



Review Article

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

Julien Barthes^{a,*}, Bernard Godelle^a, Michel Raymond^b^a ISEM-CNRS, University Montpellier II, Place Eugène Bataillon 34095, Montpellier Cedex 05, France^b CNRS, Institute of Evolutionary Sciences, CC 065, Place Eugène Bataillon, Montpellier, France

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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.

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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; Lemmola & 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; Lemmola & 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

* Corresponding author. Tel.: +33 4 67 14 46 15.

E-mail address: julien.barthes@univ-montp2.fr (J. Barthes).

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 Gavrillets 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, & Ziolkiewicz, 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:

$$r = \frac{e^{-sX}}{1 + e^{-sX}} \quad m = \frac{e^{sX}}{1 + e^{sX}} \quad f = F_{\max} \frac{e^{sX}}{1 + e^{sX}}, \quad (1)$$

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

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