doi:10.1111/j.1558-5646.2010.00985.x

MATE CHOICE AND HUMAN STATURE: HOMOGAMY AS A UNIFIED FRAMEWORK FOR UNDERSTANDING MATING PREFERENCES

Alexandre Courtiol,[1,2,3] Michel Raymond,[3] Bernard Godelle,[3] and Jean-Baptiste Ferdy[4]

[1]*CNRS, Institut des Sciences de l'Évolution, Université Montpellier II, CC065, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France*

[2]*E-mail: alexandre.courtiol@univ-montp2.fr*

[3]*Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom*

[4]*CNRS, Évolution et Diversité Biologique, Université Paul Sabatier - Toulouse III, 118 Route de Narbonne, 31062 Toulouse Cedex 9, France*

Received October 2, 2009
Accepted February 1, 2010

Assortative mating for human height has long attracted interest in evolutionary biology, and the phenomenon has been demonstrated in numerous human populations. It is often argued that mating preferences generate this pattern, but other processes can also induce trait correlations between mates. Here, we present a methodology tailored to quantify continuous preferences based on choice experiments between pairs of stimuli. In particular, it is possible to explore determinants of interindividual variations in preferences, such as the height of the chooser. We collected data from a sample of 200 individuals from France. Measurements obtained show that the perception of attractiveness depends on both the height of the stimuli and the stature of the individual who judged them. Therefore, this study demonstrates that homogamy is present at the level of preferences for both sexes. We also show that measurements of the function describing this homogamy are concordant with several distinct mating rules proposed in the literature. In addition, the quantitative approach introduced here fulfills metrics that can be used to compare groups of individuals. In particular, our results reveal an important disagreement between sexes regarding height preferences in the context of mutual mate choice. Finally, both women and men prefer individuals who are significantly taller than average. All major findings are confirmed by a reanalysis of previously published data.

KEY WORDS: Assortative mating, GLMM, height, morphological evolution, sexual selection.

Mate choice has been recognized as the most important mechanism through which sexual selection influences evolution (Andersson 1994). Individuals with trait values that increase their probability of being chosen as a mate have higher reproductive success, thus inducing direct selective pressure on traits influencing mate choice (Darwin 1879; Andersson 1994). In addition, mating patterns produced by mate choice also exert indirect effects through their influence on several genetic aspects. In particular, positive assortative mating (homogamy) on a trait increases the homozygosity of genes that determine that trait. This in turn increases the genetic additive variance and inflates the additive genetic covariance between all types of relatives (Lynch and Walsh 1997), thus influencing the response to selection.

The influence of homogamy on evolution has long attracted interest, even in the very first papers on evolutionary biology. In his 1889 book *Natural Inheritance*, Galton studied the inheritance of several continuous traits in humans, mostly for eugenicist motives. Stature was one of the traits he considered, because measuring height was easy, cheap to measure, and replicable within the same individual. In addition, he demonstrated that heights

© 2010 The Author(s).

very closely follow a Gaussian distribution, which allows for analytical analysis. To understand how height is inherited, Galton compared statures between different categories of relatives. He noted that similarities in height between relatives does result from inheritance but can also be altered by mating patterns. To quantify this later influence, he looked for potential departures from random mating in a British sample of families. Galton did not find stature similarities between mates, but Pearson and Lee (1903), after collecting additional data, did find a positive correlation between mates' statures. These authors also developed theoretical predictions on how assortative mating influences trait evolution (see, e.g., Pearson 1897); unfortunately, their approach was flawed because it was based on an incorrect theory of inheritance. A few years later, in his seminal paper *The correlation between relatives on the supposition of Mendelian inheritance*, Fisher (1918) accurately formalized the influence of assortative mating on the process of inheritance, and using Pearson and Lee's data, he demonstrated that the principles of Mendelian inheritance can explain the evolution of continuous traits.

Since Pearson and Lee's study (1903), height correlation between mates has been described in many other human populations (for a review, see Spuhler 1982). All these situations are said to correspond to assortative mating patterns, which are a property of the population, but this does not necessarily imply that individuals choose their mates according to their own height. For example, competition for mates could itself generate assortative mating patterns even if preferences are invariant in the population. Suppose, for instance, that everyone prefer to mate with a rich mate, then rich people will mate together, and poor people will mate with poor mates as a last option. Similarly, correlation between mates stature may actually result from a shared preference for tallness associated with an advantage induced by tallness. Such an advantage is well documented for many mammals (Lindenfors et al. 2007). Assortative mating patterns may also be observed in the total absence of any preference for height if heights differ between subpopulations. Local divergences of stature may indeed induce a spurious correlation between mates observed at the population level if the population structure in overlooked (as in a Wahlund effect in population genetics).

For these reasons, it is necessary to study individual preferences to understand mate choice. In comparison with other traits such as waist to hip ratio or body mass index, which have been extensively surveyed (Weeden and Sabini 2005), there are, to our knowledge, only 13 studies evaluating individual preferences for height. Overall, there is a good consensus on a female preference for tall men and an agreement that this preference seems to be influenced by the female's height. Several but not all of these studies indeed showed that the height of a woman's preferred mate is positively correlated her own height. In addition, the preferred difference in stature is higher for short women than for tall ones (see Table 1 for a summary of female studies). In men, mating preferences for height are less clear. Men seem to prefer women shorter than themselves, but authors make different conclusions that short, medium, or taller than average women are preferred overall. Several studies also report no preferences for mate height in men. Nonetheless, a man's height preferences seem to be influenced by his own height: the taller a man is, the taller the woman he prefers. Lastly, the preferred difference in stature is smaller for short men than for tall ones (see Table 2 for a summary of male studies).

Three main rules have been proposed in the literature to describe the influence of the focal individual's height on his/her preferences: (1) women prefer men taller than themselves, or reciprocally, men prefer women shorter than themselves (hereafter referred to as the male-taller norm, Gillis and Avis 1980), (2) both women and men prefer mates who resemble themselves (hereafter referred to as the matching hypothesis, see e.g., Kurzban and Weeden 2005), and (3) each person prefers a partner whose stature is close to the average population values and whose height difference is close to the average population dimorphism (hereafter referred to as the Pawlowski rule, Pawlowski 2003).

Here, we propose that the height preference of a focal individual, given his/her own height, could be described by a simple homogamy preference function, for each sex. The preferences of individuals can then be quantitatively described by the parameters defining this function. We present an empirical measurement of these parameters and suggest that this quantitative approach reveals important, but neglected, aspects of height preferences that may have important evolutionary consequences.

Methods

We used experimental mate choice to measure height preferences. Focal individuals (hereafter called judges) were presented two stimuli with different heights and asked to choose the one they preferred. This procedure was repeated several times for each judge.

THE STIMULI

We used an approach proposed by Courtiol et al. (2010) to design stimuli with controlled height and body masses based on pictures of real individuals. More precisely, silhouettes were extracted from pictures of 50 females and 33 males, and the contours of these silhouettes were approximated using elliptic Fourier descriptors (Kuhl and Giardina 1982). The coefficients of these descriptors were then related to the morphological characteristics of the pictured individuals for each sex using a multivariate linear model. This allowed us to use this model to predict the average Fourier coefficients for a given set of individual characteristics and to create the corresponding silhouettes using inverse Fourier transforms.

Table 1. Studies on female preferences for male height. N.A., unavailable information.

Population	Method	No. of judges	Favorite height (cm) or relationship between height of the stimulus and preference	Favorite height expressed relative to judge's stature (cm) or relationship between judge's height and it's favorite height	Source
US (16–24 years)	Stated preferences	39	179.7 (±5.9)	+18.1 (±6.0)	Beigel (1954, tables 4 and 5)
US (singles)	Requests in newspaper ads	<155[a]	"Tall" or >182.8	>+10.2	Cameron et al. (1977)
US (18–22 years)	Attractiveness ratings (based on nine pictures associated with false information on height)	100	Medium(175.3–180.3)> Tall(188.0–193.0)> Short(165.1–170.2)	Independent	Graziano et al. (1978, experiment 1)
Canada (students)	Stated preferences	≈64[b]	N.A.	+15.0	Gillis and Avis (1980)
US (singles)	Responses to 173 newspaper ads	N.A.	Positive linear; not quadratic	N.A.	Lynn and Shurgot (1984)
US (students)	Attractiveness ratings (based on three manipulated pictures)	60	Taller than women	N.A.	Shepperd and Strathman (1989)
US (students)	Stated preferences	60[c]	N.A.	Taller	Shepperd and Strathman (1989)
US (students)	Person Perception Questionnaire	237[d]	Tall(193.0)≥Medium (177.8)≥short(162.6)	Independent	Jackson and Ervin (1992)
US (students)	Stated preferences	145	182.8	Positive	Hensley (1994)
Poland (singles)	Responses to 551 newspaper ads	≈2937	Positive	N.A.	Pawlowski and Koziel (2002)
Poland (students)	Single attractiveness choice (based on six drawings of couples whose dimorphism vary)	363	N.A.	Negative for dimorphism	Pawlowski (2003)
US (singles)	Speed dating	>4500	Positive linear; not quadratic	Positive	Kurzban and Weeden (2005)
Germany, Austria, UK	Single attractiveness choice (based on six drawings of couples whose dimorphism vary)	646	N.A.	Negative for dimorphism	Fink et al. (2007)
US (singles)	Requests in online ads	1000	"Tall"	Positive for height; Negative for dimorphism	Salska et al. (2008, study 1)
US (students)	Attractiveness ratings (based on written descriptions with 10 different stated heights)	249	181.1	Positive for height; Negative for dimorphism	Salska et al. (2008, study 2)

[a]Among them several ads did not contain an height request.
[b]Deduced from a total of 128 individuals (males+females).
[c]Same subjects as previous line.
[d]Sexes pooled (150 females+87 males), but no gender effect.

Table 2. Studies on male preferences for female height. N.A., unavailable information.

Population	Method	No. of judges	Favorite height (cm) or relationship between height of the stimulus and preference	Favorite height expressed relative to judge's stature (cm) or relationship between judge's height and it's favorite height	Source
US (16–24 years)	Stated preferences	79	162.8 (±5.6)	−11.9 (±6.2)	Beigel (1954, tables 4 and 5)
US (singles)	Requests in newspaper ads	<192[a]	"Small" or "medium"	Independent	Cameron et al. (1977)
Canada (students)	Stated preferences	≈64[b]	N.A.	−11.3	Gillis and Avis (1980)
US (singles)	Responses to 138 newspaper ads	N.A.	Independent	N.A.	Lynn and Shurgot (1984)
US (students)	Attractiveness ratings (based on three manipulated pictures)	49	Independent	N.A.	Shepperd and Strathman (1989)
US (students)	Stated preferences	49[c]	N.A.	Shorter	Shepperd and Strathman (1989)
US (students)	Person Perception Questionnaire	237[d]	Tall(177.8)=medium (162.6)>small(147.3)	Independent	Jackson and Ervin (1992)
US (students)	Stated preferences	164	N.A.	Positive	Hensley (1994)
Poland (singles)	Responses to 617 ads	≈4603	Negative	N.A.	Pawlowski and Koziel (2002)
Poland (students)	Single attractiveness choice (based on six drawings of couples whose dimorphism varies)	161	N.A.	Positive for dimorphism	Pawlowski (2003)
US (singles)	Speed dating	5143	Independent	Positive	Kurzban and Weeden (2005)
Germany, Austria, UK	Single attractiveness choice (based on six drawings of couples whose dimorphism varies)	456	N.A.	Positive for dimorphism	Fink et al. (2007)
US (singles)	Requests in online ads	1000	N.A.	Positive for height; Positive for dimorphism	Salska et al. (2008, study 1)
US (students)	Attractiveness ratings (based on written descriptions with 10 different stated heights)	133	166.9	Positive for height; Positive for dimorphism	Salska et al. (2008, study 2)

[a]Among them several ads did not contain an height request.
[b]Deduced from a total of 128 individuals (males+females).
[c]Same subjects as previous line.
[d]Sexes pooled (150 females+87 males), no gender effect.

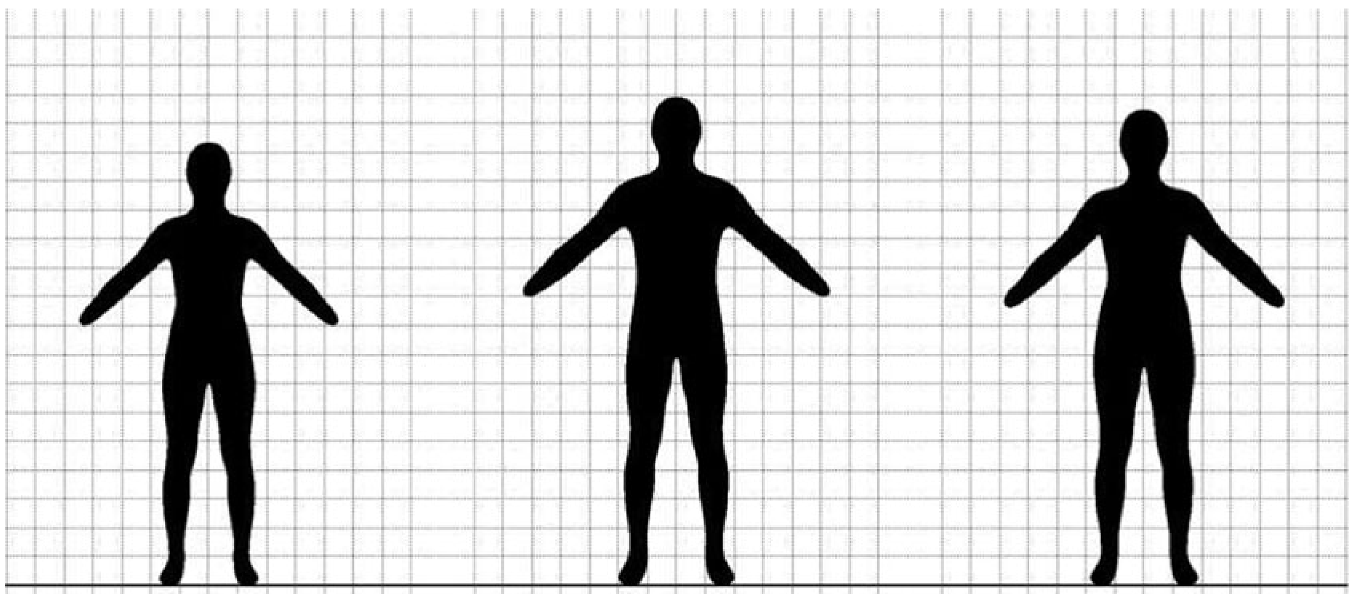

Figure 1. Example of one pairwise comparison shown to a male judge. The judge (shown in the center) has to decide which is the most attractive stimulus among the two female stimuli on each side.

We traced 16 symmetric silhouettes with different heights but constant body mass index (BMI) for both females and males. The waist-to-hip ratio (WHR) was not explicitly constrained because WHR measured on pictures is highly correlated to BMI (data not shown). Examples of such stimuli are shown in Figure 1. Apparent stimulus height ranged from 157 cm to 177 cm in 1.33 cm increments for females, and from 160 cm to 190 cm in 2 cm increments for males; these ranges correspond to 95% of the height range of the subjects in the original pictures upon which the stimuli are based. The stimulus BMI was fixed as the average of the pictured individuals (22.2 kg m^{-2} for females and 25.3 kg m^{-2} for males).

JUDGES

Judges were recruited in several public places during the winter and spring of 2008 in Montpellier, France. They were asked for their height, age, household income, and whether they were in a relationship or not. To eliminate some possible sources of variation in preferences between subjects, postmenopausal females, and individuals who were not heterosexual, were not considered in our analyses. Similarly, to reduce culturally based variation in preferences, we did not consider people with any non-European grandparent. In addition, 13 individuals were excluded because they did not report information concerning variables of interest, leading to a final set of 187 judges (95 females and 92 males).

EXPERIMENTAL MATE CHOICE

Software written in C++ using the Qt toolkit for graphical design was developed to present the stimuli to judges on a laptop. A judge had to indicate which of two stimuli of the opposite gender, which differed only in height, he/she found the most attractive. The two stimuli were always displayed surrounding a reference stimulus that matched the judge's sex and height (Fig. 1).

As most judges were only willing to engage in a relatively short experiment, we performed a sampling strategy to select which pairs of stimuli to show to each judge using the merge sort algorithm (Knuth 1998). This algorithm presents pairs of stimuli until a judges choices allow it to completely sort the 16 stimuli. It therefore allows the program to extract the same amount of information on preferences for each judge. The algorithm lowers the number of presented pairs by assuming that the choice is transitive, which allows it to deduce which stimuli a judge would have chosen for some of the comparisons based on the judges previous choices. In our experiment, a complete sort using this algorithm required on average 45.6 ± 1.8 comparisons per female and 44.0 ± 3.0 per male, where the total number of possible pairwise comparisons using 16 stimuli is 120.

STATISTICAL ANALYSIS

Each judges choices can be expressed as a variable that indicates whether the taller stimulus was chosen (outcome = 1) or not (outcome = 0). The aim was to create a statistical model that predicts the respective probabilities of these two outcomes as a function of the stimulus heights. We will consider that judges' choices involve two steps: first, judges give each of the two stimuli a unique preference score based on their respective heights, and second, they choose a stimulus based on these scores. Thus, analyzing judges' choices requires that we define two functions:

one that relates preference score to stimulus height, and another that relates the probability of choosing one of the two stimuli to preference scores. Describing the outcome of pairwise comparison by a preference and a choice function has been introduced by Kirkpatrick et al. (2006). Note that judges only express choice outcomes, not their preference scores that may be considered as internal representations.

The preference function

The preference function provides a preference score for each stimulus. The preference score of a judge n has been expressed directly as a function s_n of the stimulus height x, as this is the only trait that differs between stimuli. We considered here a quadratic preference function

$$s_n(x) = \alpha x^2 + \beta_n x + k_n. \tag{1}$$

We assumed that the quadratic coefficient α is not influenced by individual characteristics and is thus a common coefficient for all judges of a particular sex. This guarantees that a judge's preferred height is a linear function of his/her own height (see below). To study how a judge's preference depends on his/her own characteristics, we defined the linear term β_n as a function of the judge's height h_n. To limit potential bias caused by other characteristics of the judge that can influence preferences, β_n is also a function of the judge's age (a_n), household income (i_n), relationship status (m_n), and all interactions between these three variables and h_n. Of course, some characteristics that we have not measured may also influence our judges' preferences. We account for this by adding a random effect z_n to each β_n

$$\beta_n = \mathrm{b}_0 + \mathrm{b}_1^h h_n + \mathrm{b}_1^a a_n + \mathrm{b}_1^i i_n + \mathrm{b}_1^m m_n + \mathrm{b}_2^a a_n h_n + \mathrm{b}_2^i i_n h_n + \mathrm{b}_2^m m_n h_n + z_n, \tag{2}$$

where the b_0 term corresponds to the common slope of the linear term of the preference function, the b_1 terms correspond to the main effects of the judges covariates, the b_2 terms correspond to interactions between the judge's height and the judge's other covariates, and z_n is the realized value of a random effect drawn from a Gaussian distribution with a mean of zero and the between-judge variance σ_b^2. All parameters (b_0, b_1, and b_2) are the same for all individuals of the same sex, but β_n will differ because judges have different values for their covariates and z_n.

The choice function

We model the probability $p_{njj'}$ that a judge n chooses a stimulus j against a stimulus j' as a function g of that judges preference scores

$$p_{njj'} = g(s_n(x_j), s_n(x_{j'})). \tag{3}$$

This function must return values between 0 and 1, and $s_n(x_j) > s_n(x_{j'})$ must imply that $g(s_n(x_j), s_n(x_{j'})) > 1/2$. This condition corresponds to the case of a strict preference as defined by Kirkpatrick et al. (2006). This condition guarantees that a choice is transitive. The relative choice function, frequently used in the literature, satisfies these assumptions (Kirkpatrick et al. 2006). In our situation, this function would be defined as the ratio between the score of the taller stimulus and the sum of the scores of the two stimuli compared. For statistical convenience, we modified this function by expressing the scores in their exponential forms

$$g(s_n(x_j), s_n(x_{j'})) = \frac{e^{s_n(x_j)}}{e^{s_n(x_j)} + e^{s_n(x_{j'})}} \tag{4}$$

$$= \frac{1}{1 + e^{s_n(x_{j'}) - s_n(x_j)}}. \tag{5}$$

The choice function then becomes a univariate function f of the difference in preference scores

$$p_{njj'} = f(s_n(x_j) - s_n(x_{j'})). \tag{6}$$

The function f is widely used in statistics and is known as the logistic function (see Fig. 2). Many other functions satisfy the criterion mentioned above, including the cumulative density function (cdf) of the t-distribution. This function (hereafter called the inverse Gosset function) has an additional parameter ν that corresponds to the degree of freedom of the t-distribution, which makes it more flexible than the logistic function. For example, when $\nu = 1$, f corresponds to the cdf of the standard Cauchy distribution; when $\nu = \infty$, f corresponds to the cdf of the Gaussian distribution. Figure 2 illustrates how ν impacts the shape of this function.

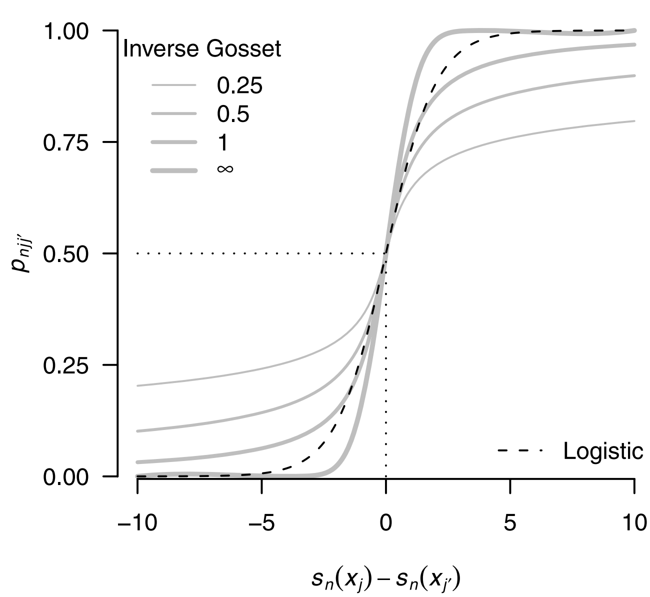

Figure 2. **Choice functions. Each function describes the probability of choosing stimulus *j* over *j*′ as the function of the difference in preference scores between these two stimuli.**

Model fit

Equations (1) and (6) were combined to express the probability that a judge n chooses stimulus j against stimulus j' as a function of the stimulus heights

$$p_{njj'} = f\left(\alpha\left(x_j^2 - x_{j'}^2\right) + \beta_n(x_j - x_{j'})\right). \quad (7)$$

In statistical terms, this equation describes a general linear model (GLM) for a binary response. If equation (7) is taken as describing a GLM, the function f corresponds to the inverse of the link function (McCullagh and Nelder 1989). When f is the logistic function, the resulting link function is the logit, and when f is the cdf of the t-distribution, the corresponding link function is called the Gosset link (Koenker and Yoon 2009). In particular, when $\nu = 1$, this is equivalent to the cauchit link, and when $\nu = \infty$, it is the probit link. The utility of expressing mate choice as a GLM is that the parameters α and β_n can be easily estimated by fitting the previous model using general tools already available in several statistical software. Here, all statistical analyses were performed using R 2.8. To implement the Gosset link, we followed the method presented by Koenker (2006); the logit, cauchit, and probit link functions are all available in R-base. Also, note that because female judges and male judges evaluated different stimuli, the two sexes have been analyzed by different GLMs.

As the term β_n involves both fixed effects and a random term, the previous GLM corresponds more precisely to a generalized linear mixed effect model (GLMM), which we fit using the function *glmmPQL()* of the *MASS* package for R (Venables and Ripley 2002). This function relies on a penalized quasi-likelihood parameter estimation, which is known to present several drawbacks in comparison with other methods (Bolker et al. 2009). Still, this tool enables to consider that each choice made by a judge depends on the choices that this judge has previously made. This relaxes the important assumption of strict preferences. Indeed, an autoregressive model revealed significant autocorrelation in our data. We used a fourth-order ARMA model to control for most of the autocorrelation using the function *corARMA(p=4)* of the *nlme* package (Pinheiro et al. 2008). This step required us to consider an additional variable that indicates the position t of the comparison involving the stimuli j and j' in the sorting sequence, to define β_n (which therefore should be called β_{nt}, but this detail is omitted for simplicity).

As we have no a priori idea about the actual choice function, we ran our analysis using the logistic function and the inverse Gosset function with a range of values for ν. Unfortunately, the *glmmPQL()* procedure used to fit the GLMM uses a penalized quasi-likelihood based method. This makes it impossible to select the best-fit choice function using the maximum likelihood criterion. Instead, we chose a function that minimizes the variance within judges σ_w^2. This leads us to choose an inverse Gosset choice function with ν values smaller than unity. As small ν values correspond to flat functions (see Fig. 2), problems with convergence can occur during the GLMM fit. Hence, results obtained using other parameter values are also presented. To some extent, this also enables us to analyze the robustness of the preference function estimates when different choice functions are considered.

Estimation of the parameters of the homogamy preference function

Once estimates of the model parameters are obtained, the preferred height of each judge n can be predicted as $-\frac{\hat{\beta}_n}{2\hat{\alpha}}$, with $\hat{\alpha}$ and $\hat{\beta}_n$ the best estimates are obtained for α and β_n, respectively. As $\hat{\beta}_n$ has been defined as a linear function of a judge's height, it follows that a judges preferred height is also a linear function of h_n. Expressed in terms relative to the average judge's height (hereafter, called $\bar{h}$), estimation of the preferred height becomes

$$-\frac{\hat{\beta}_n}{2\hat{\alpha}} = \hat{\psi}_n(h_n - \bar{h}) + \hat{\omega}_n, \quad (8)$$

where $\hat{\psi}_n$ and $\hat{\omega}_n$ are, respectively, the estimated slope and intercept of the homogamy preference function for judge n. The value of $\hat{\psi}_n$ indicates how much preferred height increases when the height of the judge increases by 1 cm. The value of $\hat{\omega}_n$ has been scaled to represent the preference of a judge whose height is $\bar{h}$. $\hat{\psi}_n$ and $\hat{\omega}_n$ can be computed as

$$\hat{\psi}_n = \frac{\hat{b}_1^h + \hat{b}_2^a\, a_n + \hat{b}_2^i\, i_n + \hat{b}_2^m\, m_n}{2\hat{\alpha}} \quad (9)$$

$$\hat{\omega}_n = \hat{\psi}_n\bar{h} + \frac{\hat{b}_0 + \hat{b}_1^a\, a_n + \hat{b}_1^i\, i_n + \hat{b}_1^m\, m_n}{2\hat{\alpha}}. \quad (10)$$

The estimates $\hat{\psi}_n$ and $\hat{\omega}_n$ correspond to the set of b_0, b_1, and b_2 that best fit our data. Of course, parameter values that are close to the best set of parameters will yield a comparable fit. However, if very different values were equally good, our estimates $\hat{\psi}_n$ and $\hat{\omega}_n$ would not be very precise.

We estimated the precision of our estimates by computing confidence intervals for $\hat{\psi}$ and $\hat{\omega}$, which were deduced from the intervals that the GLMM procedure provides for $\hat{b}_0$, $\hat{b}_1$, and $\hat{b}_2$. To do this, 200,000 sets of b'_0, b'_1, and b'_2 were obtained by adding to $\hat{b}_0$, $\hat{b}_1$, and $\hat{b}_2$ a random value drawn from a multivariate t-distribution using the covariance matrix of parameter estimates provided by *glmmPQL*. These randomly drawn parameter values were then combined with the average characteristics of judges to produce the random values $\hat{\psi}'$ and $\hat{\omega}'$. The value of z_n was fixed at zero (by setting the *level* argument to zero when using the *predict.lme()* function) so that our confidence interval would incorporate all variance due to random effects. The covariate indicating the position of the pairwise comparison was set to 1 so that we predict each judges choice independently of that judges previous choices.

We then determined joint confidence intervals for $\hat{\psi}$ and $\hat{\omega}$ from the 200,000 sets of $\hat{\psi}'$ and $\hat{\omega}'$. For that purpose, we used the function *kde2d()* from the package *MASS* (Venables and Ripley 2002). Technically, this function provides a two-dimensional kernel density estimation with an axis-aligned bivariate normal kernel evaluated on a square grid. We set the grid dimensions to 100×100.

Explanatory power of the model

To assess the quality of our predictions, we first compared the actual choices made by our judges to the probabilistic prediction associated with each pairwise comparison. Concordant matches are situations in which the chosen stimulus was the one that had the highest predicted probability. Other cases were labeled as discordant. The quality of fit can be measured as

$$\gamma = \frac{C - D}{C + D}, \qquad (11)$$

where C and D are the numbers of concordant and discordant matches. This is similar to Goodman and Kruskal's statistic (Sheskin 2007). A null γ means that there are as many concordant matches as discordant ones, that is, that model offers no explanatory power. When $\gamma = 1$, the model correctly predicts all actual choices, and its explanatory power is maximal. We computed γ for the model with all covariates and for different submodels with some covariates removed as well. This allows us to estimate the relative influence of each covariable in our model.

We also estimate the quality of our model predictions by comparing how judges rank the 16 stimuli to the rankings predicted by the model. This ranking was obtained using "virtual judges" whose preferences and choice functions correspond to those adjusted for each real judge. For each comparison proposed by the merge-sort algorithm, these judges made random choices according to the probability predicted by the model. This procedure was repeated 100 times for each virtual judge to obtain the predicted distribution of ranks for each stimulus height.

Results

JUDGES CHARACTERISTICS

Of the 95 females sampled, 30 were students, 69 were involved in a relationship, the median age was 26.0 years (mean ± SD: 27.4 ± 6.9, range: $18.1 - 53.2$), the median height was 165.0 cm (mean ± SD: 165.3 ± 6.0, range: $147 - 178$), and the median BMI was 20.9 kg m^{-2} (mean ± SD: 21.0 ± 2.3, range: $16.2 - 29.0$). Among the 92 males of the dataset, 19 were students, 68 were involved in a relationship, the median age was 30.8 years (mean ± SD: 33.0 ± 10.9, range: $16.8 - 63.7$), the median height was 178 cm (mean ± SD: 177.7 ± 7.3, range: $160 - 194$), and the median BMI was 23.1 kg m^{-2} (mean ± SD: 23.3 ± 2.7, range: $18.9 - 32.1$).

INFLUENCE OF STIMULUS HEIGHT ON EXPERIMENTAL MATE CHOICE

Stimulus heights influenced mate choice for both male and female judges (Pearson's chi-square test with simulated *P*-value based on 10,000 replicates, for masculine stimuli: $X^2 = 3467$, $P < 0.0001$; for feminine stimuli: $X^2 = 568$, $P < 0.0001$) (Fig. 3A,B). Most female judges ranked the tallest stimuli first and the lowest median of rank distributions for each stimulus height corresponds to a 190-cm-tall male. Male judges have more variable preferences, with six different stimuli equally voted the lowest median rank (namely, the 165, 166.33, 167.67, 169, 170.33, and the 173 cm stimuli). Among them, the 167.67 cm stimulus was ranked first according to the majority judgment method of classification (Balinski and Laraki 2007).

THE PREFERENCE FUNCTION

The preference score was modeled as a quadratic function of stimulus height. In both sexes, estimates of the quadratic coefficient significantly differ from zero, which means that the quadratic model fits the data better than a linear preference function (*t*-test on $\hat{\alpha}$: for females $t = -28.8$, $df = 4232$, $P < 0.0001$; for males $t = -18.5$, $df = 3950$, $P < 0.0001$).

We also considered judges' preferred height to be a linear function of their own stature. The homogamy preference function is then characterized by the slope of this function, which describes how preference for height increases when the judge's height increases by 1 cm, and also by its intercept, which is scaled to represent the preferred height of a judge of average height (see eqs. 9 and 10). The best-fit model has a slope of 0.77 (CI 95% = 0.51–1.03) and an intercept of 182.9 cm (CI 95% = 181.3–184.6) for females judging masculine stimuli, and a slope of 0.60 (CI 95% = 0.37–0.84) and an intercept of 167.7 cm (CI 95% = 166.1–169.4) for males judging feminine stimuli.

Homogamy preference functions are illustrated in Figure 4A. Situations for which both heights within a couple match the respective preferences of each partner are scarce. This only occurs when both partners are much taller than average (zone 3 in Fig. 4B).

THE CHOICE FUNCTION

Some of the possible choice functions (e.g., the logistic or the Gaussian cdf choice functions for females) could not be used here because they prevent convergence during the fit procedure. Among the other possible choice functions, the best-fit function, defined as the one that minimizes the within-judge error (see Methods), is the inverse Gosset function with a value of ν of 0.528 for females and of 0.257 for males.

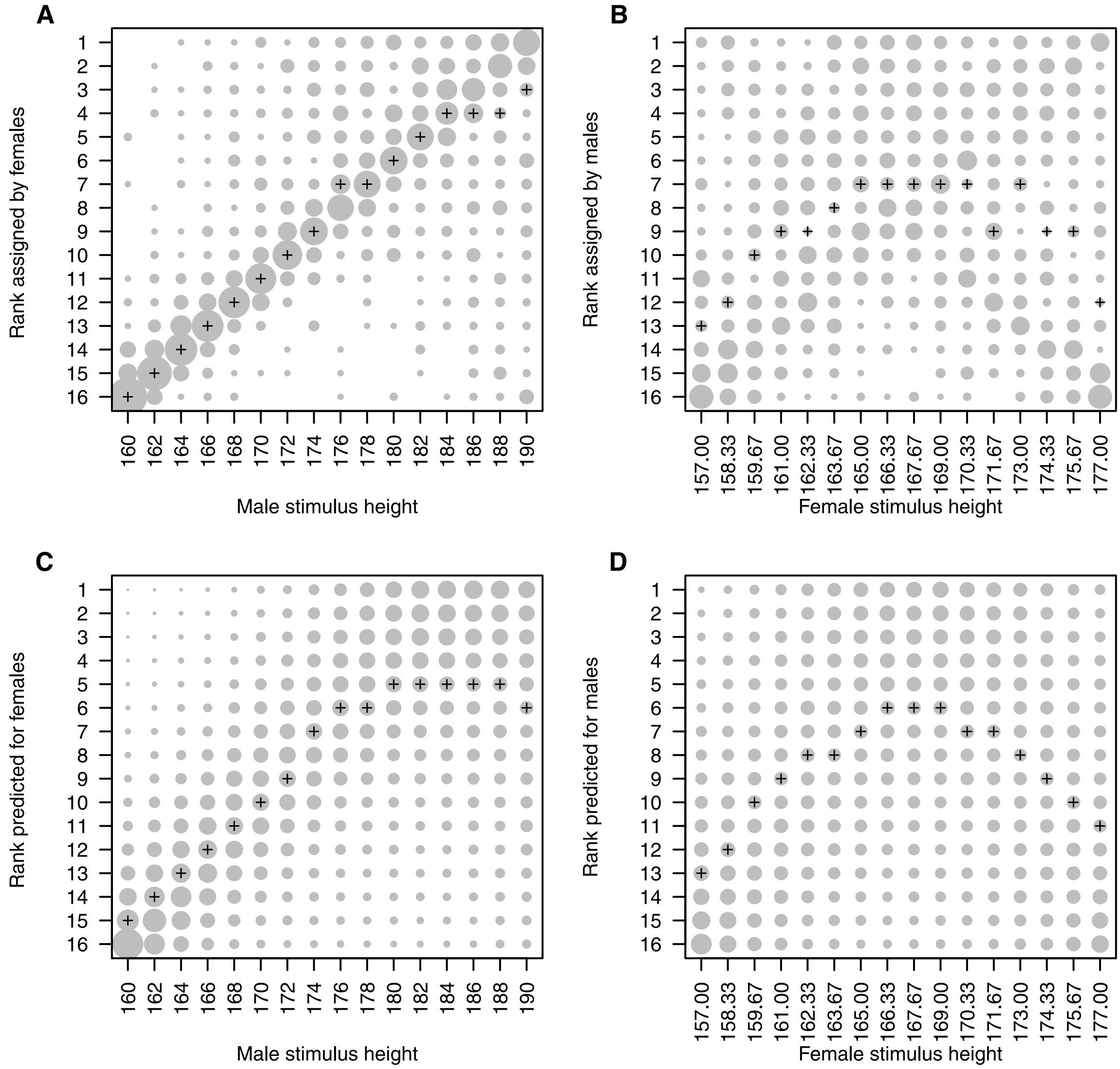

Figure 3. Distribution of ranks obtained at the end of the merge-sort procedure. For each combination of rank (*y*-axis) and stimulus height (*x*-axis), the circle area is proportional to frequency. The scale used to define circle areas is the same for the four graphics of the panel. Crosses represent the median of rank distributions for each stimulus height. Ranks have been measured using actual decisions made by the judges (A and B) or from stochastic decisions predicted by the mate choice modeling (C and D). See text for details.

Table 3 illustrates how the choice function influences estimates of the preference function parameters. For example, using an inverse Gosset choice function with a ν of 0.25 leads to the conclusion that female preference does not statistically differ from the average male height. Using the best-fit function instead (i.e., fixing ν to 0.528), female preference is significantly higher than the average male height. Overall, results are more robust with regard to variations in choice functions for males than for females.

PREDICTIONS OF EXPERIMENTAL MATE CHOICE OUTCOMES

The combination of adjusted preference and choice functions allows us to predict judges' choices during the experiment (see Methods). Figure 5 represents this prediction for a male or a female virtual individual with average characteristics (age, stature, income, and relationship status).

Using model parameter estimates, it is also possible to predict the probability of the outcome of each pairwise comparison performed by each judge. Concordant pairs, that is, pairs for which the stimulus with the highest probability has been chosen, represent 77.1% and 66.8% of all pairwise comparisons performed by female and male judges, respectively. The corresponding reduction in error compared to random choice (i.e., γ, see Methods) is 54.3% for females and 33.6% for males (Table 4). The good agreement between the model and the data can also be assessed by comparing the median predicted rank for each stimulus to its actual median rank: the Pearson correlation is $\rho = +0.96$ for

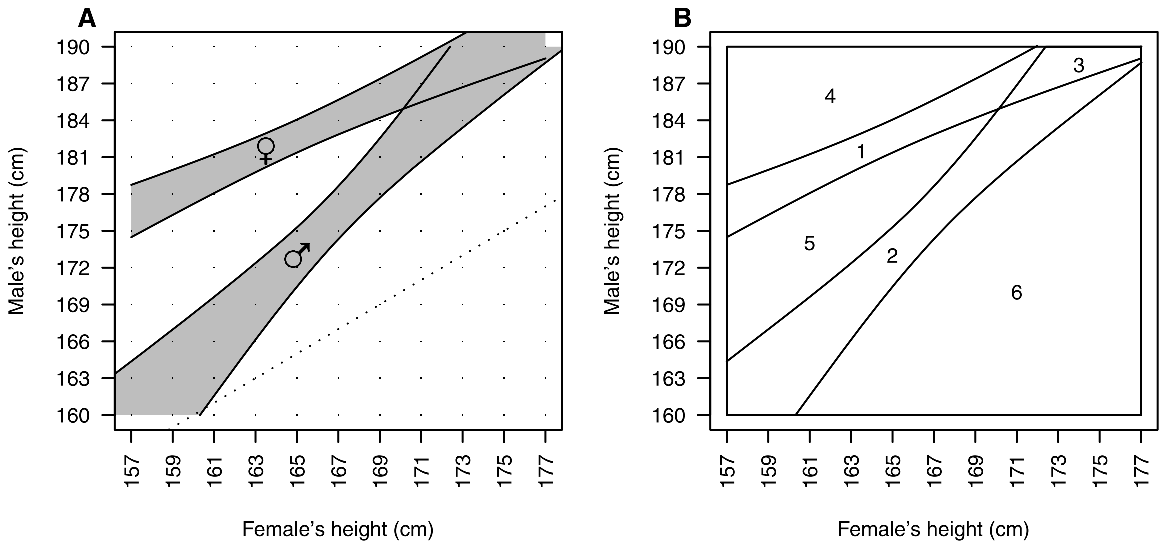

Figure 4. Estimation of the linear homogamy preference functions in both sexes. (A) Gray area labeled by the female symbol: male height preferred by females (*y*-axis) as a function of the female's height (*x*-axis). Gray area labeled by the male symbol: female height preferred by males (*x*-axis) as a function of the male's height (*y*-axis). Areas represent the 95% confidence intervals of best preference estimations. The dotted line represents the perpendicular bisector. (B) Same figure identifying how partners perceive each other within a couple compared to average preferences. Each point on the graph represents a couple, as characterized by the heights of the people involved. In zone 1, the female's preference is satisfied but she is perceived as too short by her male partner. In zone 2, the male's preference is satisfied but he is perceived as too short by his female partner. In zone 3, both preferences are satisfied. In zone 4, the male is perceived as too tall, whereas the female is perceived as too short. In zone 5, both partners find each other too short. In zone 6, the male is perceived as too short and the female as too tall.

Table 3. Influence of the choice function on parameter estimates of the homogamy preference function. For the inverse Gosset function, the shape parameter (ν) is indicated. σ_w corresponds to the estimated within-judge error standard deviation. N.A., no convergence of the model.

Sex	Choice function	Intercept (cm)	CI 95%		Slope	CI 95%		σ_w
Female	Inverse Gosset							
	ν=0.528[a]	182.94	181.31	184.59	0.77	0.51	1.03	0.729
	ν=0.25	179.54	177.56	181.66	0.50	0.21	0.81	0.866
	ν=0.50	180.94	179.15	182.91	0.64	0.40	0.89	0.832
	ν=0.75	183.43	181.70	185.16	0.85	0.57	1.13	0.736
	ν=1.0[b]	184.9	182.16	187.66	0.81	0.37	1.26	0.872
	ν=∞[c]	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
	Logistic	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
Male	Inverse Gosset							
	ν=0.257[a]	167.74	166.10	169.36	0.60	0.37	0.84	0.862
	ν=0.25	167.32	165.75	168.89	0.62	0.39	0.86	0.864
	ν=0.50	167.51	166.00	169.01	0.65	0.45	0.87	0.897
	ν=0.75	167.71	165.83	169.67	0.63	0.35	0.94	0.952
	ν=1.0[b]	167.72	165.77	169.61	0.66	0.37	0.96	0.955
	ν=∞[c]	167.55	165.57	169.50	0.73	0.44	1.04	1.078
	Logistic	167.59	165.57	169.56	0.73	0.43	1.04	0.969

[a]Values minimizing σ_w.
[b]Equivalent to a cauchit link.
[c]Equivalent to a probit link.

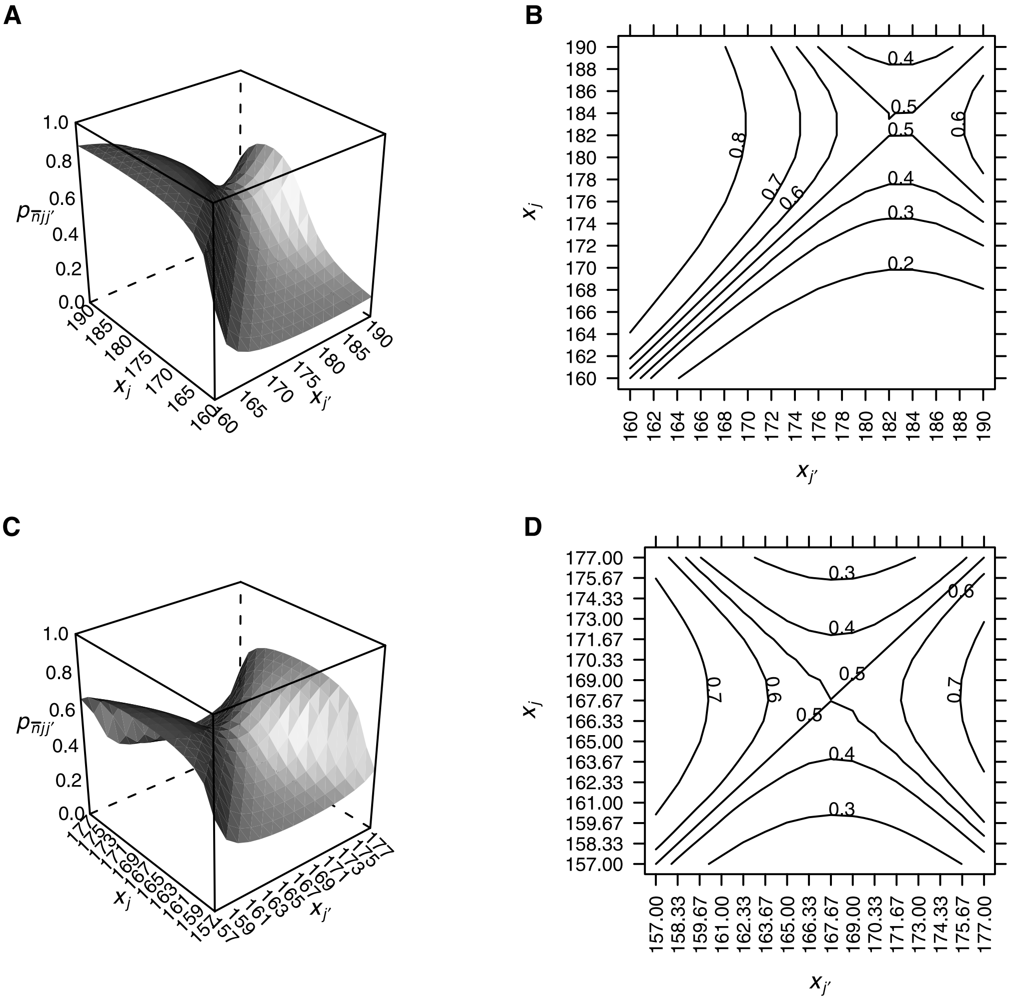

Figure 5. Model estimates of the probability ($p_{\bar{n}jj'}$) that a stimulus of height x_j will be chosen when compared to a stimulus of height $x_{j'}$. This choice probability is predicted for a female (A, B) and male (C, D) judges with average characteristics. For clarity, two different visual representations of the same data are given in each row: the three-dimensional plot and the corresponding contour plot.

females and $\rho = +0.93$ for males, with $P < 0.0001$ in both cases (compare Figs. 3C and D with Figs. A and B).

Overall, the predictive power of the model is increased by less than 5% for females and less than 15% for males when the judges individual characteristics are taken into account. The influence of the different judges characteristics are given in Table 4. Note that the percentage of concordant pairs should increase as long as new variables are included in the models, but convergence approximations introduce some noise, precluding this observation. In both females and males, height is the characteristic that contributes the most to the explanatory power of the model. Interactions between height and other characteristics do not seem to substantially increase the quality of the prediction.

Discussion

EVALUATION OF THE METHOD

Previous experimental studies of mating preferences for height (summarized in Tables 1 and 2) consisted of asking individuals to report their preferred height (stated preferences), to indicate the attractiveness of a given stimulus (attractiveness rating), or to choose their favorite stimulus among several (single attractiveness choice). Here, we studied mating preferences based on pairwise comparisons of stimuli, as is usually done to study mating preferences in nonhuman animals (e.g., Ryan et al. 2003). This methodology is probably closer to real mate choice situations than protocols using stated preferences or quotations. Still, we admit that, in real life, actual partners encounter processes probably greatly differ from simple choices between pairwise alternatives.

To analyze our data, we considered that the mate choice process obeys what Kirkpatrick et al. (2006) called "strict preferences," and that it can thus be decomposed into two distinct steps: (1) judges attach a preference score to each stimulus that depends only on its characteristics, (2) judges choose one of the two competing stimuli based on their respective preference scores. The first step involves a preference function that relates the stimulus' characteristics to its score. The second step involves a choice

Table 4. **Influence of judges' characteristics on model predictions. The different judge's covariates are: judge's age (a_n), household income (i_n), relationship status (m_n), judge's height (h_n), and all interactions between the three first variables and h_n. The "base model" includes all parameters independent of judge's characteristics. The dots (...) indicate that the model is an extension of the model given in the row above. C provides the percentage of pairwise comparisons in which the stimulus with the highest predicted probability of being chosen is actually chosen. γ corresponds to a measure of the explanatory power of the model (with γ=0 for a null power, and γ=1 for a maximal power). To enhance convergence, the Cauchy choice function has been used on all models, except for models labeled with the ♠ symbol, which correspond to models fitted with the inverse Gosset choice function parameterized with their optimal ν values. σ_w corresponds to the estimated within-judge error standard deviation, and σ_b corresponds to the estimated between-judge standard deviation of the random term (see Methods for details).**

Sex	Model	$C(\%)$	γ	σ_w	σ_b
Females	Base model	76.2	0.524	0.873	0.342
	$\ldots+a_n$	76.4	0.528	0.869	0.353
	$\ldots+i_n$	76.4	0.528	0.872	0.340
	$\ldots+m_n$	76.4	0.528	0.900	0.318
	$\ldots+h_n$	77.9	0.557	0.866	0.311
	$\ldots+a_nh_n$	78.0	0.560	0.864	0.312
	$\ldots+i_nh_n$	78.1	0.561	0.866	0.303
	$\ldots+m_nh_n$	77.6	0.552	0.872	0.291
	...♠	77.2	0.543	0.729	0.154
Males	Base model	60.5	0.211	0.958	0.215
	$\ldots+a_n$	60.6	0.213	0.958	0.216
	$\ldots+i_n$	61.9	0.238	0.957	0.213
	$\ldots+m_n$	62.3	0.247	0.957	0.213
	$\ldots+h_n$	67.5	0.350	0.954	0.183
	$\ldots+a_nh_n$	67.4	0.348	0.954	0.181
	$\ldots+i_nh_n$	67.3	0.346	0.954	0.180
	$\ldots+m_nh_n$	67.2	0.344	0.955	0.178
	...♠	66.8	0.336	0.862	0.351

function that guarantees that the most preferred stimulus has a higher probability of being chosen than the least preferred.

Using this framework, we developed a statistical approach that enables to directly obtain parameter estimates of preference functions from binary data. It provides a precise quantification of preference as a continuous function of the ornament dimension. Although we applied this methodology in the context of human mating preferences, the same method could be applied in very different contexts. Concerning mate choice, obtaining empirical estimates of preference functions is of particular interest because such functions are at the core of the main theoretical models of evolution of mating preferences (e.g., Lande 1981; Price et al. 1993; Iwasa and Pomiankowski 1999).

In the present context, this methodology allowed us to quantify how preferences vary according to stimulus height for a given individual, which gives information that cannot be obtained from single attractiveness choices. In addition, our statistical approach allowed us to relax two major assumptions. First, we considered that preferences can differ between judges because of their morphological or sociological differences (but note that any other covariate could have been used in the model). Second, we considered that a given comparison can be influenced by comparisons performed by the judge earlier in the experiment.

Of course, this method still suffers from some limitations. First, we have assumed that the preference function is quadratic with the same curvature for all judges within one sex. We have also assumed that the judges characteristics have a linear effect on their preferred height. In addition, although we considered different mate choice functions, they are all derived from two choice functions, namely the logistic and the inverse Gosset functions. Finally, we assumed that the judges' choices are transitive. This assumption is central for "strict preference" to hold (Kirkpatrick et al. 2006). It is also central in the merge-sort algorithm used in this experiment to reduce the number of experimental choices that judges had to perform. Despite all these assumptions, our model fits the data much better than a null model with random choice.

PREFERENCES FOR HEIGHT

The quadratic shape of preference functions

Based on studies on height and reproductive success, Mueller and Mazur (2001) proposed that female preference for male height should be positively directional and unconstrained, meaning that a woman's preference scores should always increase with a male judge's height. Conversely, Nettle (2002a,b) argued that in both sexes, mating preference functions could be better described by an inverted U-shape. Here, we found that for both sexes, an inverted U-shape fits our data significantly better than a simple linear relationship. This firmly demonstrates the presence of a ceiling effect on preferences for both sexes, and it does not support an unconstrained directional preference for male height.

For both sexes, our "base model," which does not take into account the judge-specific effects, fits our data much better than a null model in which mate choice is random. The quality of the fit can be further increased by taking into account the variability introduced by morphological and sociological differences among judges. This latter gain in fit quality, although moderate compared to the initial improvement, is highly significant.

Our statistical analysis also allows us to estimate the preferred height for both women and men while taking into account the variability introduced by individual differences. These estimates correspond to statures of 183 cm and 168 cm for males and females, respectively. Hence, both sexes appear to prefer heights that are significantly above the sample means, although not extremely so. More precisely, females are predicted to prefer males 3.5–6.9 cm taller than average male height, and males are predicted to prefer females 0.8–4.0 cm taller than average female height (based on 95% confidence intervals estimation, see Methods).

Our conclusion that females prefer men who are taller than average but are not extremely tall has already been proposed several times. It is sometimes referred to as the "central tendency" (Ellis 1995). However, the same conclusion has not been proposed for men in previous studies, although it is possible to deduce male preferences from some of these studies. For example, based on data presented by Beigel (1954), we found that the preferred height for men is slightly above the average height. The same conclusion is reached when looking at the second part of the study of Salska et al. (2008).

Homogamy at the level of preferences

We also assessed how a judge's height influences his/her most preferred height. This influence can be described as a homogamy preference function, which was assumed here to be linear. For both sexes, the preferred height significantly increases with the judges' height: the taller the judge, the taller his/her preferred mate. Hence, the homogamy that is often reported as a mating pattern observed at the population level can also be detected in individual preferences.

Homogamy at the individual and population levels are related but not identical. First, the actual outcome of this choice is potentially influenced by preferences expressed in both sexes that seem to disagree in our case (see below). Second, processes other than mate preferences can also influence the actual mate choice and thus lower the influence of preferences on the outcome of mate choice, such as competition for mates, availability of potential partners, or the encounter process of mates (see e.g., Gimelfarb 1988a,b). Additionally, the actual mate choice does not indeed rely on preferences for height only, but rather on numerous traits (see e.g., Buss 1989). Therefore, it is not surprising that the slope estimates of the homogamy preference function obtained here are much larger than the slopes of the regression between mates' heights in actual couples (Spuhler 1982; McManus and Mascie-Taylor 1984).

From an evolutionary perspective, the fact that preferences are function of judge's height can induce complex consequences. For instance, it might seem straightforward to interpret preference for intermediate heights as an indication of stabilizing selection (Mueller and Mazur 2001). This is indeed a possibility, but in the presence of homogamy preferred stature should vary together with height. Predictions are then hard to make, unless the details on how selection operates on both preferences and height are known.

Preference rules

Three rules have been proposed in the literature to describe how height influences preferences (see Introduction). These rules can be formulated as particular cases of the linear homogamy preference function. It is therefore possible to test each of them using our dataset and our modeling framework. First, the present model is consistent with the male taller norm rule because it indicates that females do prefer males taller than themselves, and males do prefer females shorter than themselves (see Fig. 4). Using 95% confidence intervals on the parameters of the homogamy preference function, we can define ranges of preferred height based on a given judge's height: 100% and 96% of predictions are concordant with the male taller norm for females and males, respectively. Second, both females and males do prefer partners whose height is correlated with their own height, which is consistent with the matching rule. For both sexes, this rule is satisfied for 100% of the predictions because the slopes of the homogamy functions are positive and the confidence intervals exclude zero. The hypothesis of a strict homogamy where the slope would be one is rejected for males, but not for females, even if only 1.6% of the slope estimations are greater or equal to one in this later case. Finally, we found that preferred dimorphism is influenced by judges heights, consistent with the Pawlowski rule: when the judge's height increases, preferred dimorphism decreases in females and increases in males. Here, 98.4% and 100% of the predictions agree with this rule for females and males, respectively.

The predictions obtained are therefore simultaneously consistent with all three preference rules, which means that these rules are not mutually exclusive and may therefore not actually correspond to distinct psychological mechanisms. They could rather reflect different aspects of a single homogamy preference function that have been approximated here by a linear relationship between preferred height and judge's height.

SEX DIFFERENCES

Sex differences in the choice function

A pivotal aspect in our modeling approach is that it requires a choice function to be defined before fitting the preference function to the data. Among the two functions that have been tried, the best one is the inverse Gosset. This function has a parameter that was adjusted independently for females and males. The parameter estimate is lower for males than for females. This means that for the same difference in preference scores, our models predict that females will display a more pronounced choice than males (see Figs. 2 and 5).

This difference could reflect a true biological difference in choosiness between sexes. For instance, if mate choice relies less on height for male judges than for female ones, decisions are expected to be more prone to stochastic errors in males than in females. Accordingly, measurement of intraindividual variance shows that choices of a given individual tend to be more variable in males than in females. A possible evolutionary interpretation would be that male's height can be more strongly associated with direct and/or indirect benefits. Allocation trade-offs between height and other preferred characteristics could also differ between sexes. Furthermore, it is possible that selection acts only on females but that genetic correlation between females and males leads males to express preferences for height too. If this correlation is imperfect, this could also explain sex differences in choosiness. These sex differences could explain why the literature focusing on male mating preferences seems to be inconsistent, while most studies on female preferences yield comparable conclusions (compare Tables 1 and 2). Of course, this difference between males and females might also be due to a statistical artifact. For example, this could happen if our statistical model is correct for females but poorly describes the preference function in males.

A sexual disagreement in preferences

Because males are taller than females and females prefer men taller than average, the dimorphism preferred by females is above average. Conversely, males prefer females who are shorter than themselves but taller than average. Therefore, they prefer females that are less dimorphic than average. This sexual difference on preferred dimorphism is large: the ratio between the preferred and average difference in stature ranges from 1.28 to 1.54 in females, and from 0.61 to 0.91 in males. Therefore, this yields a potentially important disagreement between sexes over preferred dimorphism.

Few previous publications based on stated preferences for ideal mates present sufficient information to quantify this disagreement. In Beigel's study (1954), women prefer men 18.1 cm taller than themselves on average, while men prefer women only 11.9 cm shorter than themselves. In Gillis and Avis's study (1980), females were found to be looking for men 15 cm taller than themselves, whereas males were looking for women 11.3 cm shorter than themselves. In addition, using data presented in the experimental study of Pawlowski (2003), we also found that women prefer a dimorphism significantly greater than the one preferred by men.

Hence, despite the low number of studies, data currently available support the hypothesis of a disagreement between sexes in height preference. This disagreement implies that most of the time, the preferences of both partners cannot be satisfied at the same time (see Fig. 4). Therefore, selection exerted on height and dimorphism will depend on the relative contribution of each sex preference to the actual outcome of mate choice. Note also that dimorphism could be itself influenced by antagonistic selective pressures, such as that potentially exerted by mating preferences (Cox and Calsbeek 2009).

CONCLUSIONS

With a quantitative approach to assess preferences applied on human height, we demonstrated that: (1) Homogamy is present at the level of preferences for both sexes, and measurements of the function describing this homogamy are concordant with several mating rules proposed in the literature. (2) Both women and men prefer individuals who are significantly taller than average. (3) There is an important disagreement between sexes regarding height preferences. It is also worth noting that all previous works on preference for height, including the present one, were performed in western societies. To assess the generality of conclusions drawn here, there is thus a need to replicate similar experiments in other populations, which differ in height distribution, environmental and socio-cultural backgrounds. In addition, this should help to identify key factors influencing the evolution of preferences for height in humans.

ACKNOWLEDGMENTS

We thank A. Alvergne, M. Chassagne-Manoukian, C. Faurie, and S. Picq for helping us to collect the data; T. Lenormand and F. Rousset for discussions concerning the analysis; and M. KirkPatrick and G. Stulp for useful discussions. This work was funded by a Ministère de l'Éducation et de la Recherche (France) studentship awarded to A.C. Contribution ISEM no. 2010-018.

LITERATURE CITED

Andersson, M. 1994. Sexual selection. Monographs in Behavior and Ecology. Princeton Univ. Press, Princeton, NJ.

Balinski, M., and R. Laraki. 2007. A theory of measuring, electing, and ranking. Proc. Natl. Acad. Sci. USA 104:8720–8725.

Beigel, H. G. 1954. Body height in mate selection. J. Soc. Psych. 39:257–268.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24:127–135.

Buss, D. M. 1989. Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. Behav. Brain Sci. 12:1–49.

Cameron, C., S. Oskamp, and W. Sparks. 1977. Courtship American style: newspaper ads. Family Coord. 26:27–30.

Courtiol, A., J.-B. Ferdy, B. Godelle, M. Raymond, and J. Claude. 2010. Height and body mass Influence on human body outlines: a quantitative approach using an elliptic Fourier analysis. Am. J. Phys. Anthropol. *In press*.

Cox, R. M., and R. Calsbeek. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. Am. Nat. 173:176–187.

Darwin, C. 1879. The descent of man. Published in 1879 by John Murray, London, 2nd edition. Penguin Classics 2004, London.

Ellis, B. J. 1995. The evolution of sexual attraction: evaluative mechanisms in women. Pp. 279–281 *in* L. C. J. H. Barkow and J. Tooby, eds. The adapted mind. Oxford Univ. Press, New York, NY.

Fink, B., N. Neave, G. Brewer, and B. Pawlowski. 2007. Variable preferences for sexual dimorphism in stature (SDS): further evidence for an adjustment in relation to own height. Pers. Indiv. Differ. 43:2249–2257.

Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. T. R. Soc. Edinburgh 52:399–433.

Galton, F. 1889. Natural inheritance. London and New York MacMillan and Co.
Gillis, J. S., and W. E. Avis. 1980. The male-taller norm in mate selection. Pers. Soc. Psychol. B. 6:396–401.
Gimelfarb, A. 1988a. Processes of pair formation leading to assortative mating in biological populations: dynamic interaction model. Theor. Popul. Biol. 34:1–23.
———. 1988b. Processes of pair formation leading to assortative mating in biological populations: encounter-mating model. Am. Nat. 131:865–884.
Graziano, W., T. Brothen, and E. Berscheid. 1978. Height and attraction: do men and women see eye-to-eye? J. Pers. 46:128–145.
Hensley, W. E. 1994. Height as a basis for interpersonal attraction. Adolescence 29:469–474.
Iwasa, Y., and A. Pomiankowski. 1999. Good parent and good genes models of handicap evolution. J. Theor. Biol. 200:97–109.
Jackson, L., and K. Ervin. 1992. Height stereotypes of women and men: the liabilities of shortness for both sexes. J. Soc. Psych. 132:433–445.
Kirkpatrick, M., A. S. Rand, and M. J. Ryan. 2006. Mate choice rules in animals. Anim. Behav. 71:1215–1225.
Knuth, D. E. 1998. The art of computer programming, vol. 3: sorting and searching, chapter Sorting by merging, Pp. 158–168. 2nd edition. Addison-Wesley, Reading, MA.
Koenker, R. 2006. Parametric links for binary response. R News 6:32–34.
Koenker, R., and J. Yoon. 2009. Parametric links for binary choice models: A Fisherian-Bayesian colloquy. J. Econometrics 152:120–130.
Kuhl, F. P., and C. R. Giardina. 1982. Elliptic Fourier features of a closed outline. Comput. Graph. Image Process. 18:236–258.
Kurzban, R., and J. Weeden. 2005. HurryDate: Mate preferences in action. Evol. Hum. Behav. 26:227–244.
Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. USA 78:3721–3725.
Lindenfors, P., J. L. Gittleman, and K. E. Jones. 2007. Sexual size dimorphism in Mammals. Pp. 16–26 *in* D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely, eds. Sex, size, and gender roles. Oxford Univ. Press, Oxford.
Lynch, M., and B. Walsh. 1997. Genetics and analysis of quantitative traits. Sinauer Associates Inc., U.S.
Lynn, M., and B. A. Shurgot. 1984. Responses to lonely hearts advertisements: effects of reported physical attractiveness, physique, and coloration. Pers. Soc. Psych. Bull. 10:349–357.
McCullagh, P., and J. Nelder. 1989. Generalized linear models. Chapman and Hall, London.
McManus, I. C., and C. G. N. Mascie-Taylor. 1984. Human assortative mating for height: non-linearity and heteroscedasticity. Hum. Biol. 56:617–623.
Mueller, U., and A. Mazur. 2001. Evidence of unconstrained directional selection for male tallness. Behav. Ecol. Sociobiol. 50:302–311.
Nettle, D. 2002a. Height and reproductive success in a cohort of British men. Hum. Nat. 13:473–491.
———. 2002b. Women's height, reproductive success and the evolution of sexual dimorphism in modern humans. Proc. R. Soc. Lond. B 269:1919–1923.
Pawlowski, B. 2003. Variable preferences for sexual dimorphism in height as a strategy for increasing the pool of potential partners in humans. Proc. R. Soc. Lond. B 270:709–712.
Pawlowski, B., and S. Koziel. 2002. The impact of traits offered in personal advertisements on response rates. Evol. Hum. Behav. 23:139–149.
Pearson, K. 1897. Mathematical contributions to the theory of evolution: on the law of ancestral heredity. Proc. R. Soc. Lond. 62:386–412.
Pearson, K., and A. Lee. 1903. On the laws of inheritance in man: i. inheritance of physical characters. Biometrika Trust 2:357–462.
Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and the R Core team. 2008. Nlme: linear and nonlinear mixed effects models, R package version 3.1-90.
Price, T., D. Schluter, and N. E. Heckman. 1993. Sexual selection when the female directly benefits. Biol. J. Linn. Soc. 48:187–211.
Ryan, M. J., A. S. Rand, and T. Tregenza. 2003. Sexual selection in female perceptual space: how female Tungara frogs perceive and respond to complex population variation in acoustic mating signals. Evolution 57:2608–2618.
Salska, I., D. A. Frederick, B. Pawlowski, A. H. Reilly, K. T. Laird, and N. A. Rudd. 2008. Conditional mate preferences: factors influencing preferences for height. Pers. Indiv. Differ. 44:203–215.
Shepperd, J. A., and A. J. Strathman. 1989. Attractiveness and height: the role of stature in dating preference, frequency of dating, and perceptions of attractiveness. Pers. Soc. Psychol. B. 15:617–627.
Sheskin, D. 2007. The handbook of parametric and nonparametric statistical procedures. Chapman and Hall, New York.
Spuhler, J. N. 1982. Assortative mating with respect to physical characteristics. Soc. Biol. 29:53–66.
Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. 4th edition. Springer, NY.
Weeden, J., and J. Sabini. 2005. Physical attractiveness and health in western societies: a review. Psychol. Bull. 131:635–653.

Associate Editor: U. Candolin