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Introduction

Vocal communication plays important roles in mediating social relationships across diverse species (Hopp, Owren, & Evans, 1997), including many primates (Clarke et al., 2006; Crockford et al., 2004; de la Torre & Snowdon, 2009; Hauser, 1992; Hauser & Marler, 1993a, 1993b; Owren et al., 1993; Seyfarth et al., 1980). Despite the relevance of communication to both sexes, the acoustic properties of adult vocalizations are often sexually differentiated. In primates, vocalizations are sexually differentiated in such species as Japanese macaques (*Macaca fuscata*: Green, 1981), lion-tailed macaques (*Macaca selenia*: Green, 1981), chacma baboons (*Papio hamadryas ursinus*: Fischer, Hammerschmidt, Cheney, & Seyfarth, 2002; Rendall, Kollias, Ney, & Lloyd, 2005; Rendall, Owren, Weerts, & Hienz, 2004), orangutans (*Pongo pygmaeus*: Delgado, 2006), chimpanzees (*Pan troglodytes*: Mitani & Gros-Louis, 1995), and bonobos (*Pan paniscus*: Mitani & Gros-Louis, 1995).

Sex differences can evolve for a variety of reasons, but sexual selection is often implicated (Andersson, 1994). Sexual selection (Darwin, 1859, 1871) favors traits that help win mating opportunities and operates through multiple

mechanisms, including mate choice, favoring sexual displays and ornaments for attracting mates, and contest competition, favoring size, strength, aggression, anatomical weapons, and threat displays for winning mates by force or threat of force. Darwin (1871) noted the pubertal enlargement of male vocal structures in many mammals and males' use of vocalizations chiefly, and sometimes exclusively, during the breeding season. These facts suggest the influence of sexual selection on male vocalizations. Yet, Darwin concluded that females were not generally attracted to male vocalizations and that, while the roaring of a male lion or stag might intimidate adversaries, this benefit would have been insufficient to account for changes in male vocal structures. Rather, Darwin hypothesized that such vocalizations were byproducts of intense nervous excitement under strong emotion, such as when preparing to fight. He suggested that the frequent use of the voice in this manner may, in Lamarckian fashion over many generations, "at last have produced an inherited effect on the vocal organs of the stag, as well as other male mammals" (Darwin, 1882, p. 527).

Subsequent researchers have generally not shared this view, and recent evidence strongly implicates sexual selection in producing sex differences in numerous acoustic signals and their anatomical substrates (Charlton, Reby, & McComb, 2007; Reby et al., 2005; Ryan & Rand, 1995), including those of many primates

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(Delgado, 2006; Snowdon, 2004). In some primates, vocalizations may function in male contest competition. For example, among orangutans, lower-ranking males avoid long calls given by higher-ranking males (Mitani, 1985), indicating that acoustic cues suggest threat potential to conspecifics. High dominance rank may be advertized partly by the fundamental and formant frequencies of vocalizations. Vocal fundamental frequency relates negatively to body size across primates (Hauser, 1993; Mitani & Stuht, 1998), and among rhesus macaques, formant frequencies indicate body size and age (Ghazanfar et al., 2007), both potential correlates of dominance. In addition, mantled guereza males possess a subhyoid air sac causing them to display lower formant spacing than would be expected given their vocal tract length (Harris, Fitch, Goldstein, & Fashing, 2006). This suggests that vocalizations may have been selected to exaggerate apparent body size among males of this species (Harris et al., 2006). Research thus indicates that, especially in males, vocalizations may serve as signals of dominance, a predictor of mating and reproductive success across primates (Cowlshaw & Dunbar, 1991). Mate choice by females has also likely been an important influence in shaping the vocalizations of male primates. Among gibbons, for instance, there is evidence that male calls signal fitness, with call quality suffering during times when food is unavailable or energy must be allocated to thermoregulation (Cowlshaw, 1996).

Sex Differences in the Human Voice

The human voice is also highly sexually differentiated (Childers & Wu, 1991; Fitch & Holbrook, 1970; Wu & Childers, 1991). Men speak at a lower fundamental frequency (F_0), the rate of vocal fold vibration during phonation and the acoustic parameter closest to what we perceive as pitch. Men also speak with lower, more closely spaced formants (e.g., Childers & Wu, 1991), frequencies of high energy that affect the perceived timbre of a vocalization. In

addition, some evidence suggests that men tend to speak in a more monotone voice, that is, F_0 varies less across an utterance in men than it does in women (Daly & Warren, 2001; Puts, Apicella, & Cárdenas, 2012), although the ubiquity of this sex difference is debated (Simpson, 2009).

These sex differences are very large, ranging from around three standard deviations in the case of monotonicity to nearly six standard deviations in the case of fundamental frequency (Puts, Apicella, et al., 2012). In a sample of 630 US university undergraduate students, there was no overlap between men's and women's mean speaking fundamental frequency when reading a standard passage (D. A. Puts, unpublished data, Fig. 3.1). In the same data set, this sex difference exceeded those of many commonly studied sexually differentiated traits, including waist-to-hip ratio, height, weight, and handgrip strength (Fig. 3.2). Vocal sex differences also do not merely reflect the sex difference in body size. Fundamental frequency and formant position (a measure of formant structure) correlate only modestly with stature within sexes—in men, these correlations are approximately -0.2 and -0.3 , respectively—and remain highly sexually differentiated after controlling for stature (Puts, Apicella, et al., 2012).

With the exception of F_0 variation (monotonicity) (Daly & Warren, 2001), the proximate anatomical and physiological substrates for these vocal sex differences are well understood. Men's vocal tracts and vocal folds are 15 % and 60 % longer, respectively, than are women's (Fant, 1960; Titze, 2000), several times the 7–8 % sex difference in stature (Gaulin & Boster, 1985). At puberty, elevated testosterone levels (Tossi, Postan, & Bianculli, 1976) acting through androgen receptors in the vocal folds (Aufdemorte, Sheridan, & Holt, 1983; Newman, Butler, Hammond, & Gray, 2000; Saez & Sakai, 1976) cause males' vocal folds to grow longer and thicker than those of females, both absolute and relative to overall body growth (Harries, Hawkins, Hacking, & Hughes, 1998; Harries, Walker, Williams, Hawkins, & Hughes, 1997; Hollien, Green, & Massey, 1994). Men's larger vocal folds consequently vibrate at an F_0

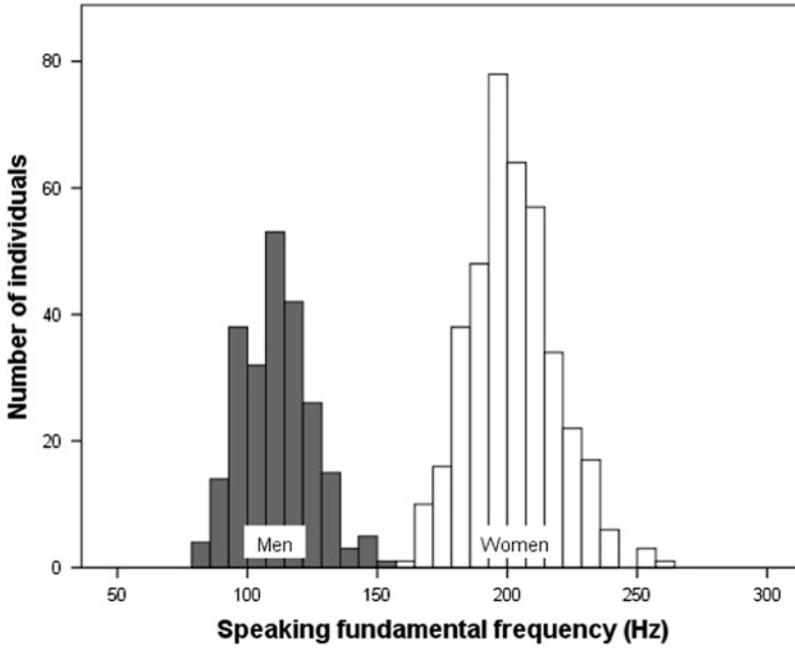


Fig. 3.1 There is almost no overlap between men’s and women’s mean habitual speaking fundamental frequency

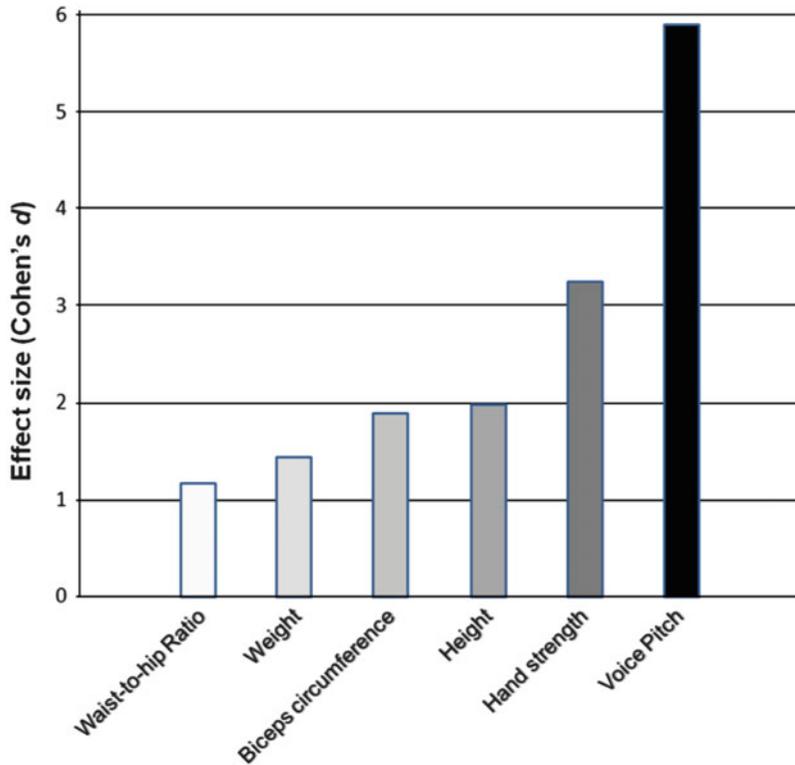


Fig. 3.2 The difference between male and female means (in pooled standard deviations, Cohen’s *d*) is larger for voice pitch (measured by F_0) than for other putative targets of sexual selection

approximately half that of females during phonation. Similarly, males' larynges descend at puberty (Fitch & Giedd, 1999), producing a longer vocal tract and resulting in lower, more closely spaced formant frequencies. Although the proximate causes of the sex difference in vocal monotonicity are unclear, the apparent cross-cultural prevalence of this sex difference (Henton, 1995) suggests that sex hormones may be involved in producing its underlying neuropsychology (Puts, Apicella, et al., 2012).

Sexual Selection and Human Voices

Vocal communication may be important for primate species generally, but in none is it more important than in humans. We are a supremely communicative species, so much so that spoken language may be regarded as *the* defining human characteristic (Pinker, 1994). It is conspicuous that men's and women's voices are so different when vocal communication is so important to both sexes. For those interested in understanding the social dynamics of human sexuality, such acoustic sexual dimorphisms are particularly relevant. As we will see, these traits affect attractiveness and perceptions of dominance and predict mate preferences and behavior related to competition for mates. Therefore, clarifying why men and women sound different will elucidate how the voice mediates vocal communication and interpersonal relationships in general, and more specifically, such relationships as dominance hierarchies, social status, and romantic relationships.

Darwin (1882) attributed human sex differences in the voice and vocal anatomy to phylogenetic inertia: humans inherited these differences from ancestral species, and ancestral sex differences evolved due to the "the long-continued use of the vocal organs by the male under the excitement of love, rage and jealousy" (p. 566). Although we now know that heredity works differently, to Darwin, it was the repeated (largely functionless) use of vocalizations by males that eventually resulted in heritable sex differences in the voice and vocal anatomy.

Humans merely inherited these sex differences. By contrast, Ellis (1905, p. 125) noted that, when one considers the development of vocal sex differences at puberty, "it is difficult not to believe that this change has an influence on sexual selection and sexual psychology." In Ellis' view, because women's voices change far less than do men's at puberty, it is unlikely that women's voices evolved to attract men. Instead, men's vocal changes at puberty make the "deeper masculine voice" a secondary sexual trait in men, a conclusion further suggested to Ellis by the fact that male mammals are generally more vocal during the rutting season.

These writers worked over a century ago and had a paucity of information at their disposal. In what follows, we review the comparative wealth of evidence that has accumulated since that time, largely in the past couple of decades. We find evidence in support of the hypothesis that sexual selection has played a major role in producing sex differences in the human voice. Ancestral men and women likely competed with their same-sex rivals for mates via both mate choice and contest competition. However, in general, mate choice appears to have been relatively more important than contests in shaping women's traits (Barber, 1995; Buss & Dedden, 1990; Cashdan, 1996, 1998; Low, Alexander, & Noonan, 1987; Schmitt & Buss, 1996), and contests appear to have been more important than mate choice in shaping men's traits (Archer, 2009; Daly & Wilson, 1988, 1990; Puts, 2010). These generalities also seem to apply to voices, as we will see.

Sexual Selection on Women's Voices: Male Mate Choice

Male mate choice for feminine voices may partly account for the evolution of sex differences in these phenotypic characters. Although he ultimately rejected sexual selection on men as the cause of sex differences in the human voice, Darwin (1882, p. 695) proposed that women acquired "sweeter" voices as a sexual ornament. Laboratory studies have shown that men indeed

prefer feminine voices (Apicella & Feinberg, 2009; Collins & Missing, 2003; Feinberg, DeBruine, Jones, & Perrett, 2008; Jones, Feinberg, DeBruine, Little, & Vukovic, 2008, 2010; Puts, Barndt, Welling, Dawood, & Burriss, 2011), particularly for short-term, purely sexual relationships (Puts et al., 2011) and when the woman's voice indicates positive social interest (Jones et al., 2008).

The relative importance of women's voices in short-term contexts may reflect associations with current fertility (Puts et al., 2011). For example, a high voice pitch partly reflects age, with voice pitch decreasing as women senesce (Awan, 2006; Decoster & DeBruyne, 1997; Nishio & Niimi, 2008). Accordingly, Röder, Fink, and Jones (2013) found that women of peak reproductive ages had more attractive voices than did either pubescent girls or postmenopausal women. In addition, Bryant and Haselton (2009) found that women's voices were higher in pitch during the fertile phase of the ovulatory cycle, although Fischer et al. (2011) found a slight decline in pitch near ovulation, and Puts, Bailey, et al. (2012) found no significant change in pitch with estradiol or progesterone levels over women's cycles. Men also find women's voices least attractive during menstruation, a time of lowered fertility (Pipitone & Gallup, 2011), and most attractive during the late follicular (fertile) phase of the cycle (Pipitone & Gallup, 2008). These changes appear to be driven by fluctuating ovarian hormones: normally cycling women's voices were most attractive when their progesterone levels were low and their estradiol levels were high, again corresponding with peak fertility in their cycles (Puts, Bailey, et al., 2012).

Consistent with the hypothesis that attractive, feminine voices increase women's competitiveness for mates, other women perceive feminine voices as more attractive to men and more flirtatious (Puts et al., 2011), that is, attractive, feminine women's voices are perceived as greater threats in competition for mates. Similarly, women perceive other women's voices to be more attractive to men when the speakers' progesterone levels are low, indicative of greater fertility in their cycles (Puts, Bailey, et al.,

2012). Feminine voices could not have evolved to help women exclude competitors from mates by force or force threat, however, because femininity in women's voices decreases the appearance of physical threat (Jones et al., 2010; Main, Jones, DeBruine, & Little, 2009; Perrett et al., 1998).

Sexual Selection on Men's Voices

Despite evidence that sexual selection has shaped women's voices, there are several reasons to expect that sexual selection operating on men, rather than on women, played a larger role in the evolution of vocal sexual dimorphisms. First, sexual selection tends to be stronger in the sex that invests less in offspring (Trivers, 1972), is capable of reproducing at a faster rate (Clutton-Brock & Vincent, 1991), and has a higher variance in reproductive success (Bateman, 1948). In humans, males invest less in offspring than females do (Eibl-Eibesfeldt, 1989; Geary, 2000; Hewlett, 1992), can reproduce at a faster rate (e.g., Chagnon, 1992; Salzano, Neel, & Maybury-Lewis, 1967), and have higher reproductive variance (Chagnon, 1990; Hewlett, 1988; Howell, 1979; Salzano et al., 1967). Thus, sexual selection has almost certainly been stronger in shaping men's traits than it has been in shaping women's. Second, sexually selected traits tend to emerge at sexual maturity, and males, much more than females, exhibit dramatic pubertal changes in vocal characteristics (Barber, 1995; Ellis, 1905). Finally, as we will see, considerable evidence indicates that masculine voices increase men's success in competition for mates.

Female Mate Choice

Men might have evolved deeper voices partly because women prefer these traits. Some correlational studies report that women prefer a more masculine than average vocal pitch (Collins, 2000; Hodges-Simeon, Gaulin, & Puts, 2010), monotonicity (Hodges-Simeon et al., 2010), and timbre (Hodges-Simeon et al., 2010, but not Collins, 2000). Women also prefer an experimentally masculinized, relative to feminized,

mean pitch (Feinberg, DeBruine, Jones, & Little, 2008; Feinberg et al., 2006; Feinberg, Jones, Little, Burt, & Perrett, 2005; Jones et al., 2010; Riding, Lonsdale, & Brown, 2006, but see Apicella & Feinberg, 2009). Additionally, women's visual object memory improves after hearing masculine male voices but not after hearing feminine male voices or female voices, suggesting that women may be particularly attuned to masculine voices (Smith, Jones, Feinberg, & Allan, 2012). However, Riding et al. (2006) did not find women to prefer men's voices masculinized (increased) in monotonicity, and Feinberg et al. (2005) did not find that masculinizing timbre increased the attractiveness of men's voices. Yet, at least three studies have found that male voices masculinized in both pitch and timbre simultaneously were more attractive to women than the same voices with these acoustic parameters feminized (Feinberg et al., 2005, 2006; Puts, 2005).

Much of the variation across studies likely results from differences in the type of study (correlational vs. experimental), manipulation sizes, the rating task (e.g., sexual attractiveness vs. attractiveness for a committed relationship), stimulus presentation (e.g., paired masculinized/feminized stimuli vs. no rater hearing the same stimulus twice), and other methodological and sampling details. In general, women appear to prefer voices slightly more masculine than average, particularly in pitch. These results suggest that if female preferences influenced the evolution of masculine voices, then men's voices are now near the optimum under this form of sexual selection.

Why does vocal masculinity matter in a mate?

A related question concerns why women's preferences for masculine voices have evolved and been maintained by selection. That is, what fitness benefits, if any, are associated with mating with deep-voiced males? Given evidence for heritability in the acoustic properties of both human and nonhuman vocalizations (e.g., DeBruyne, Decoster, Van Gijssel, & Vercammen, 2002; Forstmeier, Burger, Temnow, & Deregnacourt, 2009) and that putative biomarkers for genetic quality may predict vocal attractiveness (Hughes,

Harrison, & Gallup, 2002), a logical possibility is that men's vocal traits signal heritable fitness benefits. These benefits may partly relate to heritable dominance, social status, and associated perquisites. Evidence detailed below in the part "Male Contest Competition" suggests that a masculine voice predicts dominance in men, and the offspring (perhaps especially male offspring) might benefit from inheriting whatever alleles contributed to their fathers' dominance.

Other evidence suggests that androgen-dependent traits, such as a deep voice (Bruckert, Lienard, Lacroix, Kreutzer, & Leboucher, 2006; Dabbs & Mallinger, 1999; Evans, Neave, Wakelin, & Hamilton, 2008; Puts, Apicella, et al., 2012), signal heritable immune system efficiency (Folstad & Karter, 1992; Tybur & Gangestad, 2011). There are two possible reasons for this. First, androgens may be immunosuppressant (Grossman, 1985), and compromising the immune system by producing high androgen levels may be feasible only for otherwise healthy individuals (Folstad & Karter, 1992). Although some evidence indicates that sex steroids suppress immune function in humans (Bouman, Heineman, & Faas, 2005), a meta-analysis found that testosterone treatment had little such effect in birds (Roberts, Buchanan, & Evans, 2004). Other evidence suggests that the immunosuppressive effects of testosterone are condition-dependent, with testosterone suppressing immune function to a greater degree in males in poor condition (Moore, Al Dujaili, et al., 2011; Moore, Cornwell, et al., 2011; Roberts & Peters, 2009). If heritable immunocompetence mitigates the immunosuppressive costs of high testosterone production, then testosterone-dependent male traits such as masculine voices should signal underlying genes that would confer disease resistance to offspring.

Second, immune system activation may suppress testosterone production. A recent meta-analysis found strong support for this hypothesis across mammals and birds (Boonekamp, Ros, & Verhulst, 2008). If a male's immune system more quickly and efficiently dealt with immune threats, then testosterone production might be suppressed less frequently, less severely, and/or

for shorter durations, and a more masculine phenotype would develop. To the extent that such immune efficiency was heritable, ancestral women may have produced healthier offspring by mating with masculine men.

Thus, women's preferences for men's voices may have been shaped in part to extract heritable benefits such as dominance and immunocompetence for offspring. However, testosterone is positively correlated with male infidelity, violence, divorce, low investment in mates and offspring, and interest in extra-pair sex (Booth & Dabbs, 1993; Burnham et al., 2003; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002; McIntyre et al., 2006). Indeed, women perceive more masculine male voices as indicating a lower likelihood of male investment in relationships (O'Connor, Fraccaro, & Feinberg, 2012). Additionally, the extent to which women associate low trustworthiness with masculine voices predicts individual variation in preference for such voices (Vukovic et al., 2011). Women's preferences for masculine vs. feminine men in general, and for masculine voices in particular, may reflect this trade-off between the costs and benefits associated with choosing a masculine partner. At least three factors seem to affect how women respond to this trade-off: the type of relationship sought (especially in terms of commitment level), women's own mate value, and changes in fertility across the ovulatory cycle.

Mating context. The fitness benefits of mate choice likely depend upon the type of mating relationship under consideration (Kenrick, Groth, Trost, & Sadalla, 1993; Kenrick, Sadalla, Groth, & Trost, 1990). When the prospective relationship is purely sexual, a woman does not obtain sustained male investment, but she may obtain genetic benefits for her offspring. However, when the prospective relationship involves commitment of time and resources to a mate and mutual offspring, mate choice is expected to depend on substantially more than signs of a mate's heritable fitness. Often this distinction is discussed in terms of the temporal context of the relationship (long-term vs. short-term), but it may be more accurate to conceptualize it in terms of commitment level, as, for example, a

couple could have a long-term relationship that is nevertheless purely sexual, with no male investment.

Because women can expect to obtain little beyond genetic benefits from a purely sexual (generally short-term) relationship and because of the typically lower investment associated with masculine traits, several authors have predicted that women's preferences for masculine men will be stronger when judging men's attractiveness for a short-term, uncommitted relationship than for a long-term, committed one (e.g., Gangestad & Simpson, 2000; Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Penton-Voak et al., 2003; Puts, 2005). In fact, women show stronger preferences for masculine voices when judging men's attractiveness as short-term partners than when judging men's attractiveness as long-term partners (Puts, 2005). The temporal context of the imagined relationship thus affects women's masculinity preferences in ways consistent with trade-off theories of women's mate preferences. One study also revealed a correlation between women's reported openness to short-term relationships and their preferences for masculine characteristics in men's voices (Jones, Boothroyd, Feinberg, & DeBruine, 2010).

Women's own attractiveness. Women higher in mate value may be able to recruit and/or retain investment from more masculine men than can women lower in mate value. Indeed, several studies have shown that women's own attractiveness and beliefs about their attractiveness positively predict their preferences for masculine male voices (O'Connor, Feinberg, et al., 2012; Vukovic et al., 2008, 2010), and as one would predict, this appears to be true particularly for women's preferences in long-term, committed relationship contexts (Feinberg et al., 2012). Conversely, women's self-rated health negatively predicted their short-term vocal masculinity preferences (Feinberg et al., 2012). This preference pattern may function to promote mating with masculine males, who putatively possess heritable immunity, when the benefit is greatest, as when women have poor health themselves (Feinberg et al., 2012).

Changes across the ovulatory cycle. Other evidence indicates that women also resolve the trade-off between good genes and investment partly by preferring men with masculine voices more strongly around ovulation (when conception risk is highest) than during other cycle phases (Feinberg et al., 2006; Puts, 2005; see also Puts, 2006). Puts (2005) also found a significant interaction between imagined mating context (short-term, purely sexual vs. long-term, committed) and cycle phase, such that women significantly preferred masculinized male voices only during the fertile phase and for short-term, sexual relationships. These results complement a broader literature in which women's preferences for other male traits, such as masculine faces and bodies, are highest during the fertile phase of the cycle and in short-term mating contexts (Gangestad & Thornhill, 2008). In one study, hormone levels estimated from women's self-reported ovulatory cycle position suggested that changes in progesterone levels may drive these cyclic preference shifts (Puts, 2006). Studies of cyclic changes in women's preferences for men's faces have also implicated testosterone (Welling et al., 2007) and estradiol (Roney & Simmons, 2008; Roney, Simmons, & Gray, 2011). Similar studies measuring hormones in relation to cyclic variation in women's voice preferences have not yet been reported.

The hormonal and psychological mechanisms that drive correlations between masculinity preferences and female fertility remain poorly understood. Nevertheless, this well-established relationship constitutes evidence that women's preferences for masculine voices function at least partly in recruiting high-quality genes for their offspring. The fact that these preferences are also most pronounced for short-term, purely sexual relationships further suggests that women's mating preferences may have been shaped by selection to increase the likelihood of producing fit offspring while maintaining a relationship with an investing long-term partner. This explanation emphasizes the importance of extra-pair sex for the evolution of fertility-contingent masculinity preferences.

Women's interest in extra-pair mating is seemingly greater around ovulation than it is during other phases of the ovulatory cycle. Women report more frequent sexual fantasies about men other than their primary partner (Gangestad, Thornhill, & Garver, 2002; see also Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006) and less commitment to their romantic partner (Jones, Little, et al., 2005) during the fertile phase of their cycle than they do at other times. Women are also more receptive to men's courtship invitations (Guéguen, 2009a, 2009b), more likely to dress attractively and express interest in revealing clothing (Durante, Griskevicius, Hill, Perilloux, & Li, 2011; Durante, Li, & Haselton, 2008; Grammer, Renninger, & Fischer, 2004; Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007), more likely to attend social gatherings where they might meet men (Haselton & Gangestad, 2006), and report both greater extra-pair flirtation and mate guarding by their primary partner (Gangestad et al., 2002; Haselton & Gangestad, 2006) during the late follicular phase of the ovulatory cycle. Importantly, recent studies have found that women with more masculine romantic partners show smaller changes in their sexual interests during the ovulatory cycle (Gangestad, Thornhill, & Garver-Apgar, 2010).

While the extra-pair mating account of cyclic preference shifts predominates in the literature, a different, but not mutually exclusive, explanation focuses on the potential benefits of increased commitment and attraction to relatively feminine men when raised progesterone prepares the body for pregnancy (Puts, 2006). As mentioned above, women report greater commitment to their primary romantic partner during the luteal phase of the ovulatory cycle when the body prepares for pregnancy (Jones, Little, et al., 2005). Analyses of other aspects of women's behavior, such as their dress, sexual fantasy about extra-pair men, and extra-pair flirtation, also suggest that women's bonds with their partner are strengthened during the luteal phase of the cycle (Durante et al., 2008; Gangestad et al., 2002; Haselton & Gangestad, 2006). This

strengthened bond, together with increased preferences for men displaying cues of prosociality and commitment when progesterone levels are raised (DeBruine, Jones, & Perrett, 2005; Jones, Little, et al., 2005), may reflect adaptations designed to increase the amount of care and support available to women during pregnancy. Importantly, both the extra-pair mating and “care-during-pregnancy” accounts of cyclic shifts in women’s mate preferences may reflect the two sides of the trade-off between the costs and benefits of mating with relatively more masculine men.

Male Contest Competition

Sex differences in voices may also have evolved through male contest competition. Hypertrophic growth of male vocal folds and the descent of the larynx at puberty produce deep, resonant vocalizations that exaggerate apparent size (Fitch, 1997). Studies investigating the role of male contests have explored relationships between vocal masculinity and dominance (social influence through force or threat of force, Henrich & Gil-White, 2001). Although dominance may be less relevant to men’s mating success in modern life than it has been during most of human evolution (Puts, 2010), the underlying logic of these studies is that past contest competition would have favored signals of threat potential and deference to these signals. Indeed, men’s voices masculinized in pitch and/or timbre are perceived as emanating from men who are more dominant than are the feminized versions (Feinberg et al., 2005, 2006; Jones et al., 2010; Puts, Gaulin, & Verdolini, 2006; Puts, Hodges, Cárdenas, & Gaulin, 2007; Watkins et al., 2010; Wolff & Puts, 2010). Correlational studies have also found that more masculine (lower) within-utterance pitch variation (greater monotonicity) predicts dominance perceptions (Aronovich, 1976; Hodges-Simeon et al., 2010; but see Tusing & Dillard, 2000), and people are more likely to choose male leaders with more masculine voices (Klofstad, Anderson, & Peters, 2012), especially in wartime scenarios (Tigue, Borak, O’Connor, Chandl, & Feinberg, 2012).

Masculinity predicts dominance. Masculine voices thus convey the impression of dominance, but deference to masculine voices would not be maintained by selection unless masculinity was a reliable signal of formidability. In fact, vocal masculinity seems to indicate potential for aggressive behavior. For example, people accurately assess men’s fighting ability and physical strength from their voices (Sell et al., 2010), though it is not presently clear which acoustic variables communicate this information. Although some studies have found relationships between vocal pitch and men’s height (Graddol & Swann, 1983) and weight (Evans, Neave, & Wakelin, 2006), most have not (Bruckert et al., 2006; Collins, 2000; Kunzel, 1989; Lass & Brown, 1978; Rendall et al., 2005; Sell et al., 2010; van Dommelen & Moxness, 1995). Similarly, some studies have found relationships between vocal timbre and men’s height (Evans et al., 2006; Greisbach, 1999; Rendall et al., 2005; Sell et al., 2010), but others have not (Collins, 2000; Gonzalez, 2004), and some have found relationships between vocal timbre and weight (Evans et al., 2006; Gonzalez, 2004), but most have not (Bruckert et al., 2006; Collins, 2000; Rendall et al., 2005; Sell et al., 2010).

Puts, Apicella, et al. (2012) present evidence that mean standardized formant frequency (“formant position”) is a superior measure of masculinity in vocal timbre to mean spacing between consecutive formant frequencies (“formant dispersion”), the measure used by most previous studies. In this study, formant position was more sexually dimorphic than formant dispersion in both a US sample and a sample of Hadza foragers from Tanzania. Puts, Apicella, et al. (2012) found that masculine formant position was related to handgrip strength and height, but formant dispersion was related to neither. Masculine pitch (measured by mean fundamental frequency) was related to height and testosterone levels, and masculine vocal dynamics (measured by monotonicity, or low within-utterance variation in fundamental frequency) was related to physical aggression.

Voice pitch may also be modulated in relation to perceived relative dominance. For example,

men who perceived themselves to be better fighters than their competitor lowered their voice pitch when addressing him, whereas men who believed they were less dominant raised their pitch (Puts et al., 2006). Similarly, Ohala (1983, 1984) reviewed evidence that high pitch tends to be used to indicate deference (as when asking a question), and low pitch tends to be used to indicate assertiveness (as when making a statement) across languages. Additionally, when male observers witness a man speaking aggressively with another man, they perceive him as being more dominant (Jones, DeBruine, Little, Watkins, & Feinberg, 2011).

Also consistent with the idea that men use vocal masculinity to assess other men's competitive abilities, Watkins et al. (2010) observed that low-dominance men were particularly sensitive to the masculinity of other men's voices. However, these findings should be treated cautiously, as Wolff and Puts (2010) observed no similar relationships in two studies between men's own dominance and their sensitivity to the masculinity of other men's voices. Although more research is required to clarify discrepant findings, exploring individual differences in men's dominance sensitivity may provide important insights into the role of masculine cues in communicating dominance to potential rivals.

Female Choice Versus Male Contests

Given evidence that vocal masculinity in men has been shaped both by female choice and male contests, it is reasonable to ask which mode of sexual selection played a larger role in the evolution of these traits. Do masculine voices appear to be sexual ornaments or threat displays? As discussed above, male traits such as vocal masculinity are closer to the optimum under female choice than under male contests. Thus, on the one hand, female choice may appear more influential if it won out against male contests in moving the mean closer to the optimum under female choice.

On the other hand, many additional factors might shift masculine traits nearer the optimum under mate choice, including ecological costs

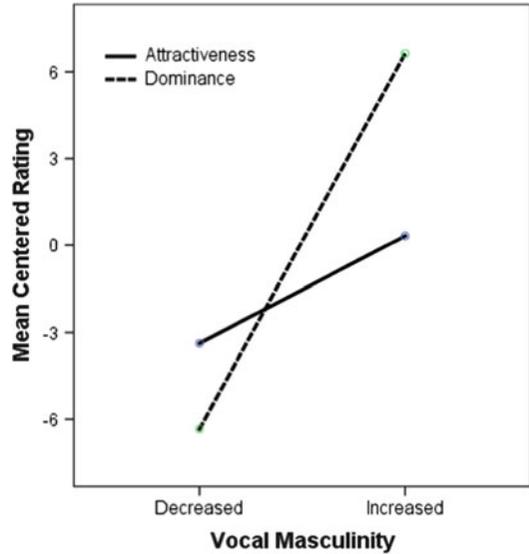


Fig. 3.3 Manipulating men's fundamental and formant frequencies has much larger effects on how other men rate the speaker's fighting ability than on how women, even those in the fertile phase of their cycles, rate his sexual attractiveness. The interaction between vocal masculinity and attribute rated is $F_{1,106} = 20.8$, $p < 0.0001$, $\eta^2 = 0.16$ (Data from Puts, 2005; Puts et al., 2006)

and benefits of producing and maintaining masculine traits and, importantly, the costs of advertising more dominance than one can back up (Rowher, 1977; Rowher & Ewald, 1981). Moreover, this reasoning based on the optimum trait value under mate choice assumes that modern female preferences are comparable to those that shaped men's voices over human evolution. Making a similar assumption, one can ask about the effect of masculinity on attractiveness to mates compared to the effect on perceptions of dominance. In other words, how well does masculinity serve the alternative (but not mutually exclusive) putative functions of mate attraction vs. dominance signaling? The answer is that across studies, masculine traits are more effective at signaling dominance (Puts, 2010), and this is particularly true of vocal masculinity. Experiments that have compared masculinized to feminized male voices have found larger positive effects on the appearance of dominance than on attractiveness (Feinberg et al., 2005, 2006; Puts et al., 2006, Fig. 3.3).

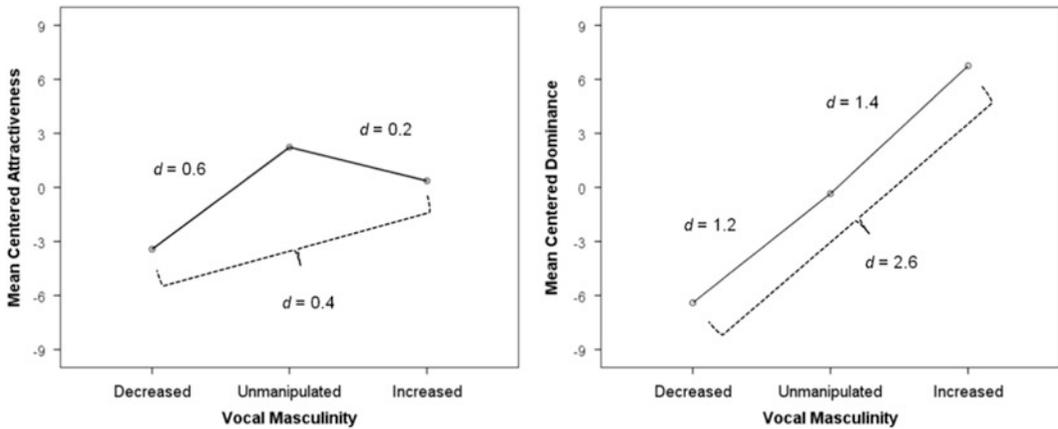


Fig. 3.4 Vocal masculinity has larger effects (measured in standard deviations, Cohen's d) on perceptions of dominance than on attractiveness. Voices were rated by women in the fertile phase of their cycle for attractiveness in a short-

term, purely sexual relationship and by men for physical dominance (e.g., fighting ability). See Puts (2005) and Puts et al. (2006) for additional methodological details. Figure redrawn from Puts, Jones, and DeBruine (2012)

However, the effect of masculinity on dominance may be more linear near the male average, and the effect on attractiveness may be more curvilinear. If so, then comparing effects on attractiveness vs. dominance using only two levels of masculinization/feminization might be misleading because such a linear comparison would adequately describe the effect of masculinity/femininity on dominance, but not the curvilinear effect on attractiveness. Figure 3.4 illustrates how the effect of masculinity on attractiveness might be underestimated by a comparison of only masculinized and feminized stimuli (data from Puts, 2005; Puts et al., 2006). In this case, it is more appropriate to compare the feminized and masculinized versions of the male trait to the unmanipulated condition. Again, however, the result is that, over the normal range of male voices, masculinity has larger effects on dominance than it does on attractiveness. Therefore, although additional research is needed, deep voices appear better designed by selection for winning male contests than for attracting mates.

Men's Voices, Mating, and Reproductive Success

If sexual selection shaped men's voices, then vocal masculinity must have contributed to

male mating and reproductive success over human evolution. Evidence that masculine voices contribute to mating opportunities in modern samples would support the possibility that these conditions held ancestrally. In fact, several studies have demonstrated that men with masculine or attractive voices report more sexual partners, and more short-term and extra-pair sexual relationships in particular, than their relatively feminine peers report (Hodges-Simeon, Gaulin, & Puts, 2011; Hughes, Dispenza, & Gallup, 2004; Puts, 2005). Complementing these findings, Apicella, Feinberg, and Marlowe (2007) observed a positive correlation between men's vocal masculinity and their reported reproductive success in a natural fertility sample of African hunter-gatherers; men with lower-pitched voices reported more children born to them and a greater number of currently living children than did men with relatively higher-pitched voices. As men's voice pitch was unrelated to the mortality rate of their children, this correlation may reflect a positive effect of masculine voice pitch on men's mating opportunities. Collectively, these findings suggest that voices evolved because they elevated reproductive success through increasing mating opportunities.

Conclusions and Directions for Future Research

In several ways, the voice represents an ideal model trait for studying human sexual selection. It is highly sexually differentiated, and vocal sex differences develop mainly at sexual maturity and are not plausibly due to ecological selection (e.g., sexual division of labor). The voice is also eminently quantifiable and highly salient due to its association with verbal communication. Evidence reviewed above indicates that sexual selection has shaped both men's and women's voices and that male contests, female mate choice, and male mate choice all played roles in the evolution of human vocal sexual dimorphisms. Feminine voices in women increase attractiveness to men, may signal fertility, and are thus likely to have been shaped by male mate choice. Masculine voices in men also affect attractiveness to women, perhaps because a masculine voice signals heritable benefits such as dominance and immune system efficiency. Consistent with the hypothesis that masculine voices signal heritable benefits, women prefer more masculine voices for purely sexual relationships and during the fertile phase of the ovulatory cycle. Thus, female mate choice is likely to have shaped men's voices over human evolution. However, masculine voices function more efficiently in signaling dominance to other men than they do in increasing attractiveness to women. Indeed, several contest-relevant traits such as size, strength, and aggressiveness can be accurately, if not precisely, assessed from men's voices, and men appear to modulate their voices in relation to their dominance relative to a competitor. Masculine voices thus appear primarily to be dominance signals.

A number of important and unresolved questions await future research. Among these are how vocal characteristics affect mating and reproductive success. For example, do masculine voices increase men's sexual opportunities, as some research suggests? If

so, to what extent are these mating advantages due to increased dominance among men and to what extent are they due to greater attractiveness to women? Because the mating environments of many modern societies are likely to differ in important ways from those in which human mating adaptations evolved, it will be essential to examine these questions cross-culturally, especially among more traditional peoples.

Future research should also determine how voice preferences and dominance perceptions relate to actual mate choices and contest outcomes. Work so far on these issues is sparse, but encouraging. Another unanswered question regards how people integrate information from cues in different domains (e.g., facial and vocal masculinity) with information about attitudes and intentions (e.g., emotional content and movement). Our understanding of social perception would also be enriched by further work exploring how familiarity with potential mates and competitors (e.g., past performance in competitive encounters with rivals or previous behavior in romantic relationships) figures in contest- and mating-related perceptions.

Although the research described above provides evidence for the ultimate functions of perceptions of men's vocal masculinity, the proximate mechanisms for individual differences in these perceptions remain unclear. Steroid hormones such as progesterone, estradiol, and testosterone (Jones, Perrett, et al., 2005; Puts, 2006; Roney & Simmons, 2008; Roney et al., 2011; Welling et al., 2007) are likely to mediate shifts in women's masculinity preferences over the ovulatory cycle, but more work is needed. Studies of social learning suggest that experience produces individual variation in voice preferences. Such studies have generally focused on mate choice (reviewed in Little, Jones, Debruine, & Caldwell, 2011), but social learning can also influence perceptions of men's dominance (Jones et al., 2011). Additionally, experience with voices can recalibrate judgments of masculinity and associated

attributions (Buckingham et al., 2006), and conditioning and associative learning can contribute to preferences and perceptions (e.g., Jones, DeBruine, Little, & Feinberg, 2007). Establishing how such relatively simple socio-cognitive processes interact to provide rich and colorful preferences and perceptions is essential to more fully understand social perception, mate preferences, and perceptions of rivals.

Future research should also continue to employ cross-species comparison to investigate the predictors of resonant and low-pitched vocalizations across primates and the possible influence of sexual selection. In addition, it will be important to utilize such data to establish whether men have particularly low voices or women have particularly high voices after controlling for these predictors, as this will help clarify whether sexual selection in men or women was more important in producing present vocal sexual dimorphisms. The identification of genetic polymorphisms associated with variation in vocal masculinity/femininity will also facilitate the search for signatures of recent selection on these traits in the human lineage.

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