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Chapter 5

AN EVOLUTIONARY PERSPECTIVE ON CHARACTERISTICS OF PHYSICAL ATTRACTIVENESS IN HUMANS

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ABSTRACT

Over evolutionary history, sexual attractiveness has had a large influence on the propagation of an organism's genes in sexually-reproducing species such as humans: individuals most desirable to members of the opposite sex were more likely to attract and retain a mate. In this chapter, we discuss the importance of attractiveness to two facets of sexual selection: intersexual selection (i.e., choosiness of potential mating partners) and intrasexual selection (i.e., within-sex competition over mating opportunities and resources). We describe how specific morphological features can provide important information about a potential partner's quality as a mate, and whether these features are in fact linked to aspects of mating success. We then describe under what conditions systematic variation in standards of attractiveness would be

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expected to occur, and how individuals compete (sometimes dishonestly) in the display of attractiveness characteristics.

In ancestral environments, individuals who mated with partners who were in poor health, low in fertility, or unable to provide the resources necessary to rear offspring, would have achieved lower reproductive success than individuals who mated with partners of higher quality (Gangestad & Scheyd, 2005; Symons, 1995). As modern humans, we are descended from ancestors who were effective at both identifying and attracting *viable* mates. In this chapter, we describe how specific morphological features have adapted to serve as signals of phenotypic quality, as well as the implications of these features for sexual attraction and competition in the realm of human mating. We begin by providing a brief overview of sexual selection theory (Darwin, 1871), highlighting the role of physical attractiveness in the process of intersexual (i.e., between sex) selection. Using examples from research on human morphological features such as facial attractiveness, skin quality, vocal attractiveness, and body attractiveness, we describe how certain physical traits convey to others important information about an organism, which may be pertinent to survival or reproductive fitness. We then describe potential reasons for variability in mate-preferences among individuals, from an evolutionary perspective. Finally, we describe how individuals compete intrasexually (i.e., within sex) along dimensions of physical attractiveness by modifying, enhancing, or drawing attention to specific morphological characteristics.

Sexual Selection and Physical Attraction

Many morphological features can be understood in light of the theory of *sexual selection* (Darwin, 1859; 1871), which, as a component of natural selection, concerns the reproductive advantages of certain individuals over others of the same sex. This differential reproductive success, in turn, leads to the heritable traits of successful reproducers being passed on and expressed with greater frequency in subsequent generations—a process that ultimately shapes the physical morphology and behavioral inclinations of that species (Darwin, 1871). Darwin noted that characteristics benefiting sexual reproduction can evolve even if they simultaneously detract from survival, provided that these traits sufficiently influence mating and reproductive success. The prototypical example is the brightly colored plumage of the

peacock (*Pavo cristatus*), which is physically-costly to produce and may detract from survival by increasing visibility to predators, but which is also highly attractive to peahens (Petrie & Halliday, 1994).

Sexual selection hinges upon *intersexual selection*, whereby the phenotypic traits held by members of one sex influence the likelihood that they will be chosen as a mate by the opposite sex. In other words, desirable characteristics confer a mating advantage. For example, female barn swallows (*Hirundo rustica*) prefer to mate with males who exhibit symmetrical tail ornamentation. As a result of this preference, the most symmetrical males are able to mate earlier and have greater reproductive success compared to less-symmetrically-ornamented males (Møller, 1992).

This raises the questions: Why do some traits bear more heavily upon intersexual selection than others? Why are female barn swallows impressed by males' symmetrical tail feathers but not the size of their beak or legs? One possible explanation is that certain traits are attractive simply because they exploit a hidden or underlying preference in the receiver that evolved in a non-mating context, or because the trait was once advantageous but may no longer be (Fisher, 1930; Kirkpatrick & Ryan, 1991). Take the guppy (*Poecilia reticulate*), for example: guppies have evolved a preference for the color orange which likely originated as a food detection mechanism for identifying fallen fruits in the water, as these provide essential nutrients in food-scarce environments. This visual bias for the color orange extended to female mate preferences for males who happened to have orange colorations (Rodd, Hughes, Grether, & Baril, 2002). Over time, males' orange colorations were selected for even though they did not confer any direct mating benefit to females; t. This is because females who preferentially mated with orange-colored males conferred a mating benefit onto their offspring, who, based on having the desired traits (i.e., orange color in male offspring), will be more attractive to the next generation of females, and hence more likely to reproduce (i.e., sexy son hypothesis; Fisher, 1930).

Traits can also be considered attractive because they are honest signals of a desirable underlying characteristic that could subsequently benefit the receiver's reproductive fitness. According to signalling theory, individuals choose "attractive" mates because the cost of producing attractive morphology is indicative of good genes, health (i.e., condition), or reproductive and parental capacity (Hamilton & Zuk, 1982). In many cases, a signal can be costly to produce, and it is this cost that ensures the honesty of the signal (Zahavi, 1975). When a particular signal is costly, only those of sufficient health or condition can afford the handicap of expended energy, resources, or

health to produce the signal. Selection should therefore favor receivers who prefer costly signals, and in turn, receivers' responses will determine whether, and which, signals evolve. For example, the darkened mane of the African lion (*Panthera leo*) is energetically costly to produce and raises the male's surface temperature beyond ideal levels. Yet the darkened mane is simultaneously indicative of the male's nutrition status and testosterone level, and therefore diagnostic of his ability to offer protection to offspring and prevent infanticide by competing males. Ultimately, dark-maned males are more often approached by females, have longer reproductive lifespans, and produce more surviving offspring compared to males with lighter manes (West & Packer, 2002). In the majority of mammalian species, females are the ones selecting males who, in turn, are the ones generating these costly signals. The reason for this general sex difference comes down to differences in the opportunity costs of reproduction (Trivers, 1972).

For most sexually-reproducing species with internal gestation, females carry the offspring. This results in a larger opportunity cost for females in that they are no longer able to reproduce again for some length of time after becoming pregnant (in humans: at least nine months but probably longer in ancestral environments due to natural ovulation suppression during lactation). Males, on the other hand, are typically immediately able to reproduce again after impregnating a female. This sex difference in reproductive biology translates into male competitiveness and female choosiness (except in sex-role reversed species in which the males gestate and are choosy while females compete). Among species in which both sexes invest heavily in offspring, competition for access to the opposite sex is selected for in both sexes (Gangestad & Scheyd, 2005). Indeed, a growing body of research has begun to highlight the importance of female-female competition (see Arnocky, Sunderani, Miller & Vaillancourt, 2012; Arnocky & Vaillancourt, 2012; Rhodes, 2006; Rosvall, 2011).

ATTRACTIVENESS AMONG HUMANS

Compared to males of most mammalian species, men engage in considerable care of offspring (Geary, 2000), and are selective in their choice of long-term mates (see Arnocky & Vaillancourt, 2012, for review). It can therefore be expected that both men and women would have evolved mate preferences for cues of a potential mate's quality, though these cues might be expected to reflect somewhat different underlying qualities in each sex. Recent

meta-analyses show that people worldwide are in general agreement about which individuals are attractive (Langlois et al., 2000), suggesting that there are universal morphological preferences that transcend cultural and contextual boundaries. We are treated differently based on these preferences (i.e., our attractiveness), which impacts mating success, friendships, and even our careers. Physically-attractive individuals are perceived by others as being more talented, friendly, competent, and pleasant than those who are less attractive (Eagly, Ashmore, Makhijani, & Longo, 1991; Landy & Sigall, 1974; Rudman, Feinberg, & Fairchild, 2002; Wade & DiMaria, 2003). Some studies have found that attractive people are more liked by others, earn more money in the workplace, and are better at attracting (and poaching) mates compared to their less-attractive counterparts (Arnocky & Vaillancourt, 2012; Judge, Hurst, & Simon, 2009; Lucker, Beane, & Helmreich, 1981; Neto, 1993; Sunderani, Arnocky, & Vaillancourt, 2013; Walster, Aronson, Abrahams, & Rottman, 1966).

Given the influence of physical attractiveness within many domains of life, it is important to understand which specific features determine one's attractiveness, and what information those features provide to others. In the following section, we review some of the most researched morphological features proposed to serve as cues of individuals' condition along with available evidence for links to attractiveness and mating success. For additional readings on this topic, we recommend: Barber, 1995; Gallup Jr. & Frederick, 2010; Gangestad & Scheyd, 2005; Grammer, Fink, Møller, & Thornhill, 2003; and Sugiyama, 2005.

Signals of Phenotypic Quality

Facial Attractiveness

Humans exhibit robust preferences for certain facial features, and these preferences tend to be consistent between raters, regardless of age or ethnicity (Chen, German, & Zaidel, 1997; Cunningham, Roberts, Barbee, Druen, & Wu, 1995; Langlois, Ritter, Roggman, & Vaughn, 1991). Facial attractiveness is highly tied to mating success: men with attractive faces have more short-term sex partners, and women with attractive faces start having sex at an earlier age and have more long-term sex partners (Rhodes, Simmons, & Peters, 2005). Faces are extremely important in judging phenotypic attractiveness because they provide a lot of information in a small amount of space via traits such as

symmetry, skin quality, and sexually-dimorphic features. These traits serve as signals of an individual's genotypic and phenotypic quality (e.g., Hume & Montgomerie, 2001).

One trait that has received much research attention for its link to underlying quality is facial symmetry. The extent to which one's facial characteristics diverge from perfect bilateral symmetry is a cue of developmental instability, exposure to environmental stressors during development, or genetic dysfunction (Gangestad & Thornhill, 2003; Møller, 1999; Sugiyama, 2005; Van Dongen, 2006; Van Dongen, 2012). Shackelford and Larsen (1997) reported that facial asymmetry was associated with various negative health indices among men and women, and our perceptions reflect this link: individuals with symmetrical features are perceived as being healthier, as well as more social, intelligent, lively, confident, and balanced, compared to less-symmetrical individuals. Both men and women have been found to rate symmetrical faces as being more attractive (Grammer & Thornhill, 1994; though a recent meta-analysis found mixed results: Van Dongen, 2012). Indeed, it has been convincingly demonstrated that, in general, higher fluctuating asymmetry is related to poorer mating outcomes across a variety of species (Møller & Thornhill, 1998; Rhodes et al., 2005), highlighting symmetry's role in attractiveness and mate- value judgments.

Other cues, such as facial averageness, are often studied within the context of signaling theory. Studies have demonstrated that average faces are not only perceived as being healthier by observers, but are indeed (as determined through the study of medical records) healthier than those with less-average faces (Rhodes et al., 2001). Other correlational studies have demonstrated that average faces are also considered attractive (e.g. Light, Hollander, & Kayra-Stuart, 1981). Using computerized morphing techniques, it has been demonstrated that the average of several faces is rated as more attractive than the original faces from which the composites were made (Langlois & Roggman, 1990; Langlois, Roggman, & Musselman, 1994). Furthermore, faces are rated as more attractive through each successive movement towards a same-sex average configuration (or less attractive when moving away from averageness) (Rhodes & Tremewan, 1996; Rhodes, Sumich, & Byatt, 1999). Some researchers have argued that the use of morphing enhances symmetry and skin smoothness and thus higher attractiveness of averaged faces could be an artifact of this process (e.g., Alley & Cunningham, 1991), but the link between facial averageness and health indicates that this artifact is not completely responsible, as does the evidence provided by studies in which averageness was preferred even when symmetry and facial smoothness

confounds were eliminated (Rhodes et al., 1999). A preference for average faces has also been observed in non-Western cultures (Rhodes et al., 2001), suggesting that facial averageness may function as a universal cue to the desirability of a mate; if this indeed is the case, average-faced men should enjoy more mating success than those with less average faces. In support of this link, recent research has shown that average-faced men do report having more short-term sexual partners and more extra-pair copulations than men with less-average faces (Rhodes et al., 2005). Future research will be necessary to determine whether these findings are robust across cultures.

The preference for facial averageness does not preclude certain distinct facial features from being considered attractive, however. Secondary sexual characteristics developed during puberty that distinguish males from females, also referred to as "sexual dimorphism," are hypothesized to contribute to facial attractiveness. One distinctive component of sexual dimorphism is the degree to which facial features are masculine or feminine.

For men, protruding cheekbones (Grammer & Thornhill, 1994), large and well-defined chins (Johnston & Franklin, 1993), heavy brow bones (Swaddle & Reierson, 2002), as well as facial hair (Neave & Shields, 2008) indicate higher masculinity. In this case, masculinity is defined as the development of facial features that are usually correlated with testosterone (T) levels. T diverts resources away from immune functioning (Grossman, 1985) and as such, is considered to be a costly signal of immunocompetence (Zahavi, 1975). Only men of sufficient genetic condition and health can 'afford' the effects of elevated T which suppresses their immune system. A man's immunocompetence could therefore be assessed in his T-linked secondary sexual characteristics (Roberts, Buchanan, & Evans, 2004). Men who have more masculine facial characteristics are presumed to be healthier, given that they can withstand the costs associated with developing these characteristics, and faces of high-testosterone men are generally seen as more masculine and more attractive by women (e.g., Penton-Voak & Chen, 2004; Scheib, Gangestad, & Thornhill, 1999). Additionally, men with characteristics indicative of higher testosterone may be perceived as stronger and healthier, and thus better suited for securing mates and protecting offspring. Some research has shown that adolescent males with more masculine faces are indeed healthier (versus less-masculine faces) based on medical examinations and health histories (Rhodes, Chan, Zebrowitz, & Simmons, 2003).

The link between health and sexually dimorphic facial features is unclear among women: there is some evidence that women's facial femininity is linked with measures of health (Thornhill & Gangestad, 2006), while other

evidence suggests there is no such link (Rhodes et al., 2003; Shackelford & Larsen, 2001). For women, sexually-dimorphic facial features such as prominent cheek bones, a narrow jaw, and short chin, indicate higher femininity (Shackelford & Larsen, 2001). In this case, femininity is characterized as the development of facial features that are usually correlated with estrogen levels. Estrogen-dependent facial features are important in mate choice because they might provide cues of the woman's underlying health and fertility (which is much more variable, especially across the lifespan, than men's fertility; O'Connor, Holman, & Wood, 1998). Recent studies have also found that hormones appear to mitigate changes in facial attractiveness across the menstrual cycle. For example, progesterone is a steroid hormone that is relatively low during the follicular phase of the menstrual cycle but increases and remains elevated during the luteal phase; not surprisingly, then, progesterone levels negatively predicted women's facial attractiveness rated by men (Puts et al., 2013). Similar to testosterone, estrogen may function as a handicap (Da Silva, 1999). Because producing estrogen is costly for a woman, it has been argued that only healthy women can develop the most feminine facial characteristics (Moore, Law Smith, Taylor, & Perrett, 2011). Accordingly, facial femininity is associated with attractiveness among women (Thornhill & Gangestad, 1999), and women's faces are perceived as being healthier when they are more feminine (Rhodes et al., 2003).

Feminine facial features also share aspects in common with neotony. Given men's preferences for relatively younger mates as a means of selecting those with higher reproductive value, perhaps women with youthful features (e.g., taller and wider eyes, small chin, small nose, small cheek width) would be viewed as more attractive. On the other hand, specific mature features (e.g., prominent cheekbones, narrower cheeks) are often preferred. This seeming contradiction might be the result of different selection pressures acting upon men's preferences for youthful yet reproductively mature female partners. Cunningham (1986) found that men rated as attractive faces faces as attractive when showcasing neotenous features, as well as faces showcasing specific mature features, but the combination of these features predicted the highest attractiveness ratings.

Women's lips, in particular, appear to be an important secondary sexual characteristic in facial attractiveness. In a novel study by Johnston and Franklin (1993), participants were able to form their ideal facial composite using a computer software program. Analysis of the composites revealed the lip size for attractive ideals was much larger than average. In a cross-cultural study, larger lower lips were rated as more attractive than smaller ones

(Cunningham et al., 1995). Given the increase in estrogen at puberty that influences lip size, full lips are argued to be indicative of fecundity (Johnston, 2006). Because the fullness and color of the lips diminishes with age (Jones, 1995) these features might be honest signals of female health and fertility (Furnham & Reeves, 2006).

Skin Quality

Skin coloring also plays a role in physical attractiveness. Skin color can be influenced by dietary carotenoids (Alaluf, Heinrich, Stahl, Tronnier, & Wiseman, 2002)—substances that might be related to disease prevention, the scavenging of free radicals, and the promotion of cardiac health (Rao & Rao, 2007; Voutilainen, Nurmi, Mursu, & Rissanen, 2006). Researchers have found that facial photos reflecting high-carotenoid coloration are rated as significantly more attractive than faces of low or unhealthy carotenoid coloration. This trend was not observed for meaningless scrambled images, suggesting that the coloration preference applies specifically to assessing the attractiveness of other humans (Lefevre, Ewbank, Calder, von dem Hagen, & Perrett, 2013). Among women, estrogen is associated with women's skin quality (Hall & Phillips, 2005), suggesting that smooth, clear skin, might serve as a cue of reproductive potential. Men do rate women with more homogeneous skin as more physically attractive (Fink, Grammer, & Thornhill, 2001).

Body Weight and Shape

Size and shape are important components of bodily attractiveness and have been linked to morbidity and mortality risk (Reilly et al., 2003) as well as to fertility in humans (Tovée & Cornelissen, 2001; Tovée, Reinhardt, Emery, & Cornelissen 1998). As such, weight may serve as an important and relatively honest visual cue to the quality of a potential mate (Abed, 1998; Brewer, Archer, & Manning, 2007). To a degree, female body fat is beneficial (and necessary) for ovulation and reproduction. In women, adequate levels of body fat are associated with regular cycling and earlier menarche, and may therefore benefit lifetime reproductive fitness (Brown & Konner, 1987). It is noteworthy that in some cultures, particularly those lacking stability of food and other resources, a relatively higher Body Mass Index (BMI: mass /

height^2) is sometimes considered attractive (e.g., Clark, Niccolai, Kissinger, & Bouvier, 1999; Mvo, Dick, & Steyn, 1999). For instance, heavier women are rated as being more attractive by hungry versus satiated men (Swami & Tovée, 2006). This preference might reflect a trade-off between the risks of maternal obesity versus the potential benefits, such as yielding children of higher birth weight (Baker, Michaelsen, Rasmussen, & Sørensen, 2004; Tovée & Cornelissen, 2001). As evidence of this context-dependent adaptive preference, when men migrate from resource-poor to resource-rich nations, their mate-preferences shift toward a thinner ideal (Tovée, Swami, Furnham, & Mangalparsad, 2006). "Because shortages were ubiquitous for humans under natural conditions, selection favored individuals who could effectively store calories in times of surplus" (Brown & Konner, 1987, pp. 38).

Despite the necessity to have a certain degree of body fat to successfully reproduce, a BMI considerably higher than the normal range can be detrimental to both health and fertility. Overweight women, compared to normal weight women, are less fertile (Chong, Rafael, & Forte, 1986; Crosignani et al., 1994; Hamilton-Fairley, Kiddy, Watson, & Franks, 1992; Zaadstra et al., 1993), and are at greater risk for miscarriage (Metwally, Ong, Ledger, & Li, 2008), as well as birth complications including spina bifida, heart defects, and omphalocele (ie., abdominal wall defects) in the newborn (Mills, Troendle, Conley, Carter, & Druschel, 2010; Watkins, Rasmussen, Honein, Botto, & Moore, 2003). Conversely, weight-loss among obese infertile women improves the reproductive outcomes of fertility treatments (Clark, Thornley, Tomlinson, & Norman, 1998). Moreover, among women, BMI tends to increase with age, and older women are also less fecund (Welon, Szklarska, Bielicki, & Malina, 2002).

Given that a woman's ability to reproduce can be influenced by her weight, it is no surprise that body size also influences her physical attractiveness. For instance, Tovée and Cornelissen (2001) found that BMI accounted for most of the variance in the attractiveness ratings of women's photographs. Men rate high BMI women as being less attractive than thinner women, even when relying solely on facial photographs with no additional information about body size and shape (Brewer et al., 2007). In a study of speed-daters, Kurzban and Weeden (2005) found high BMI to be the strongest predictor of women being viewed as undesirable by men; this effect was stronger than that of age, self-perceived facial, body, and personality attractiveness, race, education, smoking, drinking, number of children, and income combined (see also Tovée, Hancock, Mahmoodi, Singleton, & Cornelissen, 2002; Tovée, Maisey, Emery, & Cornelissen, 1999). Moreover,

the effects of BMI on attractiveness seem to be independent of other body fat and shape metrics, such as waist-to-hip ratio (WHR; e.g., Cornelissen, Hancock, Kiviniemi, George, & Tovée, 2009).

Similar findings have been observed in the study of women's body shape—which is strongly correlated with BMI (Singh & Randall, 2007). A woman's WHR can indicate her reproductive value and fertility status: prepubescent girls and postmenopausal women have higher WHRs than reproductive women, pregnant women's WHRs increase substantially, and there is preliminary evidence that WHR might slightly decrease at ovulation (Kirchengast & Gartner, 2002; although see Bleske-Recheck et al., 2011; for a failure to replicate). Women with lower WHRs reach puberty earlier, have higher estrogen levels, become pregnant more easily, and are at lower risk for diabetes, cancer, hypertension, and heart disease (Dalton et al., 2003; see Singh, 1993, for review). Reflecting these relationships, women with lower WHRs are rated as more physically attractive than women with higher WHRs (Singh, 1993), and this has been documented both cross-culturally (Singh, Dixon, Jessop, Morgan, & Dixson, 2010) and over time in Playboy centrefolds and Miss America contestants (Singh, 1993).

Men's mate preferences therefore place heavier women at a mating disadvantage. It is more difficult for overweight and obese women to attain and retain desirable male partners. For example, obese adolescent girls and women are significantly less likely to have dating and sexual partners, and are more dissatisfied with their dating status compared to their normal weight peers (e.g., Bajos, Wellings, Laborde, & Moreau, 2010; Pearce, Boergers, & Prinstein, 2002; Sheets & Ajmere, 2005). Obese adolescents are less likely to marry as adults (Gortmaker, Must, Perrin, Sobol, & Dietz, 1993), and if they do, they are more likely to be paired with obese, less attractive men (Carmalt, Cawley, Joyner, & Sobal, 2008; Silventoinen, Kaprio, Lahelma, Viken, & Rose, 2003).

Body weight and shape have also been linked to reproductive success in men. In some traditional hunter-gatherer tribes, a man's weight positively predicts his number of offspring, perhaps due to greater efficacy in intrasexual competitions (e.g., Hill & Hurtado, 1996). Obese men in Western cultures, however, have been found to have lower sperm concentration, lower sperm count, lower serum testosterone levels, higher estradiol, lower ejaculate volume, and more sperm with high DNA damage compared to normal weight men (Chavarro, Toth, Wright, Meeker, & Hauser, 2010; Jensen et al., 2004). In addition to weight, height is also associated with attractiveness among men, with taller men being preferred to shorter men in explicit preferences

(Pawlowski, 2003) and behaviorally: personal ads depicting a taller man receive more responses (Pawlowski & Koziel, 2002). These preferences do impact mating success: taller men are more likely to have offspring (Pawlowski, Dunbar, & Lipowicz, 2000), have a higher likelihood of finding a long-term mate, and have more long-term mates over the lifetime (Nettle, 2002).

Similar to context-dependent preferences for women's body size, the attractiveness of men's body size is also dependent upon available resources. In many traditional cultures, body fat can serve as an index of one's wealth and prosperity (Brown & Konner, 1987), and women's preference mechanisms are attuned to scarcity. For instance, Swami and Tovée (2005) examined the relative contributions of BMI, WHR, and Waist-to-Chest Ratio (WCR) to men's attractiveness ratings in urban versus rural regions. The researchers found that in urban areas, which tended to be of higher socio-economic status, women preferred men's bodies that reflected an 'inverted triangle' shape, whereas in poorer rural areas, women preferred a heavier body mass (i.e., higher BMI).

Nevertheless, in modern industrialized societies, women are relatively consistent in their expressed preference for mesomorphic (i.e., greater than average muscle development) rather than endomorphic (i.e., high body fat) or ectomorphic men (i.e., thin with little body fat or muscle mass; e.g., Dixson, Dixson, Bishop, & Parish, 2009). Women's attraction to muscular, mesomorphic men in resource-laden environments may reflect a preference for a mate who can best offer protection, status, and resources. Indeed, mesomorphic men are perceived as being more dominant, active, and energetic by other men, whereas ectomorphic and endomorphic men are rated as more shy and dependent (Dibiase & Hjelle, 1968).

Men's body shape does in fact predict mating success. For instance, men with a high Shoulder-to-Hip Ratio (SHR), indicating the inverted triangle shape, report sexual intercourse at an earlier age, more sexual partners, more extra-pair copulations (sex partners outside of one's own relationship), and more mate-poaching (i.e., having sex with someone who is currently in a relationship; Hughes & Gallup, 2003). In men, the development of lean muscle mass, muscle strength, and fat reduction is largely associated with T (Wang et al., 2000), suggesting that it may function as a costly signal in the body as well as in T-dependent facial features.

Breast Size and Shape

Female breasts are a secondary sexual trait that can signal the reproductive quality of a woman (Barber, 1995; Thornhill & Grammer, 1999). In a recent study by Jasieńska, Ellison, and Thune (2004), a positive relationship was found between breast size and markers of fecundity such as higher 17-β-oestradiol (E2) and for some, progesterone, implicating the function of the breast as a fertility signal, particularly when paired with a smaller WHR. Given that breast development in females begins just prior to menarche, smaller breast size could indicate youth, whereas larger breast size could indicate sexual maturity and immediate fertility (Singh & Young, 1995). A number of studies have revealed that the shape of the woman's breast (Mallucci & Branford, 2012) and the size of the breast (Gitter, Lomranz, Saxe, & Bar-Tal, 1983; Thompson & Tantleff, 1992) are related to perceptions of female attractiveness and health, with larger uplifted breasts seen as more desirable. Recent research employing eye-tracking techniques also reveals that when men view nude photographs of women, they spend significantly more time looking at the breasts than other areas of the body or head (Dixson, Grimshaw, Linklater, & Dixson, 2011), suggesting that the breasts are indeed very attractive to men.

Breast size does not indiscriminately predict attractiveness, however; other features such as total body fat must be taken into consideration for the observer. Generally, women with less body fat, low WHRs, and larger breasts are considered the most attractive, followed by women with more body fat, higher WHRs, and larger breasts (Furnham, Dias, & McClelland, 1998; Singh & Young, 1995). Some studies have found that medium rather than large size breasts are rated most favourably by members of both sexes (Kleinke & Stanesky, 1980), contradicting the notion that breast size definitively and positively relates to attractiveness. It could be that environmental challenges, such as resource scarcity, can override the importance of typical signals of fecundity in favor of more short-term fluctuations such as in body weight (Jasieńska et al., 2004). Other factors might also influence the importance of breast size for attraction; for example, men who are more interested in uncommitted sex value larger breasts more than other men (Zelazniewicz & Pawlowski, 2011).

Vocal Characteristics

Research on the human voice suggests that it may signal information about the quality of a potential mate (see Feinberg, 2008, for review). During puberty, a number of vocal changes occur as a result of the descent of the larynx and the influence of various hormones (Abitol, Abitol, & Abitol, 1999; Pinsanski, Mishra, & Rendall, 2012). For instance, in boys, the voice lowers an entire octave, whereas girls' will only lower by a few notes (Brodnitz, 1971). The typical change towards a lower sound of the voice is a result of androgens such as T, which affect vocal fold size (Jenkins, 1998) and ultimately shape a lower fundamental frequency of the voice (Evans, Neave, Wakelin, & Hamilton, 2008). By the same immunocompentence argument presented above, only those men with higher immunocompetence can afford to develop T-dependent traits such as lower vocal pitch (Folstad & Karter, 1992), and therefore, lower voices in men might be perceived as a cue to genetic quality (Puts, 2005). Among women, too, voices appear to signal condition: there is a negative correlation between women's vocal pitch and indices of health risk such as weight, BMI, and hip circumference (Vukovic, Feinberg, DeBruine, Smith, & Jones, 2010). Estrogen influences vocal femininity (higher fundamental frequency; Lindholm, Vilkman, Raudaskoski, Suvanto-Luukkonen, & Kauppila, 1997), and vocal pitch has been shown to increase around ovulation (Bryant & Haselton, 2009). Accordingly, a high-pitched female voice might signal reproductive potential and immediate fertility status to men.

Because the human voice is related to phenotypic quality (Feinberg et al., 2005; Hughes, Harrison, & Gallup Jr., 2002), it is not surprising that men and women have evolved preferences for particular voice qualities. Among a sample of Dutch women, young adult men with lower frequency voices were perceived as being more mature (older), heavier, taller, more masculine, and notably, more attractive overall (Collins, 2000). A host of other studies have replicated the tendency for women to prefer men with lower voices. For instance, Feinberg and colleagues (2005) found that male voices manipulated to be lower in fundamental frequency were rated as more attractive, and that this effect was not due to differences in the amount of time that the listener spent hearing the lower voice stimuli. Furthermore, men with lower voices were also more likely to have physical characteristics typically considered attractive by women (e.g., larger upper musculature; Evans, Neave, & Wakelin, 2006).

Consistent with the notion that lower-pitched male voices signal mate-quality and good genes, ovulating women prefer men with lower voices as short-term sexual partners (Puts, 2005). It may be that lower voice pitch is more important in short-term mating because not only do women find lower pitch voices as more sexually attractive for short-term rather than long-term partners (O'Connor, Pisanski, Tigue, Fraccaro, & Feinberg, 2014), but men with lower pitch voices also self-report more short-term sexual partners (Puts, 2005). Short-term mating with an attractive man would allow a woman to gain genetic benefits, while circumventing the associated risks of reduced commitment typically exhibited by more masculine men (O'Conner et al., 2014). Conversely, men with higher pitched voices are more likely to report being in committed relationships (Burnham et al., 2003), and to invest more in offspring (Gray, 2003). Thus, vocal attractiveness depends upon mating strategy.

Men find women with higher-pitched voices to be more attractive (Apicella & Feinberg, 2009; Collins & Missing, 2003) and voices that are electronically-manipulated to be higher-pitched are also strongly preferred by men compared to average or lower-pitched female voices (Feinberg, DeBruine, Jones, & Perrett, 2008). Additionally, men's preference for higher-pitched voices is even stronger when the speaker uses phrases indicative of interest in the listener (Jones, Feinberg, DeBruine, Little, & Vukovic, 2008); in this particular study, the effect was true only for vocal passages played forward, indicating that a preference for the combination of positive interest and high pitch were not a result of utterance length or speech rate (Jones et al., 2008). Other studies have found that in addition to voices that are higher in frequency, men also prefer those that are more "breathy," perhaps indicative of a smaller physical body size which men prefer (Xu, Lee, Wu, & Birkholz, 2013).

If vocal qualities do in fact reflect underlying qualities such as youth, health, and fertility status, individuals with more attractive voices should experience greater mating success. Indeed, Hughes, Dispenza, and Gallup Jr. (2004) found a positive association between vocal attractiveness (as rated by the opposite sex) and self-reported number of sex partners, extra-pair copulation partners, and number of sexual encounters with individuals mated to someone else. Attractive voices in this study also predicted earlier first sexual intercourse, further suggesting an adaptive advantage over less vocally-attractive peers. Research on the Hadza, a Tanzanian hunter-gatherer society, has found that for men, lower voice pitch predictsed number of offspring (Apicella, Feinberg, & Marlowe, 2007).

Other researchers have found that lower voices in men signal dominance to other men (Puts, Hodges, Cárdenas, & Gaulin, 2007), which may have functioned to deter rivals and facilitate status hierarchy negotiation (Hodges-Simeon, Gaulin, & Puts, 2011). Similarly, vocal femininity among women is known to increase rival perceptions of attractiveness and flirtatiousness, suggesting that women might also assess the quality of their intrasexual rivals based partly upon vocal characteristics (Puts, Barndt, Welling, Dawood, & Burriss, 2011).

VARIABILITY IN HUMAN MATE PREFERENCES

The consistency of attractiveness ratings within and across cultures (Langlois et al., 2000) does not preclude systematic variability in what is considered attractive in a potential mate. Characteristics of attractiveness can also vary over time within a given culture. One example is the increasing control offspring have gained over their own long-term mate selection in many Western countries: from 1939 to 1996 in the United States, men and women have increased the emphasis placed on a potential long-term mate's physical attractiveness, mutual attraction, and love (Buss, Shackelford, Kirkpatrick, & Larsen, 2001). Attractiveness preferences can also fluctuate based on contextual factors and specific challenges faced within the local environment. For example, in societies in which mortality rates are high, mating with a partner of good genetic quality should be even more important, and indeed, researchers have found that women's preferences for masculine male faces (as an indicator of good health) is higher in nations with increased mortality rates (DeBruine, Jones, Crawford, Welling, & Little, 2010) and attractiveness in general is more highly valued in nations with higher pathogen prevalence (Gangestad & Buss, 1993). Similarly, when asked to imagine living in a resource-deprived scenario, men and women prioritize wealth in a potential mate over other attributes (Marzoli et al., 2013).

Mate-preferences also appear to be sensitive to the Operational Sex Ratio (OSR), or the ratio of fertilizable females to sexually-active males in a given population (Emlen & Oring, 1977). Watkins and colleagues (2012) primed women with perceived sex-ratio differences using photographs of either same-sex or opposite-sex individuals. In this experiment, women were assigned to either a mate-abundance (i.e., many men and relatively few women) or mate-scarcity (i.e., many women and relatively few men) condition. Following exposure to one of these two conditions, participants rated their preference for

nale faces that varied in symmetry, a visible cue to genetic quality and health ıs described above. Women exposed to the mate-abundance condition :xhibited a greater preference for male facial symmetry compared to women n the mate-scarcity condition, suggesting that human mate-preferences ıdaptively respond to environmental condition: when mates are abundant, we :an afford to be choosier. In addition to the actual OSR, one's mate value (i.e., he degree to which opposite-sex individuals value the target as a mate) also letermines the size of one's mating pool, and men and women seem to adjust heir mate-preferences based upon this variable as well. Less attractive men, :ompared to attractive men, are less drawn to attractive women (Scheyd, 2004). Similarly, women who are independently rated as being physically ıttractive (i.e., of high mate-value) hold more exacting preferences than less ıttractive women for good genes, investment indicators (e.g., potential ncome), and signs of being a good partner or parent (Buss & Shackelford, 2008).

Even within a particular woman, preferences shift with fertility across the nenstrual cycle, reflecting women's orientation toward mating with genetically high-quality men around peak fertility (e.g., Puts, 2005). For nstance, when women are near ovulation and have higher levels of estradiol, heir preference for masculinity increases (in male faces: Roney & Simmons, 2008; in male voices: Feinberg et al., 2006; Puts, 2005). Men also exhibit ıttractiveness preferences based on ovulation: when asked to smell t-shirts worn by women who were not taking oral contraceptives, men rated shirts worn by ovulating women as significantly more attractive (Kuukasjärvi et al., 2004).

Examining the broader domain of mate choice, we find that individuals' nate preferences are also sensitive to changes in their mating goals. For nstance, men and women who are randomly assigned to report what they prefer in a short-term mate focus more on a partner's sexual desirability in erms of attractiveness, health, sex drive, and athleticism, whereas those randomly assigned to report what they prefer in a long-term mate focus more on a partner's desirable personality characteristics such as intelligence, ıonesty, and warmth (Regan, Levin, Sprecher, Christopher, & Gate, 2000). Taken together, these findings suggest that human mate preferences are highly sensitive to cultural, contextual, and individual differences. In the following section, we take a signalling approach to describe how these mate-preferences night determine the signaller's attempts to outcompete rivals by displaying the characteristics preferred by potential mates.

EPIGAMIC DISPLAY AND INTRASEXUAL COMPETITION

Natural selection favors signals that increase an organism's chances of reproduction. The examples mentioned throughout this chapter are proposed to reflect *honest* signalling of a potential mate's condition, whereby both the sender and receiver have the same interest in the result, and the signals themselves are a function of naturally-occurring individual differences. Yet the importance of signalling to human mating decisions also opens the door for both intrasexual competition and dishonesty. Upon exposure to members of the opposite sex, individuals alter their reported attitudes to conform to the mate preferences of the opposite sex. For instance, men filling out surveys in a mixed-sex room report more positive attitudes toward the accumulation of wealth (preferred by women in their mates) compared to men filling out surveys in a same-sex room (Roney, 2003). This finding highlights the ability and willingness of humans to alter their behavior to reflect the preferences of potential mates. Given the high degree of parental investment provided by both men and women in our species, it is not surprising to see that both men and women engage in intrasexual competition to attract and retain long-term mates; however, the attributes on which they compete differ based on the adaptive problems faced by men and women in mating.

Competition among Women

Men prioritize physical attractiveness more than women, especially in long-term mating, because the key adaptive problems men must solve are identifying and accessing women with high reproductive value (i.e., youth), fertility, and health, which are signalled via physical characteristics (Buss, 1988; Buss et al., 1990). Men's relatively greater emphasis on women's physical attractiveness suggests that women will be particularly likely to compete intrasexually in this domain. Recently, researchers have begun to consider appearance-enhancement behaviours among women as forms of intrasexual competition (Buss, 1988). It is well understood that many women use make-up, tanning, nail polish, and flattering clothing to enhance or draw attention to specific physical attributes that mimic signals of health, youth, and fertility (Tooke & Camire, 1991). Women are twice as likely as men to spend over an hour enhancing their physical appearance each day, and are willing to spend almost ten times the amount of money that men spend on appearance-enhancement products (Meston & Buss, 2009).

Appearance-enhancement behaviors among women seem to be rooted in intrasexual competition. Hill and Durante (2011) primed women with intrasexual competition motives by exposing participants to photos of attractive women; these primed women were more willing to take health risks to enhance their physical appearance (e.g., tanning, taking diet pills) than women in a control condition. Interestingly, unmated women were more likely to engage in these risky appearance-enhancement behaviors when exposed to a mating prime (i.e., viewing photos of men), indicating that appearance-enhancement might be serving multiple related functions: mate attraction *and* intrasexual competition. Many women prioritize the enhancement of their physical attractiveness even in the face of costs to themselves. Hill and colleagues (2012) have shown that while spending on most products decreases in an economic recession, women nevertheless increase their spending specifically on appearance-enhancing products. The researchers interpret this effect as driven largely by an increased desire to attract mates who have scarce resources. Women are also willing to endure the pain and discomfort of high heels which cause them to take shorter steps and increase hip sway—two factors that apparently signal femininity (Morris, White, Morrison, & Fisher, 2013). In fact, the gait of a woman wearing high heels was rated, by both men and women, as more attractive than the gait of a woman wearing flats.

Some researchers have similarly proposed that some eating disorders might be extreme manifestations of intrasexual competition among women. Abed and colleagues (2012) have argued that women exhibit a drive for thinness to preserve a nubile body shape. Disorders such as anorexia nervosa and bulimia nervosa would therefore reflect over-activation of this drive in response to perceived intrasexual competition. Recent evidence supports this view in that intrasexual competition for mates correlates positively with body dissatisfaction, drive for thinness, and disordered eating behavior in both cross-sectional and experimental studies (Faer, Hendriks, Abed, & Figueredo, 2005; Li, Smith, Griskevicius, Cason, & Bryan, 2010). Disordered eating behavior also occurs more frequently among women who exhibit greater mating effort (Abed et al., 2012).

The modern environment, with its plethora of (real or computer-generated) attractive intrasexual competitors could be exacerbating the normal operation of this competitive mechanism. The combination of intrasexual competition and the desire to display a thin body-shape ideal could explain why these behaviors are significantly more common among heterosexual women in prime reproductive years, compared to men and women at non-reproductive ages (e.g., Abed et al., 2012; Li et al., 2010).

Competition among Men

Although women are more likely to exhibit eating disorders, effort toward maintaining and enhancing physical appearance is by no means limited to women. As described in the sections above, physical features also signal important qualities in men, and men alter their behavior to conform to women's mate preferences. For example, men use clothing to accentuate features that align with female preferences for the ideal man (i.e., lean, tall, muscular; Frith & Gleeson, 2004). Women's preference for muscular men with a V-shaped physique and men's assumption that this physique is indeed preferred by the opposite sex (Jacobi & Cash, 1994) motivate men to become muscular (Parent, 2013; Pope et al., 2000) and therefore, men are more likely to consider themselves underweight than overweight (Harmatz, Gronendyke, & Thomas, 1985).

The combination of general body dissatisfaction and internalization of women's preferences for muscularity could be the cause of most muscle-building behaviors in men (Guõnadóttir & Garõarsdóttir, 2014). A study by Mealey (1997) revealed that the majority of men in their sample tailored their fitness workouts to increasing musculature mostly in the upper body—which coincides with women's preference for broad shoulders and a muscular upper body (Salusso-Deonier, Markee, & Pederson, 1993)—particularly among men who placed greater importance on their desire to be attractive to the opposite sex. Shomaker and Furman (2010) found that perceived pressure from a romantic partner to be muscular predicted greater pursuit of muscularity for adolescent boys, even after controlling for other variables such as influences from family and friends. Furthermore, men experience greater levels of muscle dissatisfaction following exposure to an ideal male body image via advertisements (Agliata & Tantleff-Dunn, 2004). Others have shown in a similar fashion that exposure to 'ideal' masculine physiques increases the discrepancy between self-perceived muscularity and the type of body one would ideally like to have (Leit, Gray, & Pope, 2002).

Men also engage in risky appearance-enhancement behaviors. Ricciardelli and McCabe (2003) found that some adolescent boys engage in excessive exercise, eat special foods such as vitamins and protein powders, and use anabolic steroids to build a more masculine physique. Some bodybuilders report using anabolic steroids to increase muscle mass and decrease body fat due to a strong desire to improve their looks (Blouin & Goldfield, 1995). A study on adolescents revealed similar findings, with 11% of a large sample of boys reporting steroid use to not only increase their personal appearance

overall, but to specifically increase muscle size (Johnson, Jay, Shoup, & Rickert, 1989). Despite the risks associated with steroid use (e.g., criminal punishment, impotence and infertility, liver tumors, psychological problems; Hoffman & Ratamess, 2006), pressures to attract high quality mates can outweigh the potential costs associated with these behaviors. Further research in other areas of physical and body image modification could provide a broader understanding of the competitive behaviours that men engage in to attract sexual and romantic partners.

Dishonest Signalling

Thus far, we have discussed many features that have seemingly evolved as signals of underlying properties of an organism for assessment by a member of the opposite sex. Some morphological features, however, can be faked. In other words, organisms can produce a dishonest signal that, over evolutionary history, previously functioned as an honest cue of quality:

> "An interaction qualifies as dishonest behaviour when, as a result of the behaviour of the signaller, the receiver registers a certain situation that is not in reality occurring. As a result of the interaction, the signaller benefits, while the receiver pays a cost." (Semple & McComb, 1996, p. 434)

One of the first empirical examples of dishonest signalling was observed in the male fiddler crabs (*Uca annulipes*), whose claw length is purported to be an honest signal of his fighting ability. Males with longer claws (in conjunction with other signals) are more attractive to females and have greater mating success (e.g., Backwell & Passmore, 1996). When a male loses a claw, he will generate a replacement that may be equal in length, but is simultaneously lighter, weaker, and a less effective weapon. Backwell and colleagues (2000) found that during mate searching, females did not discern between males with weaker regenerated claws, and males with original claws, indicating that regenerated male claws effectively disguise the true cost of claw development as a sexual signal. Therefore, to the extent that signals can be faked at a lower cost and are still rewarded with mating success, selection can favor such dishonest signals (although co-evolutionary pressures can cause the opposite sex to develop more rigorous standards to eliminate the benefit of dishonest signalling; Dawkins & Guilford, 1991).

One trend that epitomizes dishonest signalling in humans is the advent and growth of cosmetic surgery. In the United States, over 1.6 million cosmetic surgery procedures and an additional 15 million *minimally-invasive* cosmetic medical procedures were performed in 2013 alone (American Society for Plastic Surgeons, 2013). It is not surprising that the most common cosmetic surgical procedures (i.e., breast augmentation, eyelid surgery, rhinoplasty, liposuction, and facelift) involve enhancement of features previously described in this chapter as signalling information about underlying quality. Although the vast majority of cosmetic surgical procedures are performed on women, cosmetic surgery among men is on the rise (American Society for Plastic Surgeons, 2013). Men are more likely than women to have calf-augmentation surgery, pectoral implants, and hair transplants, suggesting that the cosmetic surgical procedures undertaken also reflect an attempt to enhance features that serve as (masculinity) signals to women, and which accordingly bear on their physical attractiveness. The ability to surgically-enhance signals of attractiveness allows one to dishonestly convey information about their quality over same-sex rivals. Recent empirical evidence suggests that intrasexual competition among both men and women predicts positive attitudes toward cosmetic surgery, as well as increased desired spending on cosmetic surgery in the future (Arnocky & Piché, in press). Further research would benefit from exploring whether men and women are averse to potential mating partners who are identified as having had cosmetic surgery.

CONCLUSION

Over the course of human evolutionary history, selection has favoured traits that signal qualities in a potential mate that correspond to important adaptive problems. Examining physical attractiveness from this perspective helps to explain why individuals possessing traits indicative of superior reproductive fitness often enjoy increased mating success, and why many humans are motivated to compete along the dimensions typically preferred by the opposite sex. Moreover, this approach helps to explain why some individuals go to risky lengths (e.g., anabolic steroids, cosmetic surgery) to develop dishonest signals to increase their perceived mate-value. Finally, sexual selection provides a cogent explanation as to why many preferred morphological characteristics are consistent across cultures, but also how specific contextual influences shift mate preferences in a predictable manner. Future evolutionary explorations into the nuances of mating, sexuality,

attraction, and intrasexual competition will help elucidate how physical attractiveness characteristics influence human mating behaviours.

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