

Original Article

Beards augment perceptions of men's age, social status, and aggressiveness, but not attractiveness

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The beard is a strikingly sexually dimorphic androgen-dependent secondary sexual trait in humans. Darwin posited that beards evolved in human ancestors via female choice as a highly attractive masculine adornment. Others have since proposed that beards evolved as a signal of male status and dominance. Here, we show that women from two very different ethnic groups, Europeans from New Zealand and Polynesians from Samoa, do not rate bearded male faces as more attractive than clean-shaven faces. Women and men from both cultures judge bearded faces to be older and ascribe them higher social status than the same men when clean-shaven. Images of bearded men displaying an aggressive facial expression were also rated as significantly more aggressive than the same men when clean-shaven. Thus, the beard appears to augment the effectiveness of human aggressive facial displays. These results are consistent with the hypothesis that the human beard evolved primarily via intrasexual selection between males and as part of complex facial communication signaling status and aggressiveness. *Key words:* aggressiveness, attractiveness, beard, dominance, facial hair, sexual selection. [*Behav Ecol* 23:481–490 (2012)]

INTRODUCTION

Overall reduction in body hair distinguishes *Homo sapiens* from other anthropoids. Nuclear genetic studies suggest that hairlessness in Hominids dates back to 1.2 Ma (Rogers et al. 2004). While human body hair is sparse, strictly speaking, people are not hairless. During prenatal development, the fetus is covered in primary lanugo hairs, which are replaced by secondary vellus hairs during early postnatal life (Trotter and Duggins 1948; Szabo 1967; Price and Griffiths 1985). Lanugo and vellus hairs are short, fine, unpigmented, and lack a medulla (Trotter 1938; Garn 1951). During infancy, childhood, and adolescence, vellus hairs differentiate into tertiary terminal hairs in specific parts of the body (Garn 1951; Szabo 1967). Compared with vellus hairs, terminal hairs are coarser, longer, more heavily pigmented, have thicker roots, and contain a larger medulla (Price and Griffiths 1985; Randall 2008).

Terminal hair on the head, eyelashes, and eyebrows grow under the influence of androgens and growth hormones. Androgens also promote the growth of terminal hair in other regions of the body so that both men and women grow pubic and axillary hair. However, at puberty, males undergo surges in androgens, which drive sex differences in the growth of more pronounced terminal hair on the face and body (Randall 2008). Sexual dimorphism in facial hair first appears at around age 10 in children (Trotter 1922). Beard hair continues to grow in early adolescence and is fully developed at

sexual maturity (Hamilton 1958). Beard hair is thicker, has a more complex medulla and a larger root compared with hair on the scalp and elsewhere on the head (Garn 1951; Szabo 1967; Tolgyesi et al. 1983; Thozhur et al. 2006).

People of different ethnic groups vary in pattern, distribution, and density of beard and body hair (Setty 1971; Lookingbill et al. 1991; Winkler and Christiansen 1993). However, although men's beards and body hair growth are stimulated by testosterone (Ewing and Rouse 1978; Farthing et al. 1982), ethnic differences in hirsutism should not be attributed to levels of total or free testosterone (Rosenfield et al. 1976; Ewing and Rouse 1978; Lookingbill et al. 1991). Rather, it is the conversion of testosterone into dihydrotestosterone, through the enzyme 5- α -reductase, which primes coetaneous androgen-sensitive receptor cells to invest in terminal follicle growth on the face (Randall 2007, 2008). Beard growth is almost identical in monozygotic twins, less similar between nonidentical twins, and shows the most variation between nontwin brothers (Hamilton 1958; Hamilton et al. 1958). Thus, genetic factors appear to regulate the extent to which the growth of facial and body hair occurs under the influence of androgens (Hamilton 1964).

Using natural selection as a starting point, many hypotheses have been proposed for the reduction of body hair in humans (for review, see Rantala 2007). For example, it has been suggested that as ancestral hominids transitioned from arboreal to savannah conditions, loss of body hair was adaptive for cooling (Morris 1967; Wheeler 1992a, 1992b). Another, more recent hypothesis proposes that due to the development of cooperative hunting and fixed home bases, loss of body hair may have lessened disease-carrying ectoparasites (Rantala 1999, 2007). Given that humans have lost thermoregulatory pelage important in other anthropoid primates, why have men retained conspicuous hair on the body and face? There have been attempts to account for the evolution of the beard

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via natural selection to assist in thermoregulation or protection against UV radiation (Cabanac and Brinnet 1988, 2000; Green et al. 2006). Consistent with such accounts, research shows, for example, that beard growth in men in the United Kingdom was 50–60% greater in summer months than in winter months (Randall and Ebling 1991). However, the absence of pronounced facial hair in women makes extrapolating evolutionary significance from these findings within the context of natural selection questionable.

Sexual selection, which operates both intra- or intersexually, provides an alternative evolutionary framework to natural selection for investigating the evolution of facial hair in men. Intrasexual selection among males favors the evolution of sexually dimorphic characteristics that augment, or signal, competitive ability (Darwin 1871; Andersson 1994; Hunt et al. 2004). In this vein, Blanchard (2010) suggested that the human beard evolved to protect against blows to the jaw in the same way as a lion's mane. However, studies of the attack patterns of male lions have not supported the hypothesis that the mane serves such a protective function (West et al. 2006). Zahavi and Zahavi (1997) proposed that the human beard is a costly signal of male competitive ability, as beards may be easily grasped by rival males during fights. Therefore, a man with a full beard may be advertising his confidence and higher competitive ability, despite the apparent handicap of the beard. Thus, beards may directly signal competitive ability to rival males. Indeed, Freedman (1969) argued that beards increase the perceived status of men and may increase the social distance between rival men.

Intersexual selection via mate choice may favor ornaments as indirect signals of genetic quality or as direct cues of fitness (Darwin 1871; Andersson 1994; Hunt et al. 2004). If, as Zahavi and Zahavi (1997) suggest, the human beard is a costly signal of male competitive ability, then it may be preferred by female mates as an indirect signal of fitness. Hamilton and Zuk (1982) proposed that female preferences for male secondary sexual adornments could be due to their signaling the male's ability to withstand or resist parasitic infection. Hair on the face and body are potential localized breeding sites for disease-carrying ectoparasites (Nenoff et al. 2009; Weiss 2009). Thus, hirsute men could be advertising their superior immune system through possessing a trait that is immunologically costly. Given that hirsutism develops during adolescence under the actions of androgens, and testosterone may have suppressant effects on the immune system (Grossman 1985), males displaying androgen-dependent secondary sexual traits could be indirectly advertising underlying genetic fitness to potential mates (Folstad and Karter 1992).

Research on women's sexual preferences for masculine chest and trunk hair has shown cross-cultural differences. Women from the United Kingdom stated a pronounced preference for masculine chest and trunk hair (Dixon et al. 2003). A weaker preference for male body hair was found among Bakossi women in Cameroon (Dixon, Dixon, Morgan, et al. 2007), whereas women from China, New Zealand, and the United States rated images lacking trunk hair as most attractive (Dixon, Dixon, Li, et al. 2007, Dixon et al. 2010). Recently, Rantala et al. (2010) found that among women in Finland, images of torsos depicting pronounced chest hair were judged to be most attractive by postmenopausal women and less attractive by younger women. Beards augment perceptions of male masculinity, social maturity, confidence, and age (Roll and Verinis 1971; Kenny and Fletcher 1973; Pancer and Meindl 1978; Wood 1986; Addison 1989; Reed and Blunk 1990; Wogalter and Hosie 1991; Neave and Shields 2008). Although women value these characteristics in mates (Buss 1989; Penton-Voak and Perrett 2001), studies of facial hair in relation to male facial attractiveness have

produced contradictory results. Thus, some studies have found a full beard to be attractive to women (Freedman 1969; Pellegrini 1973; Reed and Blunk 1990), while others have not (Feinman and Gill 1977; Wogalter and Hosie 1991; Muscarella and Cunningham 1996). Neave and Shields (2008) found that women rated male faces with light stubble as most attractive; perceived age rose with increasing amounts of facial hair, and a full beard was rated as looking most dominant.

The equivocal results on male facial attractiveness and beardness should be treated with caution, as the stimuli employed in some of these studies may not accurately reflect men's faces and beards as they appear in real life. One reason for this may be that beards do not exist independently of other facial traits. Facial expression plays an important role in many aspects of social communication in human beings and in other anthropoids (Darwin 1872). Cross-cultural studies have shown that many human populations share facial expressions indicative of fundamental emotions, such as fear, surprise, anger, happiness, sadness, and disgust (Ekman et al. 1969). It is thought that such facial expressions are phylogenetically ancient in humans (Ekman 1993; Schmidt and Cohn 2001). Morphologically very similar or identical facial expressions have also been described in the great apes (Burrows et al. 2006; Vick et al. 2007). Researchers have suggested that in primates, the smile originated as a rejection response to noxious stimuli (i.e., drawing back the corners of the mouth), then evolved into a ritualized signal of fear and submission (i.e., a fear grimace) before finally differentiating into graded fearful, nervous, and genuinely happy smiles in humans (Andrew 1963; Van Hoof 1972). In many species of nonhuman primates, males have striking secondary sexual adornments involving the face and head (Dixon 1998; Dixon et al. 2005). As such, facial expressions and secondary sexual adornments might act in concert for display purposes.

Although studies of female preferences for male body hair have included the preferences of people from indigenous as well as Western cultures, research on perceptions of beardedness have focused largely on the judgments of people of European descent from Western cultures. Any examination of the signaling value of beards will be greatly strengthened through establishing the similarities and differences in perceptions of male beardedness cross-culturally. As such, we carried out this research with participants of European descent in New Zealand (NZ) and with participants of Polynesian descent in Independent Samoa. These cultures differ markedly in socioeconomic status and exposure to modern mass media. NZ is a modern industrialized country with a population of more than 4 million people and has a high exposure to Western popular culture. In contrast, Samoa is a chain of islands in Western Polynesia with a population of 179 000. Compared with NZ, Samoa has far less exposure to Western popular culture, such as billboards, fashion magazines, movies, and access to the Internet is not widely available outside of the capital Apia. Bearded and clean-shaven men from both cultures were photographed posing with neutral, smiling, and angry facial expressions. The aim of this study was to test how beardedness, in concert with facial expressions indicative of anger and happiness, influence perceptions of male attractiveness, social status, age, and aggressiveness.

MATERIALS AND METHODS

Photographic stimuli

Ten NZ men of European descent (mean age = 23.50, standard deviation [SD] = 3.57, range 20–30 years) and 9 Samoan men (mean age = 23.00, SD = 2.12, range 20–27 years) were

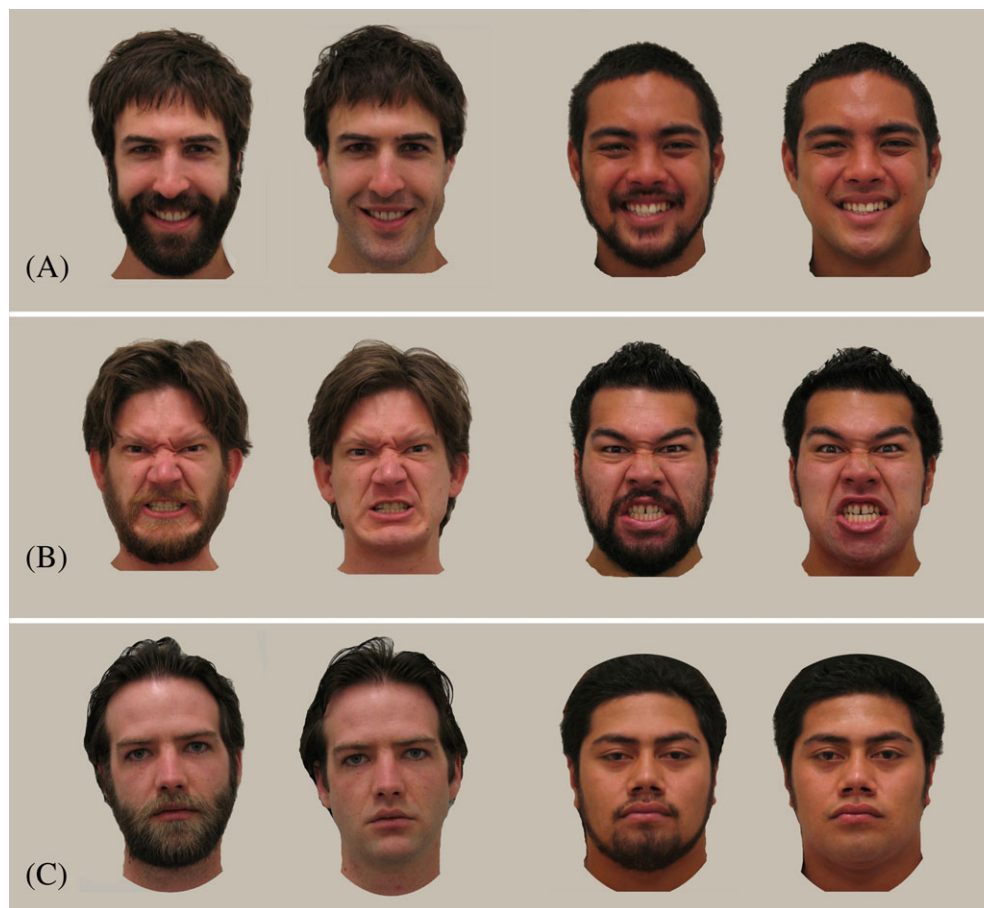


Figure 1
Examples of the facial expressions used to test the effect of the beard on perceptions of attractiveness (A), aggressiveness (B), and social status and perceived age (C) in New Zealand and Samoa.

recruited for this study. The men from these 2 cultures did not differ significantly in age ($t_{17} = 0.366$, $P = 0.713$). Participants were recruited with full beards, defined as not having shaved or trimmed the face for at least 6 weeks. These men were photographed with a full beard and then again when clean-shaven posing neutral, smiling, and angry facial expressions using a Canon PowerShot digital camera with a resolution of 8.0 megapixels. The camera was setup 150 cm from the participant, and all photographs were taken under the same controlled lighting. Figure 1 provides examples of the faces and facial expressions used in NZ and Samoa.

The Facial Action Coding System (FACS; Ekman et al. 2002) was used to produce photographs of men with standardized angry and smiling facial expressions. FACS describes the movement of groups of facial muscles or Action Units (AUs). Forty-four AUs have been identified, 30 of which relate to specified movements of suites of facial muscles and 14 that are not specifically associated with anatomy (Kanade et al. 2000). FACS does not refer to movements that are specific to an emotion, however, combinations of AUs can produce posed facial expressions that are in turn perceived as expressions of emotion (Ekman et al. 2002). In our study, we were interested in whether facial hair plays a role in communicating 2 emotional states: happiness and anger. Therefore, we used FACS to instruct participants to pose happy and angry facial expressions.

The instructions for the movement of AUs were verbally administered by a researcher, who posed the facial expressions and provided examples from FACS (Ekman et al. 2002). Figure 2 shows the AUs employed to pose an angry facial expression in this study. First, a frowning eyebrow movement requires movement of the corrugator supercilii and depressor

supercilii muscles. To achieve this pose, participants were asked to draw their eyebrows medially and down (Figure 2A). An open eye requires movement of the levator palpebrae superioris, and participants were asked to open their eyes while frowning (Figure 2B). Open eyes were posed along with a wrinkled nose, requiring the nasolabial furrow to be deepened (Figure 2B). Participants were then asked to pull down their lower lip, part their lips, and clench their teeth. This sequence requires the movement of the depressor labii inferioris, (Figure 2C). Participants repeated this combination of AUs when clean-shaven and fully bearded (Figure 2D).

Questionnaires

Each questionnaire began with a cover sheet to collect demographic information from each participant (sex, age, and ethnicity). All questionnaires were submitted anonymously, and participation was voluntary. NZ participants were interviewed at Victoria University of Wellington, New Zealand. In the Samoan sample, all the participants were Samoan citizens living on Upolu island. All participants were interviewed individually at their homes, in communal huts, or at farms using a flipbook containing the photographs. Each photograph was cropped to show only the face, from the top of the head to below the jawline (Figure 1). This research was preapproved by the Human Ethics Committee of Victoria University of Wellington and is in accordance with the Helsinki Declaration of 1975. Participants completed 4 studies, as detailed below.

Study 1 quantified women's ratings of attractiveness of men posing smiles with full beards and clean-shaven. The photographs were presented individually, in a random order and rated using a 6-point Likert Scale, where 0 = unattractive,

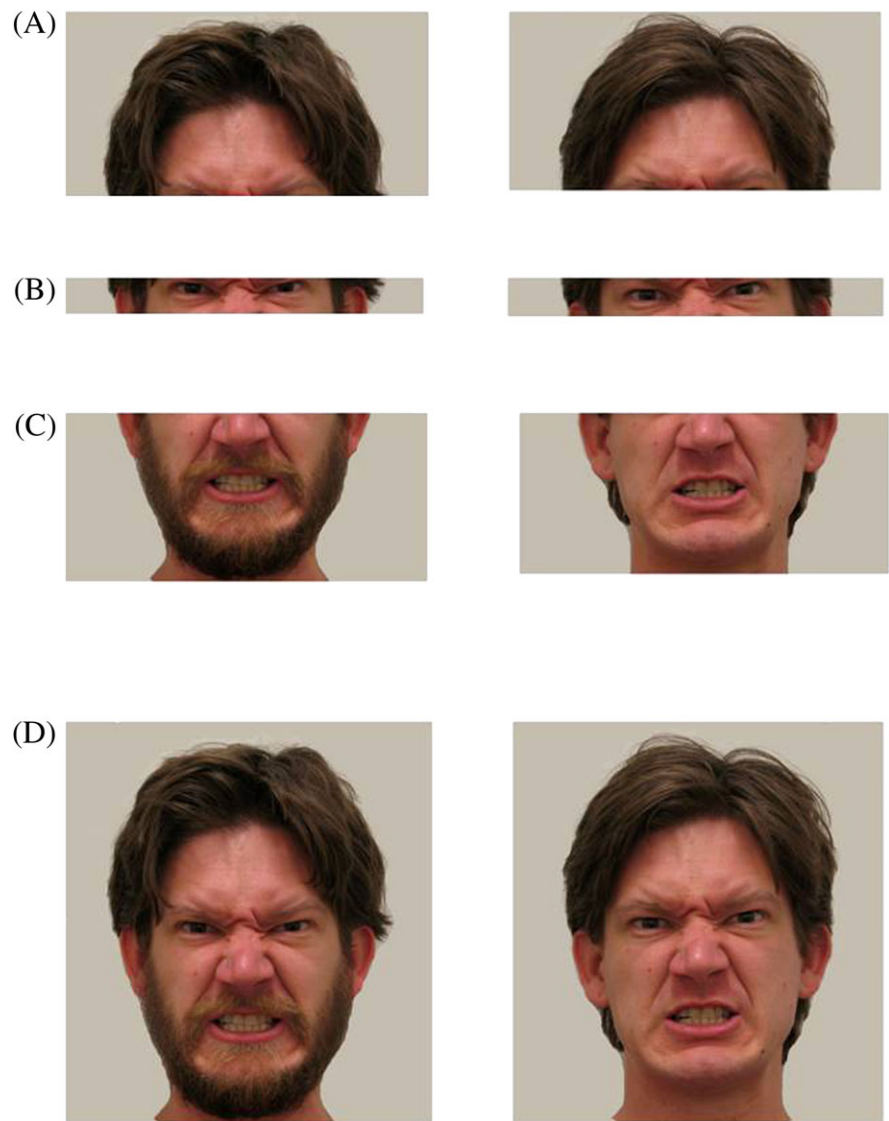


Figure 2

The FACS was used to pose angry facial expressions. Participants were asked to draw their eyebrows medially and down (A), while retaining open eyes and a wrinkled nose (B). Participants were also asked to part their lips while drawing them down and clenching their teeth (C). This combination of movements was repeated in the same participants when clean-shaven and fully bearded (D).

1 = only slightly attractive, 2 = moderately attractive, 3 = attractive, 4 = very attractive, and 5 = extremely attractive.

Study 2 measured men's judgments of physical aggressiveness of bearded and clean-shaven men. Photographs of men posing angry facial expressions were presented individually in a random sequence and rated for aggressiveness using a 6-point Likert Scale, where 0 = not aggressive, 1 = only slightly aggressive, 2 = moderately aggressive, 3 = aggressive, 4 = very aggressive, and 5 = extremely aggressive.

Study 3 assessed men's and women's judgments of social status of men with beards or clean-shaven, posing neutral expressions. Social status was defined as how likely the person in the photograph was to have a high-ranking social position and command respect over other men in the community. To simplify this, after the definition of social status was explained to participants, the word "importance" was used in the social status scale, which was as follows: 0 = low importance, 1 = only slightly important, 2 = moderately important, 3 = important, 4 = very important, and 5 = extremely important.

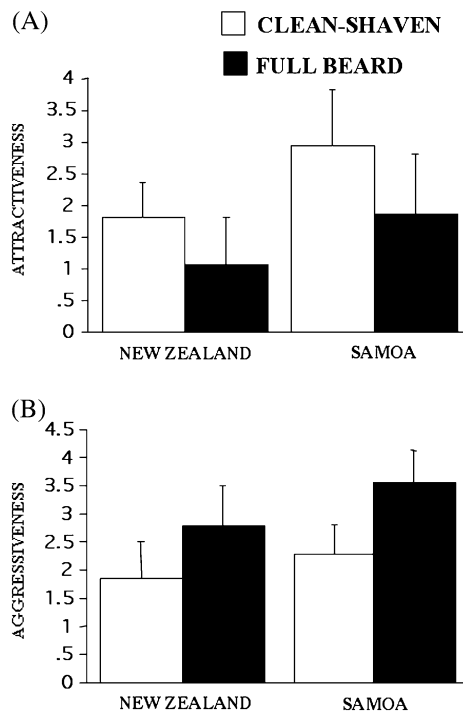
Study 4 assessed men's and women's perceived age (in years) of men photographed posing neutral facial expression with beards or clean-shaven.

For the NZ sample, participants were of European descent and rated only the images of men who were of European

descent. Samoan participants rated only the photographs of Samoan men. In Samoa, a linguistic interpreter, fluent in both English and Samoan, was present to ensure that participants understood the Likert Scales.

STATISTICAL ANALYSIS

The mean attractiveness (study 1), aggressiveness (study 2), social status (study 3), and perceived age (study 4) ratings of clean-shaven and bearded faces were entered as dependent variables in separate two-way repeated mixed measures analyses of covariance (ANCOVAs). In each, ANCOVA culture (Samoa vs. NZ) was the between-subjects fixed factor, beardedness (bearded vs. clean-shaven) was the within-subjects repeated measures fixed factor, and participant's age was a covariate. For study 3 (social status) and study 4 (perceived age), sex (male vs. female) was included as an additional between-subjects fixed factor. Post hoc two-tailed paired sample *t*-tests were used to uncover which factors were driving significant interactions within subjects. For interactions between subjects, post hoc independent samples *t*-tests were employed. For all independent samples *t*-tests, Levene's test for equality of variances was used prior to comparing the means. If this test was significant ($P < 0.05$), we have reported the

**Figure 3**

(A) Mean attractiveness scores (± 1 SD) made by women for faces posing smiling facial expressions when clean-shaven and bearded. (B) Mean aggressiveness scores (± 1 SD) made by men for faces depicting angry facial expressions when clean-shaven and bearded.

results of a modified test in which an adjusted degrees of freedom, test statistic, and P value were calculated using the Welch–Satterthwaite method. This calculation compares the means of the 2 groups without assuming equality of variances. All computations were made using PAWS Version 18 (SPSS 2009).

RESULTS

Study 1: the beard and perceived attractiveness

A total of 100 Samoan women (mean [M] = 21.36, SD = 3.30, range = 18–33 years) and 129 NZ women (M = 20.38, SD = 3.63, range = 18–38) participated in this study. The Samoan participants were significantly older than the NZ participants (Levene's test for equality of variances F = 0.029, P = 0.865; t_{227} = -2.11, P = 0.036). Age was included as a covariate in a two-way repeated mixed measures ANCOVA, in which attractiveness ratings was the dependent variable, culture (Samoa vs. NZ) was the between-subjects fixed factor, and beardedness (bearded vs. clean-shaven) was the within-subjects repeated measures fixed factor.

The ANCOVA revealed a significant main effect of beardedness ($F_{1,226}$ = 23.25, P < 0.001, η_p^2 = 0.093), so that women's attractiveness ratings were significantly higher for clean-shaven than bearded men in both NZ (t_{128} = 11.83, P < 0.001) and Samoa (t_{99} = 12.01, P < 0.001; Figure 3A). There was a significant main effect of culture on the attractiveness judgments ($F_{1,226}$ = 112.32, P < 0.001, η_p^2 = 0.332), so that Samoan women's attractiveness ratings were significantly higher, overall, for both clean-shaven and bearded men, compared with those of NZ women (Levene's test for equality of variances F = 14.62, P < 0.001; $t_{69,223}$ = -10.28, P < 0.001). There was a significant interaction between culture and beardedness ($F_{1,226}$ = 12.53, P < 0.001, η_p^2 = 0.053), which reflects that

Samoan women gave higher scores than NZ women for clean-shaven (Levene's test for equality of variances F = 20.37, P < 0.001; $t_{158,774}$ = -11.16, P < 0.001) and bearded faces (Levene's test for equality of variances F = 7.62, P = 0.006; $t_{183,814}$ = -6.92, P < 0.001). There was no main effect of age ($F_{1,226}$ = 0.01, P = 0.917, η_p^2 = 0.000). However, there was a significant interaction between beardedness and age ($F_{1,226}$ = 3.99, P = 0.047, η_p^2 = 0.017), which reflects a trend for older women to judge bearded faces as more attractive than younger women (Pearson Correlation: r = 0.120, N = 229, P = 0.07) but not for clean-shaven faces (r = 0.034, N = 229, P = 0.605).

Study 2: the beard and perceived aggressiveness

In total, 111 NZ men (M = 20.86, SD = 3.57, range = 18–39 years) and 119 Samoan men (M = 28.55, SD = 11.02, range = 18–71 years) completed this study. Samoan men were significantly older than the NZ men (Levene's test for equality of variances F = 79.00, P < 0.001; $t_{144,004}$ = -7.23, P < 0.001). Age was entered as a covariate in a two-way repeated mixed measures ANCOVA, where ratings of aggressiveness was the dependent variable, culture (Samoa vs. NZ) was the between-subjects fixed factor, and beardedness (bearded vs. clean-shaven) was the within-subjects repeated measures fixed factor.

The ANCOVA revealed a significant main effect for beardedness ($F_{1,227}$ = 66.37, P < 0.001, η_p^2 = 0.226). Men gave higher aggressiveness ratings for bearded faces than clean-shaven faces in both NZ (t_{110} = -18.31, P < 0.001) and Samoa (t_{118} = -21.70, P < 0.001; Figure 3B). There was a statistically significant main effect of culture on aggressiveness ratings ($F_{1,227}$ = 58.93, P < 0.001, η_p^2 = 0.206), revealing that Samoan men's aggressiveness ratings were higher overall for both categories of facial hair than those of the NZ men (Levene's test for equality of variances F = 20.66, P < 0.001; $t_{191,573}$ = -8.41, P < 0.001). There was also a significant interaction between facial hair and culture ($F_{1,227}$ = 13.04, P < 0.001, η_p^2 = 0.054), which reflects that Samoan men gave higher ratings than men from NZ for clean-shaven faces (Levene's test for equality of variances F = 7.02, P = 0.009; $t_{206,204}$ = -5.62, P < 0.001) as well as bearded faces (Levene's test for equality of variances F = 8.96, P = 0.003; $t_{207,919}$ = -9.10, P < 0.001). There was no significant main effect of age ($F_{1,227}$ = 0.004, P = 0.947, η_p^2 = 0.000), or a significant interaction between age and beardedness ($F_{1,227}$ = 0.73, P = 0.394, η_p^2 = 0.003).

Study 3: the beard and perceived social status

A total of 52 NZ men (M = 21.81, SD = 3.01, range = 18–28 years), 64 NZ women (M = 21.27, SD = 4.84, range = 18–42 years), 119 Samoan men (M = 28.55, SD = 11.02, range = 18–71 years), and 100 Samoan women (M = 21.36, SD = 3.30, range = 18–33 years) completed this study. Participant's age was entered as a dependent variable in a 2 culture (NZ vs. Samoa) \times 2 sex (male vs. female) analyses of variance. This revealed a significant interaction between culture and sex ($F_{1,331}$ = 15.85, P < 0.001, η_p^2 = 0.046). Thus, age was entered as a covariate, social status ratings was the dependent variable, beardedness (bearded vs. clean-shaven) was the within-subjects repeated measures fixed factor, and culture (NZ vs. Samoa) and sex (male vs. female) were between-subjects fixed factors in a two-way repeated mixed measures ANCOVA.

The ANCOVA revealed a significant main effect for beardedness ($F_{1,330}$ = 10.47, P < 0.001, η_p^2 = 0.031). Bearded faces received higher scores for social status than clean-shaven faces (t_{334} = -14.14, P < 0.001; Figure 4A). There was also a statistically significant main effect of sex ($F_{1,330}$ = 13.85, P < 0.001, η_p^2 = 0.040), so that men gave higher scores overall for both

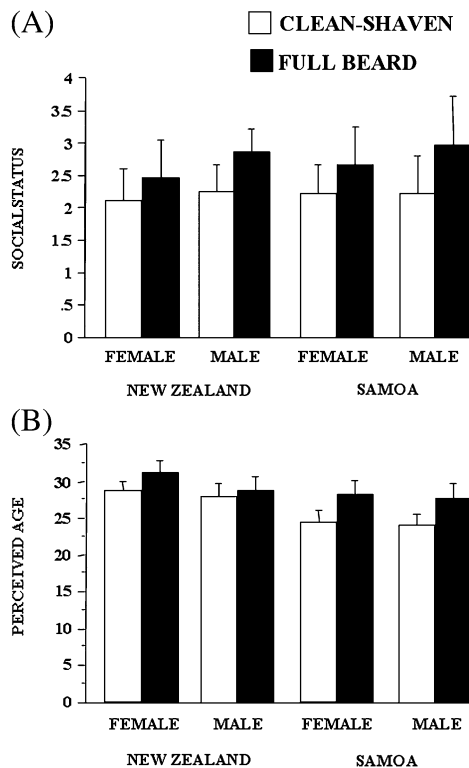


Figure 4

(A) Mean social status scores (± 1 SD) made by men and women for faces depicting neutral facial expressions when clean-shaven and bearded. (B) Mean perceived age scores (± 1 SD) made by men and women for faces depicting neutral facial expressions when clean-shaven and bearded.

clean-shaven and bearded faces than women (Levene's test for equality of variances $F = 10.05$, $P = 0.002$; $t_{317.108} = 4.25$, $P < 0.001$). There was also a significant interaction between beardness and sex ($F_{1,330} = 8.73$, $P = 0.003$, $\eta_p^2 = 0.026$), as men gave higher social status ratings for bearded than clean-shaven faces ($t_{170} = 13.16$, $P < 0.001$) as did women ($t_{163} = 7.28$, $P < 0.001$). Men also gave higher social status ratings than women for bearded (Levene's test for equality of variances $F = 2.92$, $P = 0.088$; $t_{333} = 5.02$, $P < 0.001$) but not clean-shaven faces (Levene's test for equality of variances $F = 1.87$, $P = 0.172$; $t_{333} = 1.08$, $P = 0.280$). To further investigate the sex difference in the ratings of bearded and clean-shaven faces, we calculated the differential between social status ratings within males and females by subtracting the ratings for clean-shaven faces from those of bearded faces. An independent samples t -test revealed that the differential was greater among men compared with women (Levene's test for equality of variances $F = 0.78$, $P = 0.379$; $t_{333} = 3.67$, $P < 0.001$). There were no main effects of culture ($F_{1,330} = 2.27$, $P = 0.133$, $\eta_p^2 = 0.007$) or age ($F_{1,330} = 1.79$, $P = 0.181$, $\eta_p^2 = 0.005$). There was no statistically significant interaction between beardness and culture ($F_{1,330} = 1.21$, $P = 0.273$, $\eta_p^2 = 0.004$), beardness and age ($F_{1,330} = 0.79$, $P = 0.376$, $\eta_p^2 = 0.002$), culture and sex ($F_{1,330} = 1.69$, $P = 0.195$, $\eta_p^2 = 0.005$), or any three-way interaction between beardness, culture, or sex ($F_{1,330} = 0.005$, $P = 0.942$, $\eta_p^2 = 0.000$).

Study 4: the beard and perceived age

The same participants who completed study 3 completed this study. We ran a two-way repeated mixed measures ANCOVA

in which participant's age was entered as a covariate, perceived age ratings was the dependent variable, beardness (bearded vs. clean-shaven) was the within-subjects repeated measures fixed factor, and culture (NZ vs. Samoa) and sex (male vs. female) were between-subjects fixed factors.

The ANCOVA revealed significant main effects for beardness ($F_{1,330} = 50.17$, $P < 0.001$, $\eta_p^2 = 0.132$), culture ($F_{1,330} = 328.02$, $P < 0.001$, $\eta_p^2 = 0.498$), and sex ($F_{1,330} = 27.13$, $P < 0.001$, $\eta_p^2 = 0.076$). The main effect of beardness reflects that beards were rated as looking significantly older by Samoan men ($t_{118} = -19.09$, $P < 0.001$), Samoan women ($t_{99} = -20.08$, $P < 0.001$), NZ women ($t_{63} = -11.46$, $P < 0.001$), and NZ men ($t_{51} = -2.99$, $P = 0.004$; Figure 4B). The main effect of culture reflects that NZ scores were higher overall than Samoan scores (Levene's test for equality of variances $F = 2.72$, $P = 0.100$; $t_{333} = 18.60$, $P < 0.001$). The main effect of sex reflects that women's scores were overall higher than men's (Levene's test for equality of variances $F = 14.30$, $P < 0.001$; $t_{311.768} = -4.56$, $P < 0.001$). There was a significant interaction between beardness and sex ($F_{1,330} = 21.55$, $P < 0.001$, $\eta_p^2 = 0.061$), which reflects that women gave significantly higher age ratings to both clean-shaven (Levene's test for equality of variances $F = 4.65$, $P = 0.032$; $t_{326.305} = -2.43$, $P = 0.016$) and bearded (Levene's test for equality of variances $F = 5.23$, $P = 0.023$; $t_{318.126} = -5.86$, $P < 0.001$) faces. There was also a significant interaction between beardness and culture ($F_{1,330} = 85.30$, $P < 0.001$, $\eta_p^2 = 0.205$), so that participants from NZ gave higher ratings than participants from Samoa for both clean-shaven (Levene's test for equality of variances $F = 0.07$, $P = 0.785$; $t_{333} = 23.35$, $P < 0.001$) and bearded faces (Levene's test for equality of variances $F = 3.50$, $P = 0.062$; $t_{333} = 9.08$, $P < 0.001$). Finally, there was a significant three-way interaction between beardness, sex, and culture ($F_{1,330} = 6.69$, $P = 0.010$, $\eta_p^2 = 0.020$). These interactions reflect that compared with women from Samoa, women from NZ rated clean-shaven faces as older (Levene's test for equality of variances $F = 7.83$, $P = 0.006$; $t_{159.394} = 18.95$, $P < 0.001$) as well as bearded faces (Levene's test for equality of variances $F = 0.25$, $P = 0.620$; $t_{162} = 9.40$, $P < 0.001$). Likewise, compared with Samoan men, NZ men rated clean-shaven faces as older (Levene's test for equality of variances $F = 4.24$, $P = 0.041$; $t_{80.199} = 13.78$, $P < 0.001$) as well as bearded faces (Levene's test for equality of variances $F = 0.32$, $P = 0.572$; $t_{169} = 3.45$, $P < 0.001$). Women from NZ gave higher ratings than men from Samoa for clean-shaven faces vs. bearded faces (Levene's test for equality of variances $F = 11.38$, $P = 0.001$; $t_{172.376} = 3.80$, $P < 0.001$) and bearded faces vs. clean-shaven faces (Levene's test for equality of variances $F = 3.44$, $P = 0.065$; $t_{181} = 29.47$, $P < 0.001$). Men from NZ gave higher scores than women from Samoa for bearded versus clean-shaven faces (Levene's test for equality of variances $F = 1.44$, $P = 0.232$; $t_{150} = 14.99$, $P < 0.001$) but not for clean-shaven versus bearded faces (Levene's test for equality of variances $F = 0.03$, $P = 0.862$; $t_{150} = -1.04$, $P = 0.298$). There was no main effect of the participant's age ($F_{1,330} = 1.90$, $P = 0.169$, $\eta_p^2 = 0.006$) or any interaction between facial hair and participant's age ($F_{1,330} = 0.17$, $P = 0.681$, $\eta_p^2 = 0.001$).

DISCUSSION

This study found that men and women from NZ and Samoa judged neutral faces with beards as having higher social status and being older than clean-shaven faces. Men also judged bearded faces posing angry facial expressions as more aggressive than clean-shaven faces. However, women rated the clean-shaven smiling faces as more attractive than bearded faces. This suggests that the beard plays a stronger role in intrasexual signaling than in female mate preferences.

Although beards do not directly improve fighting ability, as is the case for weaponry used in male–male competition in many animals (Emlen 2008), it has been suggested that they may intimidate rival males by increasing perceptions of the size of the jaw, overall length of the face, and by enhancing aggressive and threatening jaw-thrusting behaviors (Guthrie 1970). Among the Medlpa tribe of Papua New Guinea, when posing an aggressive and threatening facial expression, men have been observed to pull apart the beard with both hands (Eibl-Eibesfeldt 1989). Similarly, beards are sometimes incorporated into gestural “beard jutting” threat displays, which consist of flicking the back of the fingers of one hand under the chin and outward, causing the beard to become erected and thrust out toward the rival (Guthrie 1970; Morris 2002). The beard may handicap men during fighting, as it might be easily clutched by rival men (Zahavi and Zahavi 1997). Thus, bearded men may be advertising confidence as well as superior fighting ability to male rivals. Several studies have found that images of bearded men, posing neutral facial expressions, are rated as highly self-confident (Pellegrini 1973) and physically aggressive (Muscarella and Cunningham 1996; Neave and Shields 2008). The current study is the first to show that the beard augments a threatening behavioral display as bearded men with angry facial expressions received significantly higher scores for aggressiveness compared with clean-shaven faces in both NZ and Samoa. This suggests that the beard plays an important role in intermale signaling of threat and aggression.

Several authors have advanced the view that secondary sexual adornments have evolved in mammals as “psychological weapons” that act in concert with threatening or aggressive displays (Archer 2009; Darwin 1872; Guthrie 1970; Hingston 1933). Central to this view, however, is that if a trait or behavior has evolved as a signal, it should, in turn, affect the behavior of others (Maynard Smith and Harper 2003). As an example, consider songbirds, where if a song is to be classified as an aggressive signal, it should be augmented in aggressive contexts, predict aggressive intent, and elicit a response from the recipients of the display (Searcy and Beecher 2009). In humans, anger is a display of aggression and threat that may curtail the behavior of others (Averill 1983). When people view images of angry faces, neurological research has shown augmented activity in the orbitofrontal and anterior cingulate cortex with the increasing intensity of angry facial expressions, which Blair et al. (1999) suggest is a response that encourages behavioral extinction in the recipient of the signal. In this study, we tested the extent to which facial expressions and beards act in concert in the perceptions of an aggressive threatening facial expression. Research on male vocal pitch has shown that lower vocal pitch augments perceptions of dominance and aggression in men (Puts et al. 2006, 2007), and men who judge themselves as physically dominant lower their vocal pitch in response to other male competitors (Puts et al. 2006). Similar studies testing the role of beardedness in intrasexual aggressiveness signaling during competitive scenarios would be valuable to further understand the signalling value of facial hair. For example, one might predict based on the neurological studies, that men will exhibit greater orbitofrontal and anterior cingulate cortex activation in response to bearded angry facial expressions than when viewing clean-shaven angry faces.

It has been suggested that facial hair decreases a male's perceived social status because it is associated with traits such as vagrancy (Morris 2002). Our results fail to provide support for this perspective, as participants rated bearded men as having higher social status than clean-shaven men. Furthermore, we found that men ascribed higher ratings for perceived social status to bearded faces than women. Our results are

consistent with other studies that have shown the beard augments perceptions of social dominance and status (Addison 1989; Muscarella and Cunningham 1996; Neave and Shields 2008). Further evidence that beardedness is associated with augmented social status was found in a study of male academic staff at Universities in the United Kingdom, where Professors were significantly more heavily bearded than Senior Lecturers, Lecturers, and Research Fellows (Carter and Åström 2004). These findings along with those of the current study suggest that dominant men may grow facial hair in order to effectively signal their social status and dominance.

Testosterone dependent traits may augment social dominance (Mazur and Booth 1998) as well as aggressive displays (Archer 2009), and there is growing evidence that sexual dimorphism in craniofacial features and vocal pitch reflects men's actual physical strength (Sell et al. 2009, 2010). Among the Tsimane' forager farmers of Beni, Bolivia, men and women accurately assessed physical dominance (measured using midarm circumference) from photographs of the face (Undurraga et al. 2010). Furthermore, greater dominance and prestige among male Tsimane' are associated with more surviving offspring and more mating opportunities (Von Rueden et al. 2010). Beardedness appears to signal elevated social status, dominance, and the communication of aggressive intent. However, whether or not the beard honestly advertises men's actual strength or is associated with greater reproductive success, as are other masculine traits, remains to be determined.

Given that a beard makes a man look older than his real age and women typically prefer a partner who is 2–3 years older than themselves (Buss 1989; Kenrick and Keefe 1992), it seems reasonable to suspect that beards may enhance male facial attractiveness to women. However, clean-shaven faces received significantly higher scores for attractiveness than bearded faces in both NZ and Samoa. Some previous studies have found that bearded men are rated as more socially mature, sincere, masculine, self-confident, and courageous than clean-shaven faces (Kenny and Fletcher 1973; Pellegrini 1973; Neave and Shields 2008). While women may value all of these characteristics in male mates, studies of female preferences for male beardedness have produced conflicting results. Some studies have concluded that beards enhance attractiveness to women (Freedman 1969; Pellegrini 1973; Reed and Blunk 1990), whereas in other studies the opposite effect has been observed (Feinman and Gill 1977; Wogalter and Hosie 1991; Muscarella and Cunningham 1996). As well as beards, androgens drive sexually dimorphic traits such as a large jaw, narrow eyes, a pronounced brow ridge, and a longer face (Weston et al. 2007; Thayer and Dobson 2010). Men displaying these masculine traits are ranked as less “warm,” honest and cooperative (Penton-Voak and Perrett 2001), and less trustworthy (Stirrat and Perrett 2010) and are more physically aggressive (Carré et al. 2009). Some studies have found that facial masculinity does not augment perceptions of attractiveness to women (Perrett et al. 1998; Swaddle and Reiersen 2002; Neave et al. 2003). However, in mate choice, the fitness of a phenotype depends not only on the phenotype but also on the context. Female choice may be highly variable, due to individual motivation and the availability of mates carrying preferred traits (Jennions and Petrie 1997), suggesting that male ornamentation is maintained via context-specific female choice. Recent cross-cultural studies found that women in countries with lower overall health and higher income inequality judge masculine faces to be more attractive than in countries with better health care and greater income stability (DeBruine et al. 2010, 2011; Brooks et al. 2011). The strength of female preferences for beardedness may also differ cross-culturally as a result of

demographic variables, and future studies testing this hypothesis would be valuable.

A further source of context-specific variation in mate choice concerns women's preferences for androgen-dependent traits across the menstrual cycle. It has been found that women in the fertile phase of the menstrual cycle have a greater preference for masculine facial, bodily, and vocal features than women interviewed at other points of the menstrual cycle (Gangestad and Thornhill 2008). These traits may be energetically and immunologically costly and only sustainable by those males of higher genetic quality or competitive ability (Folstad and Karter 1992). Given that the growth of terminal hairs on the face and body is androgen-dependent (Randall 2008) and by consequence might incur physiological costs for males, it is possible that female preferences for body hair and beardedness will vary depending upon the phase of the menstrual cycle. Rantala et al. (2010) showed that women at the low-fertility phase of the menstrual cycle stated a higher preference for male torsos with pronounced body hair than women at the high-fertility phase of the menstrual cycle. Interestingly, this study also revealed that postmenopausal women had a higher preference for body hair than premenopausal women. It will be important for future studies to uncover the extent to which women's preferences for beardedness vary due to menstrual cycle phase and reproductive status.

For centuries, fashion, religious values, and political agendas have shaped the social significance of man's facial hair (Peterkin 2001; Reynolds 1949). A study, quantifying styles of facial hair (e.g., mustaches, sideburns, and full beards) in men photographed for the *Illustrated London News* between 1842 and 1971, showed that the popularity of facial hair and particular styles of facial hair, fluctuated over time (Robinson 1976). In the current study, it is possible that women from Wellington, New Zealand, which is a modern industrialized city with high exposure to "Western" popular media, rated clean-shaven faces as more attractive than bearded faces because it is currently more fashionable for men to be clean-shaven in Western society. However, in Samoa, there is far less exposure to Western popular media. For example, it is difficult, even in the capital of Apia, to find magazines of any sort (including fashion magazines) that can be easily acquired in Western societies. Equally, there are no large billboards advertising fashion, and there is only one movie theater in the entire country. Outside of the capital, access to the Internet is sparse. Nevertheless, like NZ women, Samoan women also rated clean-shaven faces as more attractive. Indeed, Samoan women's attractiveness ratings for clean-shaven male faces were higher than those of NZ women. However, in Samoa the presence of Missionaries may have brought Western ideologies of dress and influenced men's shaving habits (Mageo 1994). Thus, although preferences for clean-shaven faces appear to be cross-culturally robust, it would be beneficial to test this hypothesis in a culture where beards are commonly worn.

It is conceivable that secondary sexual traits such as the beard in *Homo sapiens* were present in the ancestral hominids. However, the fossil record cannot answer this question, as cutaneous tissue does not fossilize. Thus, comparative studies of human beings and extant nonhuman primates may shed light on the possible functions of visually conspicuous secondary sexual traits in threat or dominance displays (Dixson et al. 2005). For example, mature male gorillas (silverbacks) are larger, more muscular than females, adorn a gray covering on their backs, and an adipose crest on top of the head. Adipose crests are largest in those males having the most females in their one-male units (Caillaud et al. 2008). In the orangutan, adult males develop full expression of their "cheek flanges" and beards only when they achieve dominant

positions in the social system (Galdikas 1985; Kingsley 1982; Utami Atmoko and Van Hoof 2004). Male mandrills (*Mandrillus sphinx*) exhibit spectacular red and blue facial coloration, the red coloration being most pronounced in dominant males having higher testosterone levels (Wickings and Dixson 1992; Setchell and Dixson 2001). Dominant male hamadryas baboons (*Papio hamadryas*) also develop large androgen-dependent capes of hair that appear to be sexually selected as a dominance signal between males (Zuckerman and Parkes 1939; Kummer 1990). Although secondary sexual facial coloration and capes of hair in nonhuman primates are not strictly homologous to the beards of the human male, they may have arisen via similar selective mechanisms. Such traits are visually conspicuous and communicate an individual male's age and dominance status. Compared with many nonhuman primates, men exhibit relatively well-developed secondary sexual traits (e.g., facial and body hair) such as those that occur in polygynous species (Dixson 1998; Dixson et al. 2005). Although further evidence is required, the results of the present study suggest that the human beard plays an important role intrasexually as a signal of age, social status, and aggressiveness.

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REFERENCES

- Addison WE. 1989. Beardedness as a factor in perceived masculinity. *Percept Mot Skills*. 68:921–922.
- Andersson MB. 1994. Sexual selection. Princeton (NJ): Princeton University Press.
- Andrew RJ. 1963. The origin and evolution of the calls and facial expressions of the primates. *Behaviour*. 20:1–109.
- Archer J. 2009. Does sexual selection explain human sex differences in aggression? *Behav Brain Sci*. 32:249–311.
- Averill JR. 1983. Studies on anger and aggression. *Am Psychol*. 38:1145–1160.
- Blair RJR, Morris JS, Frith CD, Perrett DI, Dolan RJ. 1999. Dissociable neural responses to facial expressions of sadness and anger. *Brain*. 122:883–893.
- Blanchard CD. 2010. Of lion manes and human beards: some unusual effects of the interaction between aggression and sociality. *Front Behav Neurosci*. 3:45.
- Brooks R, Scott IM, Maklakov AA, Kasumovic MM, Clark AP, Penton-Voak IS. 2011. National income inequality predicts women's preferences for masculinized faces better than health does. *Proc R Soc Lond B Biol Sci*. 278:810–812.
- Burrows AM, Waller BM, Parr LA, Bonar CJ. 2006. Muscles of facial expression in the chimpanzee (*Pan troglodytes*): descriptive, comparative and phylogenetic contexts. *J Anat*. 208:153–167.
- Buss DM. 1989. Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. *Behav Brain Sci*. 12:1–49.
- Cabanac M, Brinnet H. 1988. Beards, baldness, and sweat secretion. *Eur J Appl Physiol*. 58:39–46.
- Cabanac M, Brinnet H. 2000. Beard vs. forehead, ten years later. *Am J Hum Biol*. 12:460–464.
- Caillaud D, Levréro F, Gatti S, Ménard N, Raymond M. 2008. Influence of male morphology on male mating status and behavior during interunit encounters in western lowland gorillas. *Am J Phys Anthropol*. 135:379–388.
- Carré JM, McCormick CM, Mondloch CJ. 2009. Facial structure is a reliable cue of aggressive behavior. *Psychol Sci*. 20:1194–1198.

- Carter S, Åström K. 2004. A cross-sectional study of UK academics suggests Santa Claus might be a professor. *Pharm J*. 273:897–899.
- Darwin C. 1871. The descent of man and selection in relation to sex. London: John Murray.
- Darwin C. 1872. The expression of emotions in man and animals. London: John Murray.
- Debruine LM, Jones BC, Crawford JR, Welling LLM, Little AC. 2010. The health of a nation predicts their mate preferences: cross-cultural variation in women's preferences for masculinized male faces. *Proc R Soc Lond B Biol Sci*. 277:2405–2410.
- Debruine LM, Jones BC, Little AC, Crawford JR, Welling LLM. 2011. Further evidence for regional variation in women's masculinity preferences. *Proc R Soc Lond B Biol Sci*. 278:813–814.
- Dixon AF. 1998. Primate sexuality: comparative studies of the prosimians, monkeys, apes, and human beings. Oxford: Oxford University Press.
- Dixon AF, Dixon BJ, Anderson MJ. 2005. Sexual selection and the evolution of visually conspicuous sexually dimorphic traits in male monkeys, apes and human beings. *Annu Rev Sex Res*. 16:1–19.
- Dixon AF, Halliwell G, East R, Wignarajah P, Anderson MJ. 2003. Masculine somatotype and hirsuteness as determinants of sexual attractiveness to women. *Arch Sex Behav*. 32:29–39.
- Dixon BJ, Dixon AF, Bishop P, Parrish A. 2010. Human physique and sexual attractiveness in men and women: a New Zealand–U.S.A comparative study. *Arch Sex Behav*. 39:798–806.
- Dixon BJ, Dixon AF, Li B, Anderson MJ. 2007. Studies of human physique and sexual attractiveness: sexual preferences of men and women in China. *Am J Hum Biol*. 19:88–95.
- Dixon BJ, Dixon AF, Morgan B, Anderson MJ. 2007. Human physique and sexual attractiveness: sexual preferences of men and women in Bakossiland, Cameroon. *Arch Sex Behav*. 36:369–375.
- Eibl-Eibesfeldt I. 1989. Human ethology. New York: Aldine de Gruyter.
- Ekman P. 1993. Facial expression and emotion. *Am Psychol*. 48:384–392.
- Ekman P, Friesen WV, Hager JC. 2002. Facial action coding system (FACS): manual, Salt Lake City (UT): A Human Face.
- Ekman P, Sorenson RE, Friesen WV. 1969. Pan-cultural elements in facial displays of emotion. *Science*. 164:86–88.
- Emlen DJ. 2008. The evolution of animal weapons. *Annu Rev Ecol Syst*. 39:387–413.
- Ewing JA, Rouse BA. 1978. Hirsutism, race and testosterone levels: comparison of East Asians and Europeans. *Hum Biol*. 50:209–215.
- Farthing MJG, Mattei AM, Edwards CRW, Dawson AM. 1982. Relationship between plasma testosterone and dihydrotestosterone concentrations and male facial hair growth. *Br J Dermatol*. 107:559–564.
- Feinman S, Gill GW. 1977. Females' response to males' beardedness. *Percept Mot Skills*. 44:533–534.
- Folstad I, Karter AJ. 1992. Parasites, bright males, and the immunocompetence handicap. *Am Nat*. 139:603–622.
- Freedman DG. 1969. The survival value of the beard. *Psychol Today*. October:36–39.
- Galdikas BMF. 1985. Adult male sociality and reproductive tactics among orangutans at Tanjung Puting Reserve. *Folia Primatol*. 45:9–24.
- Gangestad SW, Thornhill R. 2008. Human oestrus. *Proc R Soc Lond B Biol Sci*. 275:991–1000.
- Garn SM. 1951. Types and distribution of the hair in man. *Ann N Y Acad Sci*. 53:498–507.
- Green AC, Kimlin M, Siskind V, Whiteman DC. 2006. Hypothesis: hair cover can protect against invasive melanoma on the head and neck (Australia). *Cancer Causes Control*. 17:1263–1266.
- Grossman CJ. 1985. Interactions between the gonadal steroids and the immune system. *Science*. 227:257–261.
- Guthrie RD. 1970. Evolution of human threat display organs. In: Dobhansky T, Hecht MK, Steers WC, editors. *Evolutionary biology*. New York: Appleton-Century-Crofts. p. 257–302.
- Hamilton JB. 1958. Age, sex and genetic factors in the regulation of hair growth in man: a comparison of Caucasian and Japanese populations. In: Montagna W, Ellis RA, editors. *The biology of hair growth*. New York: Academic Press. p. 399–433.
- Hamilton JB. 1964. Racial and genetic predisposition. *Clin Obstet Gynaecol*. 7:1075–1084.
- Hamilton JB, Terada H, Mestler GE. 1958. Studies of growth throughout the life span in Japanese II: beard growth in relation to age, sex, heredity and other factors. *J Gerontol*. 13:269–281.
- Hamilton WD, Zuk M. 1982. Heritable true fitness and bright birds: a role for parasites. *Science*. 218:384–387.
- Hingston RWG. 1933. Psychological weapons in animal fight. *J Pers*. 2:3–21.
- Hunt J, Bussière LF, Jennions MD, Brooks R. 2004. What is genetic quality? *Trends Ecol Evol*. 19:329–333.
- Jennions MD, Petrie M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev*. 72:283–327.
- Kanade T, Cohn JF, Tian Y. 2000. Comprehensive database for facial expression analysis. *IEEE Proceedings of the Fourth International Conference on Automatic Face and Gesture Recognition (FG'00)*; 2000 Mar 28–30; Grenoble (France); The Institute of Electrical and Electronics Engineers, Inc. p. 484–490.
- Kenny CT, Fletcher D. 1973. Effects of beardedness of person perception. *Percept Mot Skills*. 37:413–414.
- Kenrick DT, Keefe RC. 1992. Age preferences in mates reflect sex differences in human reproductive strategies. *Behav Brain Sci*. 15:75–133.
- Kingsley S. 1982. Causes of non-breeding and the development of the secondary sexual characteristics in the male orang-utan: a hormonal study. In: de Boer LEM, editor. *The orang-utan: its biology and conservation*. The Hague (The Netherlands): Junk Publishers. p. 215–229.
- Kummer H. 1990. The social system of hamadryas baboons and its presumable evolution. In: de Mello MT, Whiten A, Byrne RW, editors. *Baboons: behavior and ecology, use and care: selected proceedings of the 12th Congress of the International Primatological Society*. Brasilia, Brazil. p. 43–60.
- Lookingbill DP, Demers LM, Wang C, Leung A, Rittmaster RS, Santen RJ. 1991. Clinical and biochemical parameters of androgen action in normal healthy Caucasians versus Chinese subjects. *J Clin Endocrinol Metab*. 72:1242–1248.
- Mageo JM. 1994. Hairdos and don'ts: hair symbolism and sexual history in Samoa. *Man*. 29:407–432.
- Maynard Smith J, Harper D. 2003. *Animal signals*. Oxford: Oxford University Press.
- Mazur A, Booth A. 1998. Testosterone and dominance in men. *Behav Brain Sci*. 21:353–397.
- Morris D. 1967. *The naked ape*. London: Triad Grafton Book.
- Morris D. 2002. *People watching*. London: Vintage.
- Muscarella F, Cunningham MR. 1996. The evolutionary significance and social perception of male pattern baldness and facial hair. *Ethol Sociobiol*. 17:99–117.
- Neave N, Laing S, Fink B, Manning JT. 2003. Second to fourth digit ratio, testosterone, and perceived male dominance. *Proc R Soc Lond B Biol Sci*. 270:2167–2172.
- Neave N, Shields K. 2008. The effects of facial hair manipulation on female perceptions of attractiveness, masculinity, and dominance in male faces. *Pers Indiv Differ*. 45:373–377.
- Nenoff P, Handrick W, Krüger C, Hermann J, Schmoranz B, Paasch U. 2009. Ectoparasites. Part 2: bed bugs, Demodex, sand fleas and cutaneous larva migrans. *Hautarzt*. 60:749–760.
- Pancer SM, Meindl JR. 1978. Length of hair and beardedness as determinants of personality impression. *Percept Mot Skills*. 46:1328–1330.
- Pellegrini RJ. 1973. Impressions of the male personality as a function of beardedness. *Psychol*. 10:29–33.
- Penton-Voak IS, Perrett DI. 2001. Male facial attractiveness: perceived and shifting female preferences for male traits across the menstrual cycle. *Adv Study Behav*. 30:219–259.
- Perrett DI, Lee KJ, Penton-Voak I, Rowland D, Yoshikawa S, Burt DM, Henzi SP, Castles DL, Akamatsu S. 1998. Effects of sexual dimorphism on facial attractiveness. *Nature*. 394:884–887.
- Peterkin A. 2001. *One thousand beards: a cultural history of facial hair*. Vancouver (Canada): Arsenal Pulp Press.
- Price ML, Griffiths WAD. 1985. Normal body hair—a review. *Clin Exp Dermatol*. 10:87–97.
- Puts DA, Gaulin SJC, Verdolini K. 2006. Dominance and the evolution of sexual dimorphism in human voice pitch. *Evol Hum Behav*. 27:283–296.
- Puts DA, Hodges CR, Cárdenas RA, Gaulin SJC. 2007. Men's voices as dominance signals: vocal fundamental and formant frequencies influence dominance attributions among men. *Evol Hum Behav*. 28:340–344.
- Randall VA. 2007. Hormonal regulation of hair follicles exhibits a biological paradox. *Semin Cell Dev Biol*. 18:274–285.

- Randall VA. 2008. Androgens and hair growth. *Dermatol Ther.* 21:314–328.
- Randall VA, Ebling FJG. 1991. Seasonal changes in human hair growth. *Br J Dermatol.* 124:146–151.
- Rantala MJ. 1999. Human nakedness: adaptation against ectoparasites? *Int J Parasitol.* 29:1987–1989.
- Rantala MJ. 2007. Evolution of nakedness in *Homo sapiens*. *J Zool.* 273:1–7.
- Rantala MJ, Pölkki M, Rantala LM. 2010. Preference for human male body hair changes across the menstrual cycle and menopause. *Behav Ecol.* 21:419–423.
- Reed JA, Blunk EM. 1990. The influence of facial hair on impressions formation. *Soc Behav Person.* 18:169–176.
- Reynolds R. 1949. Beards: their social standing religious involvements, decorative possibilities, and value in offence and defence through the ages. New York: Harcourt Brace Jovanovich.
- Robinson DE. 1976. Fashions in shaving and trimming the beard: the men of the *Illustrated London News*, 1842–1972. *Am J Sociol.* 81:1133–1141.
- Rogers AR, Iltis D, Wooding S. 2004. Genetic variation at the MC1R locus and the time since loss of human body hair. *Curr Anthropol.* 45:105–108.
- Roll S, Verinis JS. 1971. Stereotypes of the scalp and facial hair as a measured by the semantic differential. *Psychol Rep.* 28:975–980.
- Rosenfield RL, Kubota T, Fang VS. 1976. Plasma unbound and unconjugated androgens in oriental men. *J Endocrinol.* 68:165–166.
- Schmidt KL, Cohn JF. 2001. Human facial expressions as adaptations: evolutionary questions in facial expression research. *Yearb Phys Anthropol.* 44:3–24.
- Searcy WA, Beecher MD. 2009. Song as an aggressive signal in songbirds. *Anim Behav.* 78:1281–1292.
- Sell A, Bryant AG, Cosmides L, Tooby J, Sznycer D, von Rueden C, Krauss A, Gurven M. 2010. Adaptations in humans for assessing physical strength from the voice. *Proc R Soc Lond B Biol Sci.* 277:3509–3518.
- Sell A, Cosmides L, Tooby J, Sznycer D, von Rueden C, Gurven M. 2009. Human adaptations for the visual assessment of strength and fighting ability from the body and face. *Proc R Soc Lond B Biol Sci.* 276:575–584.
- Setchell JM, Dixon AF. 2001. Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Horm Behav.* 39:177–184.
- Setty LR. 1971. Hair patterns of the face of white and negro males. *J Natl Med Assoc.* 63:128–131.
- SPSS. 2009. PASW Statistics, release version 18.0.0. Chicago (IL): SPSS Inc. [cited 2011 December 16]. Available from: <http://www-01.ibm.com/software/analytics/spss/>.
- Stirrat M, Perrett DI. 2010. Valid facial cues to cooperation and trust: male facial width and trustworthiness. *Psychol Sci.* 20:349–354.
- Swaddle JP, Reiersen W. 2002. Testosterone increases perceived dominance but not attractiveness in human males. *Proc R Soc Lond B Biol Sci.* 269:2285–2289.
- Szabo G. 1967. The regional anatomy of the human integument with special reference to the distribution of hair follicles, sweat glands and melanocytes. *Philos Trans R Soc Lond B Biol Sci.* 252:447–489.
- Thayer ZM, Dobson SD. 2010. Sexual dimorphism in chin shape: implications for adaptive hypotheses. *Am J Phys Anthropol.* 143:417–425.
- Thozhur SM, Crocombe AD, Smith PA, Mullier KC. 2006. Structural characteristics and mechanical behaviour of beard hair. *J Mater Sci.* 41:1109–1121.
- Tolgyesi E, Coble DW, Fang FS, Kairinen EO. 1983. A comparative study of beard and scalp hair. *J Soc Cosmet Chem.* 34:361–382.
- Trotter M. 1922. A study of facial hair in the White and Negro races. *Wash Univ Stud.* 9:273–289.
- Trotter M. 1938. Anthropometry: a review of the classifications of hair. *Am J Phys Anthropol.* 24:105–126.
- Trotter M, Duggins OH. 1948. Age changes in head hair form from birth to maturity. 1. Index and size of hair of children. *Am J Phys Anthropol.* 6:489–506.
- Undurraga EA, Eisenberg DTA, Magvanjav O, Wang R, Leonard WR, McDade TW, Reyes-García V, Nyberg C, Tanner S, Huanca T, et al. 2010. Human's cognitive ability to assess facial cues from photographs: a study of sexual selection in the Bolivian Amazon. *PLoS One.* 5(6):e11027.
- Utami Atmoko S, Van Hoof JARAM. 2004. Alternative reproductive tactics: male bimaturism in orangutans. In: Kappeler P, Van Schaik C, editors. *Sexual selection in primates: new and comparative perspectives*. Cambridge (UK): Cambridge University Press. p. 196–207.
- Van Hoof JARAM. 1972. The phylogeny of laughter and smiling. In: Hinde RA, editor. *Non-verbal communication*. Cambridge (UK): Cambridge University Press. p. 209–241.
- Vick SJ, Waller BM, Parr LA, Smith Pasqualini MC, Bard KA. 2007. A cross-species comparison of facial morphology and movement in humans and chimpanzees using the Facial Action Coding System (FACS). *J Nonverbal Behav.* 31:1–20.
- Von Rueden C, Gurven M, Kaplan H. 2010. Why do men seek status? Fitness payoffs to dominance and prestige. *Proc R Soc Lond B Biol Sci.* 278:2223–2232.
- Weiss RA. 2009. Apes, lice and prehistory. *J Biol.* 8:20.
- West PM, Maccormick H, Hopcraft G, Whitman K, Ericson M, Hordinsky M, Packer C. 2006. Wounding, mortality and mane morphology in African lions, *Panthera leo*. *Anim Behav.* 71: 609–619.
- Weston EM, Friday AE, Liò P. 2007. Biometric evidence that sexual selection has shaped the hominin face. *PLoS One.* 2(8):e710.
- Wheeler PE. 1992a. The influence of loss of functional body hair on the energy budgets of early hominids. *J Hum Evol.* 23:379–388.
- Wheeler PE. 1992b. The thermoregulatory advantages of large body size for hominids foraging in savannah environments. *J Hum Evol.* 23:351–362.
- Wickings EJ, Dixon AF. 1992. Testicular function, secondary sexual development, and social status in male mandrills (*Mandrillus sphinx*). *Physiol Behav.* 52:909–916.
- Winkler EM, Christiansen K. 1993. Sex hormone levels and body hair growth in !Kung San and Kavango men from Namibia. *Am J Phys Anthropol.* 92:155–164.
- Wogalter MS, Hosie JA. 1991. Effects of cranial and facial hair on perceptions of age and person. *J Soc Psychol.* 131:589–591.
- Wood DR. 1986. Self-perceived masculinity between bearded and non-bearded males. *Percept Mot Skills.* 62:769–770.
- Zahavi A, Zahavi A. 1997. *The handicap principle*. Oxford: Oxford University Press.
- Zuckerman S, Parkes AS. 1939. Observations on the secondary sexual characters in monkeys. *J Endocrinol.* 1:430–439.