

Is plasticity in mating preferences adapted to perceived exposure to pathogens?

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Abstract Humans are unique among primates due to a lack of typical thermally insulating fur. The ectoparasite avoidance mediated by the mate choice hypothesis suggests that the loss of body hair reduces the risk of infection by ectoparasites and that the movement toward nudity may have been enforced by parasite-mediated sexual selection. In this study, we investigated two possible predictions of this hypothesis: (1) that preferences for hairless bodies increase with exposure to environmental pathogens and (2) that disgust sensitivity to the pathogens' threat predicts the degree to which a woman will prefer hairless bodies. Using an experiment comparing the preferences of 88 women for shaved vs. hairy pictured versions of 20 male torsos, we found that exposure to the visual cues of pathogens does not predict preferences for a male chest nor does the individual disgust sensitivity to disease-related invertebrates. Overall, the results suggest that female perception of male trunk hair is not associated with a risk of contamination, which questions the salience of the ectoparasite avoidance hypothesis in explaining the loss of body hair in humans.

Keywords *Homo sapiens* · Mate preferences · Nakedness · Pathogens · Trunk hair

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Introduction

The loss of body hair in modern humans, about 1.2 Ma ago (Rogers et al. 2004), has been the target of controversy since Darwin (for reviews, see Rantala 1999, 2007). It has been suggested, for example, that bareness was an adaptation to a hot savannah environment (e.g. Morris 1967; Wheeler 1984; for a detailed review, see Rantala 2007). However, this hypothesis is based on the fallible idea of bareness as a cooling factor (Amaral 1996; Rantala 2007). At present, the most prominent hypothesis is the ectoparasite avoidance hypothesis originally proposed by Belt (1874) and recently rediscovered and elaborated by Rantala (1999). This hypothesis proposes that the loss of body hair reduces the risk of infection by ectoparasites, a number of which have been responsible for pandemics (Pagel and Bodmer 2003; Rantala 1999, 2007). For example, in the 1300s, a plague transmitted by fleas was estimated to have killed between 25% and 50% of the populations of Europe, Asia and Africa (Gottfried 1983). This suggests that the selection of hairy individuals as mates could be risky in terms of transmission of deadly diseases particularly in a pathogen-rich environment.

Parasitic and infectious diseases have had a major impact on human population demography around the world (Anderson and May 1991; Ewald 1994). They have been identified as drivers of religious diversity (Fincher and Thornhill 2008), political stability of countries (Thornhill et al. 2009), the size (Thomas et al. 2004) and the number of human offspring (Guégan et al. 2001), parenting (Quinlan 2007) and cooking practises (Sherman and Billing 1999), marriage structures (Low 1990) and mate preferences (Gangestad and Buss 1993; Gangestad et al. 2006; DeBruine et al. 2010a). Parasite diversity (the number of kinds) and prevalence (number of cases) in the world vary

greatly; the diversity increases as one proceeds from the poles to the equator (Guernier et al. 2004), while the prevalence is influenced by pathogen richness and disease control efforts (Dunn et al. 2010), leading to socio-ecological variation in selective pressures across time and space. This suggests that flexibility in behavioural response to parasitic threat could have been favoured (Murray and Schaller 2010; DeBruine et al. 2010a).

Mate choice criteria are thought to reflect the selection of traits that advertise aspects of mate quality (Andersson 1994). However, judgements of attractiveness, as cues of mate quality or fertility (e.g. Rhodes et al. 2003; Lie et al. 2010; Prokop and Fedor 2011) may vary depending on the environment. For example, cues associated with physical attractiveness, such as masculinity in males, or facial symmetry, are more desirable in environments with high pathogen prevalence than in environments with low pathogen prevalence (Gangestad and Buss 1993; Penton-Voak et al. 2004; Gangestad et al. 2006; Little et al. 2007; DeBruine et al. 2010a). Laboratory studies have supported these findings: female participants exposed to visual cues of environmental pathogens preferred more masculine and more symmetrical male faces (Little et al. 2011). Finally, women who perceived themselves as more vulnerable to diseases preferred masculine male faces more than females less vulnerable to diseases (DeBruine et al. 2010b). This suggests that mate choice criteria are influenced by environmental and individual conditions regarding the pathogen threat.

In this study, we used a controlled experiment to examine whether female mating preferences for male body hair vary with visual cues of pathogens (the ectoparasite avoidance mediated by mate choice hypothesis) and with individual predispositions regarding sensitivity to cues of pathogens. We predicted that preferences for hairless bodies increase with exposure and sensitivity to cues of environmental pathogens.

Methods

Participants

The research was carried out in a lecture hall in April 2011 over four occasions (~20 students per session) at the University of Trnava, Slovakia. Eighty-eight female students (aged between 21 and 23 years, $M=21.21$, $SE=0.15$) took part in the study on a voluntary basis. All the participants were reported to be heterosexuals and earned an extra credit course for their participation. The participants were randomly divided into the two treatments described below: high pathogen group ($n=40$) and low pathogen group ($n=48$).

Chest hair stimuli

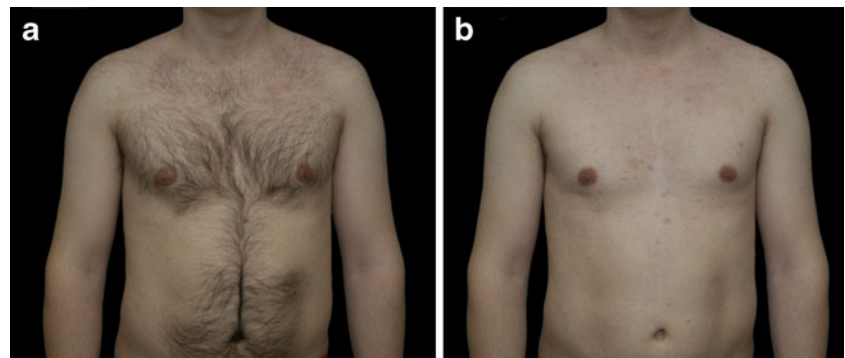
We used the photographs of male participants which were used by Rantala et al. (2010) in their research on female preferences for male body hair. Briefly, 20 Finnish males with visible chests aged 20–32 years participated in the research. Front views of male torsos were taken under symmetrical lighting conditions from a fixed distance of 200 cm. Immediately after the photo session, the men were asked to shave their abdomen with a shaver, finishing with a razor blade and shaving cream. After shaving, a new set of pictures was taken with an identical setup (Fig. 1). More details can be found in Rantala et al. (2010).

Cues to the high/low pathogen incidence

Images of objects holding a potential disease threat were predominantly taken from a published study examining peoples' perception of pathogens (Curtis et al. 2004). The images were pairs depicting, for example, a plate of viscous liquid colour-morphed like bodily fluids (high pathogen) or a blue chemical dye (low pathogen). For our study, the ten image pairs which were consistently seen as differing in disgust perception were extracted from the high-quality PDF of the stimuli. Specifically, six pairs were taken from Curtis et al. (2004) and four additional pairs were downloaded from available web sites. These additional pairs were taken in order to increase the number of disease-relevant insects that are hypothesized as having been responsible for body hair loss in humans (Rantala 1999, 2007).

Overall, five out of the ten pictures presented to each participant were insects, either disease-relevant (human flea (*Pulex irritans*), human louse (*Pediculus humanus*), German cockroach (*Blattella germanica*), common tick (*Ixodes ricinus*) and mosquito (*Anopheles maculipennis*)) (high pathogen group) or their disease-irrelevant antipodes (ladybird beetle *Coccinella septempunctata*, leaf beetle *Chrysomela fastuosa*, azure damselfly *Coenagrion puella*, rhinoceros beetle *Oryctes nasicornis* and Old World swallowtail *Papilio machaon*) (low pathogen group). Similar invertebrates were used by Prokop and Fančovičová (2010). The remaining five pictures were: a plate of viscous liquid (described above), a male face (healthy in high pathogen and ill in low pathogen), *Ascaris* worms (high pathogen) or a wasp (*Polistes* sp.) (low pathogen), a white cloth with either a stain resembling body fluid (high pathogen) or a stain of blue liquid (low pathogen), a metro full of people and one that is empty (high and low pathogen, respectively).

Fig. 1 Paired photographs of a male body before (a) and after (b) the removal of body hair. The photographs were presented to women in the forced-choice trial



Procedure

This study followed a similar research design as those used by Little et al. (2011). The participants were administered a short questionnaire assessing age and sexual orientation, followed by the main test. The main test consisted of three parts: an initial test that assessed the participants' preferences for male body hair (the pre-exposure test), a slide show of either high- or low-pathogen images (the exposure phase) and a post-exposure test which was identical to the pre-exposure test. The inclusion of a pre-exposure test is potentially important as it allowed us to control for possible preexisting individual differences in female preferences for male body hair, such as those related to the menstrual cycle, age or sexual imprinting (see Rantala et al. 2010). Finally, in order to investigate (1) whether women perceive variation in the disease threat and (2) whether female preferences for male body hair are driven by individual susceptibility to pathogens, the participants were asked to rate the disgust of five disease-relevant and five control (disease-irrelevant) invertebrates on a seven-point Likert scale (1=not at all, 7=extremely disgusting). Previous research indicated that disgust sensitivity is related to actual susceptibility to disease (Stevenson et al. 2009; Prokop and Fančovičová 2011). These ratings were only performed in the post-exposure phase.

In the pre- and post-exposure phase, the participants were presented with PowerPoint presentation slides projected on a screen with forced-choice paired image trials of 20 males with and without trunk hair and consequently asked to choose between the hairy and the completely bare (shaved) version of the same body. In order to exclude the effect of skin irritation caused by shaving, the photographs were black-and-white similarly as in Rantala et al.'s (2010) study. The pairs of pictures as well as the presence of a picture within each pair (to the left of the right side) in each phase were presented in a random order. In each trial, the participants were asked to choose the image that they found sexually most attractive. The participants were not told whether the males in the pairs were identical or not, or

whether the photographs presented in the pre- and post-exposure phase were the same. No other information regarding why the slideshow was presented was provided.

In the exposure phase, participants saw a slideshow of ten images repeated three times (for a total of 30 images). The high pathogen group was presented with pictures with cues of a high incidence of pathogens, while the low pathogen group was presented with pictures with cues of a low incidence of pathogens. The images were presented for 3 s each (for a total of 90 s of exposure) with instructions following Little et al. (2011): 'Please try and look at these images carefully'. The image order in the pre- and post-exposure phase was randomized.

Statistical methods

A generalized linear mixed model (GLMM) with a logit link function was used to examine how the treatment (high pathogen/low pathogen) and the phase (pre-exposure/post-exposure) influenced preferences for male trunk hair (dependent variable with binomial distribution, 0 for hairy and 1 for bare). The participant ID and picture ID were treated as random factors in order to take into account the pseudoreplication of the data. The correlation between the disgust of invertebrates and preference for male trunk hair was calculated by using the percentage of bodies with trunk hair chosen out of the 20 pairs of male bodies. These data could not be included into the GLMM because they were only gathered in the post-exposure phase.

Results

Figure 2 shows a preference for male trunk hair suggesting that the probability of choosing a bare body is different from 0.5. Bare bodies were preferred more than males with trunk hair in both the pre-exposure and post-exposure tests.

1. Exposure to visual cues of pathogens. The Cronbach alpha for the pre- and post-exposure phase was high

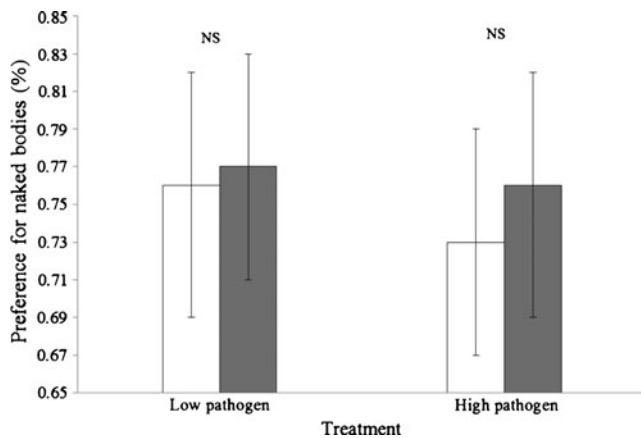


Fig. 2 Differences in preference for naked bodies before (*open bars*) and after exposure (*grey bars*) to high and low pathogen conditions. *Error bars* are 95% confidence intervals. *NS* not statistically significant

(0.80 and 0.82, respectively). The test–retest reliability was also high (Guttman split-half reliability=0.90), indicating that environmental exposure to pathogens has no influence on mate preferences. GLMM resulted in a nonsignificant model ($F_{3,3516}=1.19$, $p=0.31$). Neither the effect of the treatment and the phase nor the interaction between the variables influenced the preference for male trunk hair ($F_{1,3516}=1.793$, 1.39 and 0.21, all $p>0.18$, respectively). This is not due, however, to the fact that women fail to perceive a variation in the disease threat. Disease-relevant invertebrates were rated as more disgusting than the control invertebrates in both high pathogen ($M=25.67\pm0.75$ vs. 10.81 ± 0.65 , paired $t=16.55$, $df=47$, $p<0.001$, respectively) and low pathogen conditions ($M=28.48\pm0.69$ vs. 10.90 ± 0.75 , paired $t=19.18$, $df=39$, $p<0.001$, respectively). Participants in high pathogen conditions rated disease-relevant invertebrates as less disgusting than participants in low pathogen conditions ($M=25.67\pm0.70$ vs. 28.48 ± 0.76 , $t=-2.71$, $df=86$, $p=0.008$, respectively), whereas the control animals were rated similarly in both conditions ($M=10.81\pm0.67$ vs. 10.9 ± 0.73 , $t=-0.09$, $df=86$, $p=0.93$, respectively). This indicates that visual exposure to pathogens leads to habituation to disease-relevant stimuli.

- The influence of individual sensibility to pathogens for chest hair preferences. In light of the fact that the perceived disgust of invertebrates was measured in the post-exposure phase, only the post-exposure score of preferences for male trunk hair was included in the subsequent statistical analyses. There were no correlations between the disgust ratings of disease-relevant or control invertebrates and trunk hair preference in the post-exposure test neither in high pathogen ($r=0.05$ and 0.13 , both $p>0.37$, respectively) nor in low pathogen conditions ($r=-0.23$ and -0.09 , both $p>0.15$, respectively). When participants in both conditions were divided into two groups with high

and low disgust sensitivity to disease-relevant invertebrates according to the median split, we failed to discover any differences in the preference of male trunk hair in the post-exposure test between these groups neither in the high ($M=23.13\pm4.24$ vs. 28.33 ± 4.24 , $t=0.87$, $df=46$, $p=0.39$, $n_1=n_2=24$, respectively) nor in the low pathogen group ($M=22.50\pm4.29$ vs. 26.50 ± 4.29 , $t=0.66$, $df=38$, $p=0.51$, $n_1=n_2=20$, respectively).

Discussion

This study examined the salience of ectoparasite avoidance mediated by the mate choice hypothesis (Pagel and Bodmer 2003; Rantala 1999, 2007) in order to explain the loss of body hair in humans. Female preferences for the male chest were quantified based on their recent experience with visual cues to environmental pathogens. When considering that hairlessness could have a naturally selected advantage, it has been speculated that increasing the reproductive success of hairless women, who were in their home bases under a heavier ectoparasite threat than males (Rantala 1999, 2007), resulted in stronger preferences of hairless women by men (Rantala 2007; Pagel and Bodmer 2003).

We predicted that mate choice preferences were flexible and can quickly respond to subtle exposure to visual stimuli during adulthood (DeBruine et al. 2010a, b; Little et al. 2011). Our prediction was not supported, however, as female preferences for hairless male bodies were not influenced by exposure to visual cues to environmental pathogens, which contrasts with other research works on preferences for masculine traits (Gangestad and Buss 1993; Penton-Voak et al. 2004; DeBruine et al. 2010a,b; Little et al. 2011). It is possible that the ectoparasite avoidance mediated by the mate choice hypothesis is not applicable to the male chest at least in an environment with a low pathogen threat. This possibility remains open as preference for the male chest varies across cultures (Dixson et al. 2003, 2007a, b, 2010), and cultures are influenced by parasites (e.g. Gangestad et al. 2006; Quinlan 2007; Fincher and Thornhill 2008; Thornhill et al. 2009), suggesting that a preference for the male chest would be influenced by the parasite threat. In Slovakia, where our experiment was performed, the estimated pathogen prevalence and richness are relatively lower than in countries closer to the equator (Guernier et al. 2004; Murray and Schaller 2010; Prokop et al. 2010); thus, sensitivity to pathogens is expected to be relatively lower. In such an environment which is almost free of parasites, male hairiness is expected to be stronger than in environments rich in parasites. Further cross-cultural research is needed to examine female sensitivity to pathogens and whether male hairiness correlates with the parasite threat.

The present study indicated that females consistently preferred the torsos of shaved males more than the torsos of hairy males, suggesting that the male chest has a negative effect on female ratings of attractiveness (Dixson et al. 2007a; Rantala et al. 2010; but see Dixson et al. 2003) and supporting the idea that the male chest plays a role in mate choice. This, however, does not seem to result from the perception of hair as indicative of the pathogen load. If male chests are cues to parasite threat, then the correlation between the disgust for disease-relevant insects and the preference for shaved male bodies is expected, although no evidence was obtained in the present study. When considering research on disgust sensitivity, it was determined that repeated contact with disgusting stimuli obviously results in habituation (Rozin 2008; Adams et al. 2011), suggesting that potentially disgusting stimuli (i.e. male bodies with chest hair) should show the same or a higher preference in the second exposure. We found that repeated exposure to the male chest resulted in a similar preference and that females in the high pathogen treatment rated disease-relevant invertebrates as less disgusting than females from the low pathogen group supporting the effect of habituation. However, the women in our study who were the most disgusted by disease-relevant invertebrates showed no stronger preference for shaved male bodies than their less sensitive counterparts. All these evidences suggest that female perception of male trunk hair is not psychologically associated with the risk of contamination.

As far as we are aware, this is the first study which investigated the origin of human hairlessness from an evolutionary psychological perspective. Our results provide no evidence for ectoparasite avoidance mediated by the mate choice hypothesis as the experience with visual cues to environmental pathogens resulted in similar preferences for shaved male bodies as in the control group. Moreover, it seems that sensitivity to disgust does not mediate preferences for male trunk hair, suggesting that male body hair is not associated with the risk of contamination. Future research should investigate preference for body hair in humans with data from larger, more diverse samples and particularly among cultures that differ in risk of parasite infection.

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