.4		Female coital orgasm before/total	Female coital orgasm after/during	Female non-coital orgasm
t7.5		EV=1.9, 32.2%	EV=1.4, 23.4%	EV=1.1, 18.6%
Q12 t7.6	Frequency of coital orgasm	.809	.442	027
t7.7	Frequency of coital orgasm before partner	.901	182	036
t7.8	Frequency of coital orgasm after partner	196	.816	.169
t7.9	Frequency of simultaneous coital orgasms	.330	.724	148
t7.10	Frequency of partner orgasm, other than intercourse	263	063	.731
t7.11	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, 373 along with relationship length, predicted a component of 374 women's copulatory orgasm related to frequency during or 375 after male ejaculation. Baker and Bellis (1993) found greater 376 sperm retention associated with women's orgasms occurring 377 between 1 min before and 45 min after male ejaculation, a 378 window roughly corresponding to the orgasm component 379 that we identified. Indeed, Thornhill et al. (1995) found that 380 men's attractiveness marginally significantly predicted, and 381 low male FA significantly predicted, the occurrence of 382 women's orgasms during or after male ejaculation, although 383 FA did not load heavily onto any component of male quality 384 in the present study.

Whereas men's masculinity and attractiveness predicted 386 the frequency and timing of women's copulatory orgasms, 387 these components did not predict women's orgasms 388 achieved through self-masturbation or non-coital sexual 389 activity with a partner. This suggests that male sire quality 390 increases female orgasm specifically during sexual behaviors 391 that could result in conception, thus supporting the sire 392 choice hypothesis.

4.1. Limitations 394

The present data do not address by which proximate 395 mechanisms men's attractiveness, dominance, and mascu-396 linity may affect the timing and frequency of their partners' 397 orgasms. Several possibilities exist, including greater 398 psychological excitement resulting from the male's visual 399 (e.g., Penton-Voak & Perrett, 2000), acoustic (e.g., Puts, 400

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

t.8.1

	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

t10.1

t10.2

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t9.1	Table 9
	Results of multiple regression predicting Female Coital Orgasm After/
t9.2	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

2005) or olfactory (e.g., Wedekind, Seebeck, Bettens, & 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

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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 460 role of its timing in relation to ejaculation.

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