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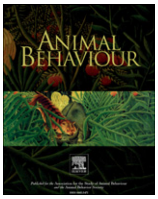

Is genetic diversity associated with mating success in humans?

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Human mating success has been associated with phenotypic characteristics proposed to signal genetic quality. However, whether genetic quality is directly associated with mating success in humans is unknown. Genetic diversity in general, and particularly at genes important for immune functioning within the major histocompatibility complex (MHC), has been associated with individual fitness and opposite-sex preferences for facial appearance, and may therefore be subject to sexual selection in humans. We investigated whether general and/or MHC genetic diversity, measured as microsatellite heterozygosity and standardized mean d^2, was associated with mating success, defined as number of sexual partners and age of first sex. Both measures of MHC diversity predicted number of sexual partners in females. Females with greater MHC diversity were more successful at obtaining mates than less diverse females. Mating success in males, however, was not significantly associated with any of the genetic diversity measures. These results provide partial support for a role of genetic diversity in human mating success.

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Recent evidence indicates that sexual selection may be acting on a range of phenotypic characteristics in contemporary human populations (Nettle & Clegg 2006; Jokela 2009). Because contraceptive use and family planning constrain numbers of offspring in modern societies, number of sexual partners and age of first sex are commonly used as proxy measures of mating success (e.g. see Thornhill & Gangestad 1994; Faurie et al. 2004; Rhodes et al. 2005; Nettle & Clegg 2006; Peters et al. 2008). These measures of mating success have been positively associated with body symmetry (Thornhill & Gangestad 1994), personality and creative ability (Nettle & Clegg 2006), sports performance (Faurie et al. 2004) and facial attractiveness (Rhodes et al. 2005; Peters et al. 2008).

It has been argued that phenotypic characteristics are under sexual selection in humans because they signal mate quality, including genetic quality (Thornhill & Gangestad 1993; Rhodes 2006). However, no studies have directly tested whether genetic quality is associated with mating success in humans. Genetic quality may include heterozygosity (or individual genetic diversity) at many loci, or at key loci such as those associated with immune functioning within the major histocompatibility complex (MHC; Thornhill & Gangestad 1993; Brown 1997, 1999). If heterozygosity is under sexual selection, then we predict that heterozygosity should be associated with individual variation in mating success.

Provided heterozygosity is associated with fitness, then heterozygous mates should be preferred because such mates could potentially enhance the chooser's reproductive success directly, through enhanced fertility, reduced risk of contagion, provisioning of quality resources and parental care (Thornhill & Gangestad 1993; Sauermann et al. 2001) and/or indirectly, by producing offspring that are on average more heterozygous (Mitton et al. 1993; Hoffman et al. 2007). There is some evidence that heterozygosity, both in general and at the MHC, is associated with fitness as well as mate preferences in some nonhuman animals. Genome-wide heterozygosity has been associated with fitness-related traits, including fertility and reproductive success, in many species (reviewed in Charlesworth & Charlesworth 1987; Keller & Waller 2002; Coltman & Slate 2003; Kempenaers 2007). For example, reduced heterozygosity associated with inbreeding predicted reduced sperm quality and smaller testis size in male wild rabbits, *Oryctolagus cuniculus* (Gage et al. 2006), while increased heterozygosity was associated with increased reproductive success in both male and female mandrills, *Mandrillus sphinx* (Charpentier et al. 2005). Heterozygosity within the MHC (or human leukocyte antigen, HLA in humans) should be especially advantageous for an individual's fitness. Because each MHC allele can only detect a restricted range of pathogens, MHC heterozygotes should be able to detect, and thereby initiate an immune response towards, a broader range of

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pathogens than homozygotes (Doherty & Zinkernagel 1975). There is evidence linking MHC heterozygosity to enhanced pathogen resistance in both humans (e.g. Carrington et al. 1999; Hraber et al. 2007; but see Hill et al. 1991) and other species, for example in mice, *Mus musculus* (Penn et al. 2002; McClelland et al. 2003), fat-tailed dwarf lemurs, *Cheirogaleus medius* (Schwensow et al. 2007) and water voles, *Arvicola terrestris* (Oliver et al. 2009). However, other studies have failed to find such an MHC-heterozygote advantage, for example in yellow-necked mouse, *Apodemus flavicollis* (Meyer-Lucht & Sommer 2005) and three-spined sticklebacks, *Gasterosteus aculeatus* (Rauch et al. 2006).

There is also evidence that sexual selection favours heterozygous individuals. For example, female fur seals, *Arctocephalus gazella*, actively choose mates that are more heterozygous across the genome (Hoffman et al. 2007). Moreover, preferences for MHC-heterozygous mates have been found in the Seychelles warbler, *Acrocephalus sechellensis* (Richardson et al. 2005) and fat-tailed dwarf lemurs (Schwensow et al. 2008). However, some species show no such preferences, including Soay sheep, *Ovis aries* (Paterson & Pemberton 1997) and great reed warblers, *Acrocephalus arundinaceus* (Westerdahl 2004; see also Sommer 2005). In addition, MHC heterozygosity was the best predictor of reproductive success in male rhesus macaques, *Macaca mulatta* (Sauermann et al. 2001; Widdig et al. 2004), but whether or not this effect reflects female choice is not clear from these studies.

In humans, mate preferences have recently been associated with heterozygosity in some laboratory studies. Women prefer the odour of MHC-heterozygous men (Thornhill et al. 2003), and they find the faces of MHC-heterozygous men more attractive than the faces of less heterozygous men (Roberts et al. 2005; Lie et al. 2008; but see Thornhill et al. 2003). Men, however, tend to prefer phenotypic cues to allelic distance (standardized mean d^2), another measure of genetic diversity, at loci outside the MHC in women's faces (Lie et al. 2008, 2010), perhaps because inbreeding, which reduces levels of allelic distance and genetic diversity, is related to fertility problems (Ober et al. 1999). Although humans appear sensitive to both olfactory and visual cues to genetic diversity in opposite-sex individuals, it is not yet clear whether genetic diversity, either in general or at the MHC, is associated with success in obtaining sexual partners.

Here we investigated whether two measures of genetic diversity (microsatellite heterozygosity and standardized mean d^2) at loci within and outside the MHC are sexually selected in humans. If they are, then more genetically diverse individuals should be more attractive as partners and should therefore enjoy greater mating success than less diverse individuals. We measured mating success as number of sexual partners and age of first sex. Age of first sex is also a measure of mating success because both sexes can enhance their reproductive potential by becoming sexually active earlier (e.g. Rhodes et al. 2005).

Past studies of human mating success controlled for the individual's age in relation to their cumulative mating success. However, an individual's attitude towards sexual behaviour could also influence whether and when they have sexual relationships. Indeed, individuals with more conservative attitudes towards sexual relations typically report having had fewer sexual partners (e.g. Thornhill & Gangestad 1994; Rhodes et al. 2005). Thus, we also included a measure of attitudes towards sexual behaviour in our study.

Specifically, we asked whether individuals with greater genetic diversity have greater mating success in terms of being more successful at having access to or attracting opposite-sex sexual partners and becoming sexually active earlier than individuals with less diversity. We included age and attitudes towards sexual behaviour as covariates because they influence the number of sexual partners obtained (Thornhill & Gangestad 1994; Rhodes et al. 2005). We also examined the independent contributions of general genetic diversity (nonMHC) and MHC diversity to the two measures of mating success. To our knowledge, this is the first study to investigate the impact of genetic diversity on mating success, assessed here as number of sexual partners and age of first sex.

METHODS

Participants

The participants were 145 (74 female) heterosexual, Caucasian students at the University of Western Australia (the sample has been described elsewhere, Lie et al. 2008). The experiment was advertised across the university campus, and participants were recruited from a wide range of departments including Psychology, Human movement, Physics, Medicine and Engineering. Participants received course credit and/or 10 Australian dollars for their participation. Each participant provided a DNA sample and details regarding their sexual behaviour and attitudes towards sex.

The study was reviewed and approved by the University Human Research Ethics Committee of The University of Western Australia.

DNA Samples and Genetic Diversity Measures

The procedures for DNA collection and genetic analyses are described in Lie et al. (2008). In brief, we used 12 microsatellite markers (average number of alleles 12; heterozygosity 0.83) across the MHC region, most of which are in strong linkage disequilibrium with one or more HLA genes (Malkki et al. 2005), and 11 nonMHC microsatellite markers (average number of alleles 14; heterozygosity 0.84) located on 11 different chromosomes. All loci are in Hardy–Weinberg equilibrium (Lie et al. 2008).

We calculated two measures of individual genetic diversity separately for the MHC and nonMHC loci: heterozygosity (referred to as H), which refers to the proportion of loci at which each individual is heterozygous, and standardized mean d^2 (referred to as d^2) following Amos et al. (2001) and Lie et al. (2008). The latter measure, d^2, reflects the genetic distance between microsatellite alleles at a given locus, averaged across all sampled loci (Coulson et al. 1998).

Sexual Behaviour and Attitudes

Sexual behaviour and attitudes to sexual relationships with the opposite sex were assessed via a questionnaire used in previous studies (Rhodes et al. 2005; Peters et al. 2008). Participants indicated the age at which they first had sexual intercourse, and how many sexual partners they have had since becoming sexually active. To obtain a measure of their attitude to sexual relationships, participants indicated the degree to which they agreed or disagreed on a nine-point Likert scale ($1 = $ strongly agree, $9 = $ strongly disagree), to the following four statements: sex without love is ok; casual sex outside an existing relationship is ok; sex on the first date is ok; and I would need to know my partner emotionally and psychologically before having sex (reverse scored). The ratings were then summed so that a higher score indicates a more conservative attitude towards sexual relations with the opposite sex (referred to as attitudes). This scale has moderate internal consistency and excellent test–retest reliability (Rhodes et al. 2005). We also obtained information regarding the participants' age, sex, ethnicity and sexual orientation (only heterosexuals were included in our analyses).

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