Evolution and Human Behavior 34 (2013) 155–163

Contents lists available at SciVerse ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Review Article

Human social stratification and hypergyny: toward an understanding of male homosexual preference

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ARTICLE INFO

Article history:
Initial receipt 5 October 2012
Final revision received 21 January 2013

Keywords:
Male homosexual preference
Hypergyny
Social stratification
Darwinian paradox
Sexually antagonistic gene
Fertile sister effect

ABSTRACT

Male homosexual preference (MHP) challenges evolutionary thinking because the preference for male–male relationships is heritable, implies a fertility cost (lower offspring number), and is relatively frequent in some societies (2%–6% in Western countries) for a costly trait. Proximate explanations include the hypothesis of a "sexually antagonistic factor" in which a trait that increases fertility in females also promotes the emergence of MHP. Because no animal species is known to display consistent MHP in the wild (only transient and contextual homosexual behavior has been described), additional human-specific features must contribute to the maintenance of MHP in human populations. We built a theoretical model that revealed that, in a stratified society, a relatively high frequency of MHP could be maintained as a result of the social ascension of females signaling high fertility (hypergyny). Additional computer simulations confirmed that this result applies to populations with various numbers of classes, conditions of demographic regulation, and mating systems. The prediction that MHP is more prevalent in stratified societies was significantly supported in a sample of 48 societies for which the presence or absence of MHP has been anthropologically documented. More generally, any traits associated with up-migration are likely to be selected for in a stratified society and will be maintained by frequency dependence even if they induce a pleiotropic cost, such as MHP. These results offer a new perspective for understanding seemingly paradoxical traits in human populations.

1. Introduction

Male homosexual preference (MHP) is a poorly understood trait despite decades of research efforts. This trait challenges evolutionary thinking because the preference for male–male relationships is heritable (Bailey, Dunne, & Martin, 2000; Kendler, Thornton, Gilman, & Kessler, 2000; Långström, Rahman, Carlström, & Lichtenstein, 2010), implies a lower offspring number and thus a reproductive cost (Bell & Weinberg, 1978; Iemmola & Camperio-Ciani, 2009; Rieger, Blanchard, Schwartz, Bailey, & Sanders, 2012), and is relatively frequent in some societies (2%–6% in Western countries, Berman, 2003). In addition, MHP has been documented in some human societies during several millennia (Crompton, 2003). The relatively high prevalence of an apparent deleterious and heritable trait suggests that a pleiotropic advantage must exist.

Several evolutionary explanations have been proposed to explain the maintenance of MHP in human populations. First, men displaying a homosexual preference could redirect their parental investment toward nephews and nieces, thereby compensating for their reduced direct reproductive expectations by increasing their inclusive fitness (Wilson, 1975). This kin selection hypothesis has received little empirical support in Western societies and is still debated (Bobrow & Bailey, 2001; Rahman & Hull, 2005; Vasey & VanderLaan, 2010). Second, overdominance has been proposed to explain the maintenance of MHP (MacIntyre & Estep, 1993). According to this hypothesis, a gene-inducing MHP in its homozygous form would be maintained because of a selective advantage provided by its heterozygous form. This hypothesis has been theoretically explored but has restricted conditions of where it is applicable (Gavrilets & Rice, 2006; Camperio-Ciani, Cermelli, & Zanzotto, 2008). The third hypothesis is drawn from the theory of sexually antagonistic selection (for a review, see Bonduriansky & Chenoweth, 2009). This hypothesis postulates that male homosexual preference could be genetically associated with a higher expected fertility in their female relatives. It has been supported by several independent studies (Camperio-Ciani, Corna, & Capiluppi, 2004; Rahman et al., 2008; Iemmola & Camperio-Ciani, 2009; VanderLaan & Vasey, 2011; VanderLaan, Forrester, Petterson, & Vasey, 2012; but see Blanchard, 2011). In addition to these evolutionary explanations, a poorly understood "fraternal birth order effect" has been observed. Here, the probability of displaying a homosexual preference increases with the number of older brothers. This effect has been tentatively explained by assuming an increase in maternal immunity against male specific antigens during successive

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http://dx.doi.org/10.1016/j.evolhumbehav.2013.01.001

male pregnancies, leading to a modification in the developmental pathway of the brain (Blanchard & Bogaert, 1996; Vasey & VanderLaan, 2007; Bogaert & Shorska, 2011). The "fraternal birth order effect" may account for 15%–29% (Cantor, Blanchard, Paterson, & Bogaert, 2002; Blanchard & Bogaert, 2004) of the cases of MHP but is not sufficient to explain why homosexual preference also appears in firstborn children (Blanchard, 2011; Rieger et al., 2012). Furthermore, no clear reproductive advantage is known to be associated with the fraternal birth order effect. Why and how this effect could have evolved remains a puzzling question.

Interestingly, the above explanations could potentially operate in other species. It is necessary to make a clear distinction between *homosexual behavior* and *homosexual preference*. Homosexual behavior could be defined as non-exclusive same-sex sexual behavior in specific social contexts generally related to the paucity of accessible females. Male homosexual preference is the long-lasting preference for same-sex partners even if accessible females are present.

Male homosexual behaviors have been reported many times in animals (Bagemihl, 1999; Van Gossum, De Bruyn, & Stoks, 2005; MacFarlane, Blomberg, Kaplan, & Rogers, 2007; Bailey & Zuk, 2009), often with an age-specific expression (Bailey & Zuk, 2009). Homosexual behaviors have also been reported in humans under similar conditions, for example, when the access to females was restricted, as in prison (Sagarin, 1976), or when it was socially institutionalized. Institutionalized homosexual behaviors in humans have been described, for example, in Melanesia, where young men only became social adults after a compulsory period of semen ingestion, which is a prerequisite to later marry heterosexually (Herdt, 1993). If homosexual behavior is commonly reported in animals, it is interesting to note that no clear cases of exclusive *homosexual preference* (i.e., preference for same-sex partners even if opposite-sex partners are available) have been documented in any species observed in natural populations (excluding zoo and domesticated animals) (Bagemihl, 1999; Bailey & Zuk, 2009). Why MHP seems restricted to humans is currently unknown. We tested the hypothesis that specific features of human societies can explain the occurrence of MHP.

One of these specific features is the importance of social stratification in most human societies. Social stratification appeared in human societies when access to concentrated, predictable, defensible, and heritable resources was possible (Kaplan, Hooper, & Gurven, 2009), generally just after the rise of agriculture (Gupta, 2004). In a stratified society, populations are organized into different groups (or classes) in which people share similar socio-economic conditions. These groups can be ranked hierarchically depending on their access to resources (with more resources for the top class). This social inequality also affects the expected reproductive success of each group (with higher reproductive success associated with the top class) (Vandenberghe & Mesher, 1980; Betzig, 1986; Betzig, 1993; Nettle & Pollet, 2008; Rickard, Holopainen, Helama, Helle, Russell, & Lummaa, 2010). In all known highly stratified societies, past or present, the majority of marriages take place between people of the same social class (Davis, 1941; Van Leeuwen & Maas, 2010). Only a small proportion of marriages occur between classes. In these cases, the dominant pattern is hypergyny, that is, the union of a woman with a man of higher social status (Davis, 1941; Dickemann, 1979; Boone, 1986; Wooding et al., 2004). In stratified societies, there is a general reproductive advantage to migrating upwards; selection should therefore promote any trait increasing up-migration. Hypergyny presents the interesting possibility that a trait enhancing the probability of females marrying up could be selected for, even if this trait has an antagonistic effect in males. A likely candidate could be the heritable factor described above that would increase female fertility and decrease male reproductive value (e.g., by increasing the probability of displaying a homosexual preference). Here, "fertility" refers to the intrinsic ability to produce children either as a potential or a realized production. It is thus a component of the reproductive value of the individuals.

In this paper, we propose that social stratification and hypergyny could be the mechanisms favoring the emergence and maintenance of MHP in humans. These parameters have not been taken into account in the models of Gavrilets and Rice (2006) and Camperio-Ciani et al. (2008), which describe the evolution of genetic factors favoring the maintenance of MHP, nor in the abundant literature on MHP. If highly fertile females have a greater probability of up-migrating—according to the well-established link between fertility, femininity, and attractiveness (Buss, 2005; Jasienska, Lipson, Ellison, Thune, & Ziomkiewicz, 2006; Jokela, 2009; Singh, Dixson, Jessop, Morgan, & Dixson, 2010)—this could simultaneously promote the presence of males with lower expected direct reproductive success. Such a sex-antagonistic effect could lead to an intermediate equilibrium value that could potentially explain the observed prevalence of MHP. To investigate the validity of this verbal argument, a formal theoretical model was first built, describing the evolution of a sexually antagonistic gene in a two-class stratified society in the presence or absence of hypergyny. To further explore the different factors affecting the evolution of such a gene, an individual-based model was then built, taking into account a higher number of classes, and various hypergyny modalities. Finally, a strong prediction from these models was tested empirically using anthropological data.

2. Materials and methods

2.1. ESS model: effect of hypergyny

Our aim was to determine the conditions under which a rare mutant does not invade a population of resident alleles in a stratified society. This information would allow us to determine the evolutionary stable strategy (ESS). Let us consider a two-class stratified society with a resident genotype *aa* and a mutant genotype *Aa* (genotype *AA* is considered too rare). The model describes the evolution of the frequency of the mutant after one generation. The mutant allele slightly modifies three life history traits: hypergyny, i.e., the female probability to up-migrate (m); female fertility (f); and male heterosexual mating success (r). Allelic variation is assumed to occur along a one-dimensional gradient of genetic value (X) from high femininity (female: very fertile and attractive) to low femininity (female: weakly fertile and not attractive) values.

The r, f and m values are obtained from the genotypic value (X) as follows:

$$r = \frac{e^{-s*X}}{1+e^{-s*X}} \quad m = \frac{e^{s*X}}{1+e^{s*X}} \quad f = F_{\max}\frac{e^{s*X}}{1+e^{s*X}}, \tag{1}$$

with s being the parameter controlling the slope of the function linking the phenotype to the genotype and $F_{\max}$ being the maximal number of offspring.

The model passes through three successive stages: female up-migration, intra-class reproduction and demographic regulation. During the female up-migration stage, some females will migrate from the C2 class (lower class) to the C1 class (upper class). The probability of up-migrating depends on the genotype. Mutant females have a probability of up-migrating that differs from that of the resident female. Then, the population passes to the intra-class reproduction stage in which the couples reproduce. The number of offspring produced depends on the genotype of the females. Furthermore, the probability of a man finding a mate and transmitting his genes to the next generation also depends on his genotype. The last step is the demographic regulation stage in which the demographic excess of the upper class is poured into the lower class and the demographic excess of the lower class is removed. For simplicity, all individuals are assumed to have the same survival rate to adulthood, and the sex ratio is balanced; it is then possible to solely consider females in the model without loss of information.

The initial situation is described by Ini_Y^Z, which is the number of females in class Z (C1 or C2) with the Y genotype (aa or Aa). The number of females is described by Mig_Y^Z after migration, by Rep_Y^Z after reproduction and by Reg_Y^Z after regulation.

The recurrence relation can thus be written:

$$\begin{pmatrix} \mathrm{Reg}_{Aa(t+1)}^{C1} \\ \mathrm{Reg}_{Aa(t+1)}^{C2} \end{pmatrix} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} \mathrm{Reg}_{Aa(t)}^{C1} \\ \mathrm{Reg}_{Aa(t)}^{C2} \end{pmatrix} \tag{2}$$

with

$$a = \frac{1}{2}\left(\frac{k\frac{r'}{r}}{\frac{r'}{r}+k-1} + \frac{f'}{f}\varphi\right) \qquad b = \frac{1}{2}\frac{(1-\varphi)}{\rho}\frac{f'm'}{fm}$$

$$c = \frac{1}{2}w\rho\left(\frac{k\frac{r'}{r}}{\frac{r'}{r}+k-1} + \varphi\frac{f'}{f}\right) \qquad d = \frac{1}{2}w(1-\varphi)\frac{f'm'}{fm} + \frac{1}{2}(1-w) \times \left(\frac{k\frac{r'}{r}}{\frac{r'}{r}+k-1} + (1+\mu)\frac{f'}{f} - \mu\frac{f'm'}{fm}\right)$$

and

$$\mu = \frac{m_0}{1-m_0}$$

$$\rho = \frac{\mathrm{Ini}_{aa}^{C2}}{\mathrm{Ini}_{aa}^{C1}}$$

$$\varphi = \frac{\mathrm{Ini}_{aa}^{C1}}{\mathrm{Ini}_{aa}^{C1} + m_0\mathrm{Ini}_{aa}^{C2}}.$$

The parameters m_0, w and k control the female up-migration basal rate (proportion of females that migrate from the lower class to the upper class), the demographic down-regulation rate (proportion of males and females that migrate from the upper class to the lower class), and the limit number of reproductive partners for men, respectively.

The dynamics of the mutant *Aa* genotype are driven by the highest eigenvalue λ of the matrix $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$, which verifies:

$$\det\left[\begin{pmatrix} a & b \\ c & d \end{pmatrix} - \lambda I\right] = 0 \tag{3}$$

(*I*: identity matrix)

If $\lambda > 1$, the mutant allele increases in frequency when rare. If $\lambda < 1$, the mutant allele approaches extinction. The limit condition of invasion is thus given by $\lambda = 1$ or:

$$(a-1)(d-1) = bc. \tag{4}$$

The mutant's life history traits are considered to be close to those of the resident. It is then possible to reduce Eq. (4) by a first-order approximation (see electronic supplementary material, available on the journal's Web site at www.ehbonline.org).

Thus, Eq. (4) becomes:

$$\alpha\frac{\delta r}{r} + \beta\frac{\delta f}{f} + \gamma\frac{\delta m}{m} = 0 \tag{5}$$

with

$$\alpha = (\varphi - w - w\varphi - 1)\left(\frac{1}{4k} - \frac{1}{4}\right)$$

$$\beta = \frac{1}{2}w + \frac{1}{4}(1-w)(1-\varphi)$$

$$\gamma = \frac{1}{2}w(1-\varphi) - \frac{1}{4}\mu(1-w)(1-\varphi)$$

(see electronic supplementary material, available on the journal's Web site at www.ehbonline.org).

Eq. (5) reduces to

$$\delta\ln\left(r^{\alpha}f^{\beta}m^{\gamma}\right) = 0, \tag{6}$$

which gives

$$r^{\alpha}f^{\beta}m^{\gamma} = K, \tag{7}$$

with K as a constant.

When *r*, *f* and *m* are replaced with their values as functions of the genotypic value (X) (see Eq. (1)) and with $V = e^{s*X}$, the following equation is obtained:

$$V^{\beta+\gamma}(1+V)^{-\alpha-\beta-\gamma} = K, \tag{8}$$

which means that the function $V^{\beta+\gamma}(1+V)^{-\alpha-\beta-\gamma}$ necessarily increases during the selective replacement of one allele by another: this is a Lyapunov function. The convergence stability equilibrium is obtained at the maximum of the Lyapunov function.

This maximum is obtained when the derivative of the Lyapunov function is zero, yielding

$$V = \frac{\beta+\gamma}{\alpha}. \tag{9}$$

Furthermore, Eq. (9) can be developed, and the following equation is obtained:

$$V = \frac{2kw + k\rho m_0\left(3w + 1 + (w-1)\frac{m_0}{1-m_0}\right)}{(-2w - \rho m_0 w - \rho m_0)(1-k)}. \tag{10}$$

Thus

$$X = \ln\left(\frac{2kw + k\rho m_0\left(3w + 1 + (w-1)\frac{m_0}{1-m_0}\right)}{(-2w - \rho m_0 w - \rho m_0)(1-k)}\right)/s, \tag{11}$$

with X being the genotypic value at equilibrium. The genotypic value (X) in Eq. (11) corresponds to the highest individual fitness for a given set of parameters (m_0, ρ, w, k) with the corresponding r^*, f^* and m^* values of the individual life history traits describing the ESS (see electronic supplementary material, available on the journal's Web site at www.ehbonline.org). Hypergyny was studied by varying the rate of females' up-migrating in a plausible range of values (0–0.1) (Wooding et al., 2004) in order to understand its effect on the genetic value of the population at equilibrium.

2.2. Simulation model

Individual-based models were then built to further scrutinize the effect of different parameters on the evolution of this sexually antagonistic gene and to take into account stochasticity. The aim was to confirm and extend the results obtained with the theoretical model. Various types of demographic regulation could be explored, and up-migration could be made dependent on or independent from the individual genetic value. The individual-based models were made with the same structure as the theoretical model (code available upon request). For each generation, there are four successive steps: mutation, female up-migration, intra-class reproduction and demographic regulation.

Mutation: There is no genetic variation in the initial condition, but mutation generates random variation at each generation (see electronic supplementary material, available on the journal's Web site at www.ehbonline.org).

Female up-migration: In the female up-migration stage, some females will migrate from their social class to an upper social class. Two distinct cases of female up-migration have been explored: an indiscriminate migration (Fig. 1C), in which each female has the same probability of up-migrating, and a fertility-oriented migration (Fig. 1D), in which the probability m for a female to up-migrate increases with her genotypic value (as in the theoretical model; see Eq. (1)).

Intra-class reproduction: The genotype affects the r value, which determines the probability of a man finding a mate. An increase in the genotypic value decreases the probability of a man finding one or several mates. The number of children is calculated from the f value of the woman, which stems from the genotypic value (as in the theoretical model, see Eq. (1), and see electronic supplementary material, available on the journal's Web site at www.ehbonline.org).

Demographic regulation: Demographic regulation begins in the upper class. The individuals of the next generation are randomly drawn from the pool of all upper-class offspring. Those individuals who are not drawn at this stage are added to the pool of offspring from the class above and thus have a probability to be selected to enter a lower class. The same process applies to the middle class and then to the lower class. The individuals who are not chosen to enter the next generation are removed (see electronic supplementary material, available on the journal's Web site at www.ehbonline.org).

2.3. Anthropological data

Anthropological monographs from the Human Relations Area Files (eHRAF, http://www.yale.edu/hraf/) and Descola (1993) were analyzed for clues about the presence/absence of MHP. Additional information was gathered from Damas (1984), Ford and Beach (1951) and Berman (2003). Special attention has been paid to specifically identify homosexual preference. Positive clues included the description of individuals with MHP or certain forms of transvestism associated with homosexual preference (e.g., the "Berdache" or "Two-spirit" of North America or the "Hombre-mujer" of Central America), the existence of a word for MHP or the institutionalized expression of a "third gender" for individuals with MHP (e.g., the "Fa'afafine" of Samoa or the "Kathoey" of Thailand). Negative clues included the absence of a word or concept for homosexuality (see electronic supplementary material, available on the journal's Web site at www.ehbonline.org) or the direct conclusion of the anthropologist after having explicitly asked for the existence of homosexuality. Dubious cases (e.g., when homosexual behavior could not be unambiguously attributed to a homosexual preference) have not been considered further. The level of social stratification of each society has been gathered from the Standard Cross Cultural Sample (SCCS) using the variable V237. The degree of stratification of the different societies ranges from "no stratification," that is, no political authority beyond the local community, to "four levels" of stratification, that is, a large state. Several potentially confounding variables of the SCCS were also considered: geographical area (V200), population density (V64) and presence of moralizing gods (based on V238) (Roes & Raymond, 2003) (see electronic supplementary material, available on the journal's Web site at www.ehbonline.org). A logistic regression was performed with the presence/absence of MHP as the response variable and the level of stratification as the explanatory variables, as well as several putative confounding variables (geographical area, population density, and presence of moralizing gods). The data were analyzed by multimodel inference (Burnham & Anderson, 2002). The fit of all possible models was compared using the corrected Akaike information criterion (AICc) to calculate their Akaike weights. Model averaging was performed on all models by weighting the contribution of each model according to its Akaike weight (Hegyi & Garamszegi, 2011). The relative importance of each variable (sum of the Akaike weights of the model in which the variable appears) has been calculated to assess its explanatory power. The explained deviance of each model has been evaluated using the pseudo-R^2 (Crawley, 2007), and a weighted mean across all models, using the Akaike weight, was calculated to estimate the overall explained deviance. More classical methods of tests of significance were also performed for comparison. All analyses were conducted using R version 2.13.2.

3. Results

3.1. ESS model: effect of hypergyny

The equilibrium value of the sexually antagonistic gene was obtained from the theoretical model (Eq. (11)). The results demonstrated that in a stratified society, when hypergyny increased, the genetic value at equilibrium increased (Fig. 2). In a class-

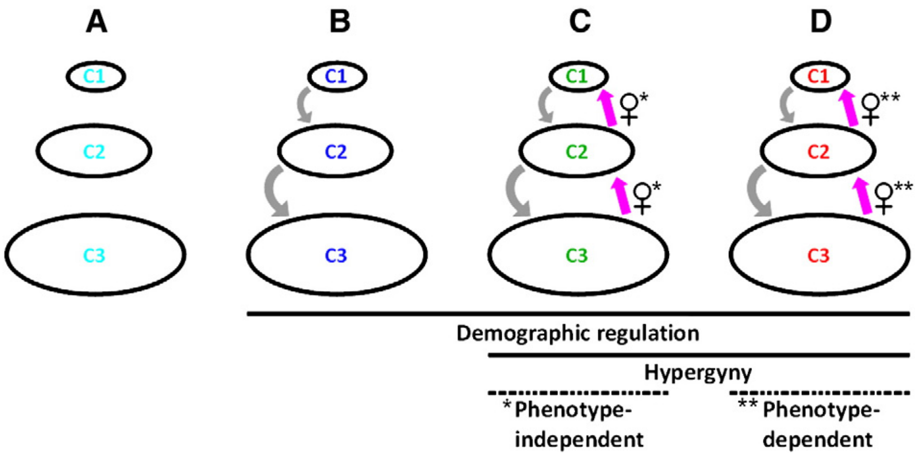

Fig. 1. Individual-based model: different connections between classes. (A) No link. (B) Demographic down-regulation only. (C) Demographic down-regulation and indiscriminate up-migration. (D) Demographic down-regulation and fertility-oriented up-migration. C1: upper class, C2: middle class, C3: lower class.

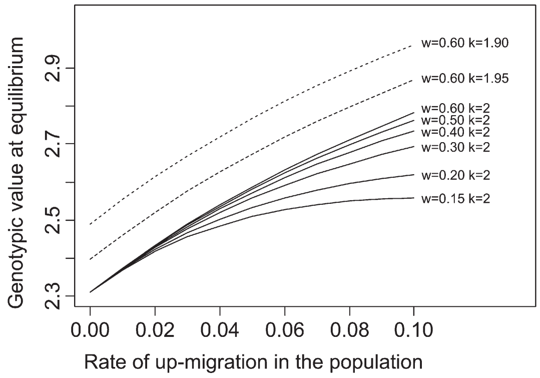

Fig. 2. Hypergyny and genotypic value at equilibrium. When the rate of female up-migration increases, the genotypic equilibrium shifts to a higher fertility value. The model was computed with the following parameter values: size of the lower class was twice the size of the upper class, and $s = 0.3$. The results are presented for different values of w (proportion of the lower class, after demographic regulation, composed of descendants of upper-class parents) and k (parameter limiting polygyny).

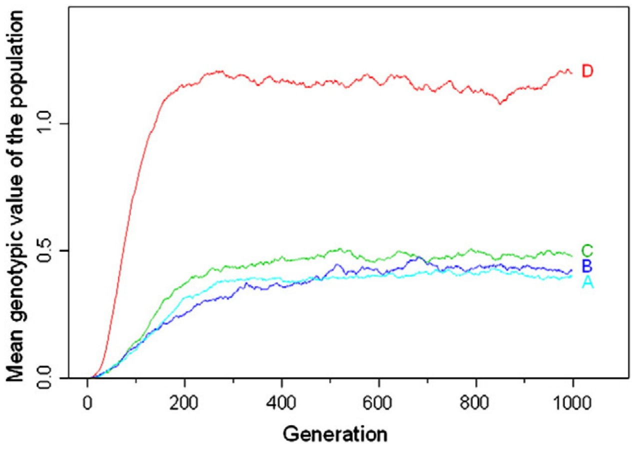

Fig. 3. Individual-based model: evolution of the mean genotypic value of the population. (A–D) Conditions depicted in Fig. 1. Class sizes of 2000, 4000, and 8000 individuals were entered for the upper, middle and lower classes, respectively. Each curve is the mean of 10 independent runs.

structured population, a gene for higher female fertility and attractiveness can therefore invade the population despite its negative effect on male reproduction.

The effect of the rate of hypergyny (m_0)—in a plausible range of values, from 0% to 10% (Wooding et al., 2004)—was explored under different conditions by varying the demographic regulation parameter (w), which controls the number of individuals migrating downward, from 0.15 to 0.6, and the parameter k, which limits the number of mating partners for men, from 1.01 to 2.5. The population size of the C2 class was twice that of the C1 class: $\rho = 2$. The parameter (s) controlling the slope of the function linking the phenotype to the genotype (for the female probability to up-migrate, the female fertility and the male heterosexual mating success) did not qualitatively affect the results (details not shown). In all cases, a shift toward higher fertility values was observed when the hypergyny rate increased (Fig. 2). This result means that stratification, together with discriminate hypergyny, allowed the selection of more fertile female phenotypes even if this selection induced a reproductive cost in men. In other words, the alleles of a sexually antagonistic gene promoting a higher fertility could have been selected for, thus producing MHP in some men.

4. Simulation model

4.1. Hypergyny

The simulation model showed that, in a three-class stratified society, the genetic value at equilibrium was approximately the same when the classes are i) not connected (Fig. 3A), ii) connected only by demographic down-regulation (Fig. 3B) or iii) connected by demographic down-regulation and female indiscriminate up-migration in which up-migrating females are chosen at random (Fig. 3C). The rate of female up-migration at each generation was 4%, a value that fell in the range of plausible values proposed by Wooding et al., (2004) on the basis of a genetic analysis of female inter-caste mobility in the Indian caste system. This measure in a system known for its social rigidity is, perhaps, in the lower part of the distribution of possible hypergyny values in stratified societies and could thus be considered conservative. Female indiscriminate up-migration resulted in an approximately 1.17-fold increase in the average equilibrium value (Fig. 3C). However, when the probability of up-migrating (keeping the rate of up-migration at 4%) depended on the genotypic value and thus more fertile females had a higher probability of up-migrating (Fig. 1D), an approximately 2.8-fold increase was observed (Fig. 3D), indicating that more fertile phenotypes were favored. Thus, the effect of hypergyny on the evolution of the sexually antagonistic gene depended on the characteristic that determined which females were chosen to up-migrate (fertility/femininity/attractiveness) and not solely on the demographic movement of females. The evolution of this antagonistic gene was therefore driven by its positive effect on up-migration.

As in the theoretical model, the simulation model showed that in a stratified society, discriminate hypergyny allowed for the selection of alleles of a sexually antagonistic gene promoting a higher fertility, even if it induced a reproductive cost in men.

4.2. Social stratification and hypergyny

The importance of social stratification was further scrutinized. The effect of the number of classes was studied, keeping the size of the population constant, by comparing three different cases: i) one class (6000 individuals), ii) two classes (3000 individuals each) connected by demographic down-regulation and female up-migration, and iii) three classes (2000 individuals each, connected as in the case of two classes). When the female up-migration did not depend on the genotype, there was no difference in the genetic equilibrium values among the three conditions, i.e., one, two or three classes. However, when the probability of female up-migration depended on their fertility (discriminate hypergyny), the equilibrium value for the two-class system was twice the value obtained for the one-class system; the value for the three-class system was not different from the value for the two-class system (see Figs. A1, A2 and A3 in electronic supplementary material, available on the journal's Web site at www.ehbonline.org).

Thus, social stratification was a necessary condition for the emergence of an allele of a sexually antagonistic gene promoting higher fertility. These data also confirm that the characteristic on which females are chosen to up-migrate, that is, fertility/femininity/attractiveness, was important for observing a selection for alleles promoting higher fertility, despite their pleiotropic cost.

4.3. Anthropological data

Using anthropological data for 48 societies worldwide (Fig. 4), the influence of several variables (level of stratification, geographical location, population density and presence of moralizing gods) on the probability of the occurrence of MHP was evaluated by multimodel inference. The relative importance of each variable (sum of the Akaike weights of the model in which the variable appears) revealed that the level of stratification had a probability higher than 0.97 of being in the best approximating model, indicating that it was important across the models considered. The averaged parameter estimate (β) for the

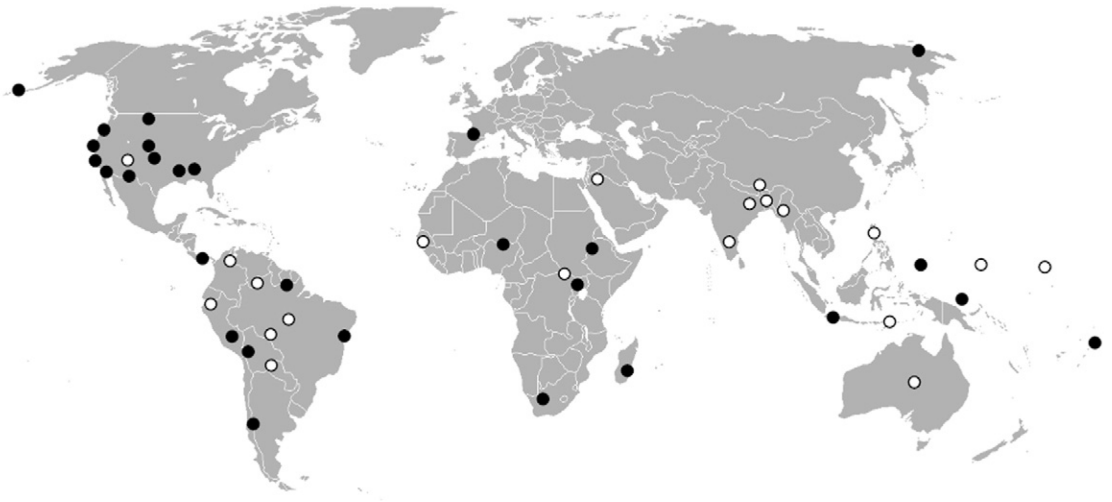

Fig. 4. Geographical distribution of the sampled societies. Full circles: societies with MHP; empty circles: societies without MHP. See Table A1 for details.

level of stratification was 1.63 (SE = 0.72). The probability of finding MHP in a given society increased with the level of stratification, with each additional level of stratification increasing the odds ratio by 5.1 (95% CI: 1.2–21.9). The effect of geographical area was also important (>0.90), principally because of the high prevalence of MHP among the indigenous peoples of North America, where there was a high acceptance of MHP, possibly due to its institutionalization under a third gender status (e.g., the "Berdache" or "Two-spirit," Callender & Kochems, 1983; Désy, 1978). The relative importance of the other variables was low (<0.28). The weighted value of the explained deviance was 35.4%.

These results are consistent with those obtained by testing the significance of the effect of the variables in the full model in terms of the level of stratification ($\chi^2 = 5.25$, $df = 1$, $P = 0.022$) and geographical area ($\chi^2 = 15.1$, $df = 5$, $P = 0.010$). The other variables did not have any significant effects (see electronic supplementary material, available on the journal's Web site at www.ehbonline.org). The full model explained 46% of the deviance.

5. Discussion

There are several examples in humans of the social environment affecting the evolution of biological traits (Gibbons, 2007; Perry et al., 2007; Itan, Powell, Beaumont, Burger, & Thomas, 2009). An influence of the social environment is most likely also the case for male homosexual preference (MHP), a notorious Darwinian paradox. We propose that, in a stratified society, females signaling a higher fertility (through a higher attractiveness) have a higher probability of marrying up. Thus, genetic factors promoting this higher female fertility are selected for, even if these factors have a sexually antagonistic cost in males (such as MHP).

The theoretical and individual-based models suggest that such a sexually antagonistic factor is indeed selected for in a stratified society in which hypergyny favors the up-migration of the most fertile females. The fact that both the theoretical model and a simulation-based model reached the same conclusion offers an interesting cross-validation. This sexually antagonistic factor confers the direct advantage of increasing fertility and the indirect advantage of increasing the probability of moving to a higher class, which leads to better access to resources. The cost for a male is a lower probability of finding a heterosexual mate for reproduction (a way to model MHP). Selection favors alleles with a higher female fertility and a low male heterosexual mating probability, resulting in a proportion of males that do not reproduce.

Hypergyny must be associated with the most fertile women because indiscriminate hypergyny provides no substantial change in the equilibrium value compared with the absence of hypergyny (Fig. 3). There is a large body of anthropological literature supporting discriminate hypergyny, which means that females who marry-up are particularly attractive (Ames, 1953; Betzig, 1986; Betzig, 1992). For example, in the Wolof society in Gambia: "The principal exception to [the] pattern of class rigidity is the socially accepted marriage between freeborn men and jam [lowest class] women. Such women, called 'tara', are selected for their beauty. They are regarded as wives, not concubines, and by virtue of their marriage with a freeborn person, they and their children attain freeborn status and are not discriminated against […] In any case, these marriages are rare, and only chiefs and other wealthy freeborn men can afford them; and none of these was observed to have more than two or three 'tara'. Marriage between a jam male and a freeborn female is prohibited." (Ames, 1953). Due to the link between attractiveness and fertility (Buss, 2005; Jasienska et al., 2006; Jokela, 2009; Singh et al., 2010), the prevalent discriminate hypergyny observed in stratified societies suggests that the most fertile females have a higher chance of marrying up.

The effect of social stratification was also studied by varying the number of class divisions with a constant total population size. The selection of more fertile alleles was only observed when there was more than one class; this result was only observed in the presence of fertility-oriented hypergyny. Increasing the number of classes from two to three did not change the results, suggesting that a two-class system with fertility-oriented hypergyny represents a minimum condition and that a higher class number will not qualitatively change the results. It is, however, possible that some ecological parameters have more quantitative impacts on the equilibrium value of female fertility, such as the carrying capacity of each class, the total amount of resources produced and the proportion of resources diverted from the lower strata toward the upper classes. Social rules may have an impact on this equilibrium value. For example, inheritance rules could favor one sex (generally males) or only one child (unigeniture), thus promoting social mobility (up or down) for the other siblings Furthermore, social rules can facilitate hypergyny, either by institutionalizing it or by enforcing the prohibition of males marrying up (e.g., the Wolof case above). Further work is needed to better appreciate the importance of these ecological and social parameters. In any case, the robust prediction from both the theoretical approach and the modeling is that the probability of observing MHP will be higher in a stratified society compared to a non-stratified society.

The anthropological data cited here are supportive of a higher probability of finding MHP in a stratified society, although there are some limitations. The present result is based on only 48 societies due to the scarcity of available data. It is important to keep in mind that the information used in this study is drawn from different ethnologists, who adhere to different schools of thought. The consideration given to the topic of homosexuality, as well as the set of theoretical ideas with which the researchers approached this topic, may have varied. Furthermore, the reports were not gathered at the same time; thus, each report reflected the particular situation of an ethnic group during a given period of time (Weston, 1993). Because the difference between homosexual preference (at least partially biologically induced) and homosexual behavior (socially promoted) had not yet been established, many anthropological reports could not be used to ascertain the presence or absence of MHP in a given society. This is particularly problematic because both types of homosexuality could have coexisted in a given society. Nevertheless, there are several firm cues suggesting the presence or absence of MHP. For the societies in which MHP was considered absent, some anthropologists reported that there was no word or concept for homosexuality. This result is most likely a strong argument supporting the absence of homosexuality (including MHP) from such societies. For example, this was the case for the Aka from Central Africa: “We asked Aka men about homosexuality and masturbation and were surprised that they were not aware of these practices, did not have terms for them and how difficult it was to explain both sexual practices. […] The Aka, in particular, had a difficult time understanding the concept and mechanics of same-sex relationships. No word existed and it was necessary to repeatedly describe the sexual act.” (Hewlett & Hewlett, 2010). It is also possible that the probability of an anthropologist observing and reporting MHP in a society is dependent on the size of the group studied, which is not independent from the level of stratification. This possibility is particularly true because MHP is generally observed at a low frequency (e.g., 2%–6% in Western countries). However, the density of the population (a good proxy of the number of indigenous people met by the anthropologist) has been statistically controlled for, and the relative importance of this variable was very low (~0.23), suggesting that it had, at most, a very limited explanatory power. It is possible that other variables could confound the present result, although they remain to be identified and tested.

Social stratification is a recent phenomenon, which was only possible when resources could be accumulated and monopolized. This phenomenon has been documented since the rise of agriculture, that is, after 10,000 years BP in the Middle East and more recently in other areas (Gupta, 2004; Kaplan et al., 2009). This date represents fewer than 500 generations (considering a minimum generation time of 20 years) and perhaps fewer than 400 (with a generation time of 25 years). This is a sufficient period for positive selection to operate because several genes providing an adaptation to the new agriculture or husbandry-based diet have already been identified, such as the gene for lactose tolerance and the amylase gene amplification (Perry et al., 2007; Itan et al., 2009). Any pleiotropic cost associated with an adaptive gene is expected to be selected against, in particular with the occurrence of modifier factors (Kirkpatrick, 1996; Orr, 1998; Bonduriansky & Chenoweth, 2009). However, this selection takes place on a larger time frame (the cost-inducing gene must first be selected for) and is necessarily weaker (otherwise, the cost-inducing gene would not have been selected for in the first place). For example, after ca. 300 generations of selection in natural populations, a pleiotropic cost was still apparent for mosquitoes adapted to the presence of insecticide (Lenormand & Raymond, 2000; Raymond, Berticat, Weill, Pasteur, & Chevillon, 2001; Labbe, Sidos, Raymond, & Lenormand, 2009), although the selection coefficient for this example is perhaps not applicable in the case of humans. This suggests, nevertheless, that a time frame of 400–500 generations is most likely too short for a complete suppression of the pleiotropic cost associated with high female fertility. Thus, the recent modification of the human social environment, which is characterized by the emergence of stratification, explains MHP as a pleiotropic cost associated with high female fertility.

Because social stratification has appeared several times independently, it is possible that MHP has been selected for independently in the various stratified societies. This situation would be an example of convergent evolution, although it is currently difficult to test this hypothesis due to the paucity of data from non-occidental societies. A similar sexually antagonistic factor (VanderLaan & Vasey, 2011; VanderLaan et al., 2012) and a similar older brother effect have been described in Samoa, although an older sister effect has also been found (VanderLaan & Vasey, 2011), suggesting that slightly different determinants of MHP have been selected for in Samoa. A broader intercultural comparison is required to settle this point. No current theory is able to explain why MHP is not documented in wild animals (Bagemihl, 1999; Bailey & Zuk, 2009) or why MHP seems to be absent from some human societies (e.g., Hewlett and Hewlett (2010). The present results suggest that homosexual preference could be found in animals, particularly in a situation where a high female fertility has been selected for. Sexually antagonistic factors are readily apparent when selection on pleiotropic traits occurs. One example is the artificial selection for high or low levels of testosterone in the bank vole leading to a sexually antagonistic effect on fitness (Mills, Koskela, & Mappes, 2012); there are many other examples in various laboratory animals (Rice, 1992; Chippindale, Gibson, & Rice, 2001) and in natural populations of animals, such as the cricket (Fedorka & Mousseau, 2004), adder (Forsman, 1995), lizard (Calsbeek & Sinervo, 2004), soay sheep (Robinson, Pilkington, Clutton-Brock, Pemberton, & Kruuk, 2006) and red deer (Foerster, Coulson, Sheldon, Pemberton, Clutton-Brock, & Kruuk, 2007). Thus, we would expect to observe male homosexual preference when a recent selection for high female fertility has taken place. The possible paucity of such recent changes in selection in the wild most likely explains why male homosexual preference has not been described yet. However, high fertility is certainly one trait under strong selection in domesticated animals, and large pleiotropic costs would be expected. Why male homosexual preference is not commonly observed in the various domesticated animals (Roselli, Resko, & Stormshak, 2002) remains to be understood. One possibility is that such a trait was strongly selected against due to the cost of raising non-reproductive males, thus accelerating the selection of cost modifiers. In addition, the number of generations since the beginning of domestication, in most cases, is far more than 1000; for example, sheep were domesticated approximately 11,000 years ago (Kijas, Lenstra, Hayes, Boitard, Porto Neto, et al., 2012). When considering a generation time of 3.5 years—the time to reach maturity plus the gestation period of the mouflon *Ovis orientalis* (cf. Festa-Bianchet in http://www.arkive.org/mouflon/ovis-orientalis/)—this would represent more than 3000 generations. This rough estimation can be considered conservative because the generation time of the Mouflon is greater than that of the domestic sheep.

The three approaches used here, namely formal modeling, individual-based modeling, and anthropological data, all support the importance of social stratification and hypergyny in a better understanding of male homosexual preference.

This solution to the Darwinian paradox offers a new way to understand why MHP is found in some human societies and not in others and why it seems hard to find a similar phenomenon in wild animals. More generally, any traits (e.g., behavioral or cognitive traits) increasing the chance of up-migrating, for males or females, will be selected for, even if these traits are costly. If the increase in fitness obtained by up-migrating is high enough, the trait promoting this upward migration will increase in frequency and will be maintained by frequency dependence as long as cost modifiers are not selected for. Thus, in the human population, we expect to observe many polymorphic traits, which are best understood by considering the recent occurrence of a stratified society.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.arth.2012.07.004.

Acknowledgment

We are very grateful to Christiane Cunnar for access to the HRAF database, Charlotte Faurie, Alexandra Alvergne, Pierre-André Crochet and two anonymous reviewers for useful comments on the manuscript, and Valérie Durand for bibliographic help. Contribution ISEM 2013-015.

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