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Response to comment on "Human social stratification and hypergyny: toward an understanding of male"

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VanderLaan et al. have challenged our recent work, which offers an evolutionary explanation for the existence of male homosexual preference (MHP) in humans. They maintain that our research is not sound because (A) empirical evidence of the existence of a sexually antagonistic genetic effect (SAGE) is weak; (B) social stratification is not a specific human feature, so our hypothesis does not explain the uniqueness of MHP in humans; (C) female relatives of homosexual males are not more attractive than those of heterosexual ones; (D) there is no link between female attractiveness and fertility; (E) the offspring of hypergynous women are often subject to infanticide thus reducing/cancelling the reproductive advantage of these women; (F) the assumptions of the mathematical model are not grounded; (G) some anthropological biases were not considered when gathering data from original anthropological sources; (H) the Standard Cross Cultural Sample (SCCS) should have been used instead of Human Relations Area Files (HRAF) to code for homosexuality, and (I) VanderLaan, Ren, and Vasey (2013) present results on transgenderism that contradict our results.

A. VanderLaan et al. acknowledge that three previous publications support the existence of a SAGE (Camperio Ciani, Corna, & Capiluppi, 2004; Camperio Ciani & Pellizzari, 2012; Iemmola & Camperio-Ciani, 2009), and they state that Rahman et al., 2008 provide supporting results only with a "White sample" but "*contrary evidence in a non-White sample*". However, several problems have been identified in this non-White sample. The results derived from it are most likely erroneous (see Camperio Ciani & Pellizzari (2012) for details). They neglect to acknowledge other results that are consistent with predictions from the SAGE hypothesis (Blanchard & Lippa, 2007; King et al., 2005; Schwartz, Kim, Kolundzija, Rieger, & Sanders, 2010; VanderLaan, Forrester, Petterson, & Vasey, 2012; VanderLaan & Vasey, 2011; Vasey & VanderLaan, 2007). Interestingly, a maternal inheritance of the antagonistic factor, as proposed from the empirical evidence, is not a pivotal issue: a biparental inheritance would not change the conclusion of our model. A review of the current available results (see Table 1, Supplementary Online Materials) suggests that the SAGE hypothesis remains a viable working hypothesis for further work on the evolution of MHP in humans. Additional data are obviously required, particularly from non-western cultures, to better understand and challenge the SAGE hypothesis. At this stage, it would be unwise, however, not to evaluate what the SAGE hypothesis could tell us on the evolution of MHP in humans.

B. The type of social stratification currently found in some human societies is most likely unprecedented. For example, social class is often defined across generations, and upper class members can control and concentrate resources due to conventions such as the social rules of wealth distribution and inheritance (Boone, 2000; Wooding et al., 2004). Additionally, reproduction is mainly intra-class. There is no equivalent, qualitatively or quantitatively, of this type of social structure in any non-human primate. In humans, social class is the same for sisters and brothers, whereas in other primates, such as the macaque matriline, the rank of a daughter is determined by the rank of her mother and ranks are not transgenerational for males. Some lineages may rule the upper class for decades and across many generations, such as in European royal families, whereas the alpha position in non-human primates is always transient, held during a small part of the animal's life. It is in these specific stratified human societies that selection driven by class structure could emerge. This situation is explored in our paper.

C. It is correct that there is no empirical support for the notion of greater attractiveness of female relatives of homosexual men; although, to our knowledge, this has never been tested. We are currently collecting data with which to evaluate this hypothesis.

D. There are several lines of evidence linking female attractiveness to fertility. For example, a high level of estradiol is associated with a female's likelihood of becoming pregnant (Lipson & Ellison, 1996), less fluctuating asymmetry, which is considered as attractive (Jasienska, Lipson, Ellison, Thune, & Ziomkiewicz, 2006; Rhodes, 2006), a more attractive face (Law Smith et al., 2006), larger breasts and a low waist to hip ratio (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004). Estradiol is also associated with higher attractiveness self-rating and selectivity in partner choice (Durante & Li, 2009). A link between attractiveness and reproductive success has also been directly demonstrated in a pair of studies (Jokela, 2009; Pflüger, Oberzaucher, Katina, Holzleitner, & Grammer, 2012). Taken together, these lines of evidence strongly support the hypothesis of a link between attractiveness and fertility in women (see Singh and Singh (2011) and Buss (2005) for a review).

E. One of the papers cited by VanderLaan et al. concludes: "*…dowry can be useful in attracting a wealthier son-in-law and in marrying one's daughter up in terms of income, both of which have been shown to have positive effects on the education, income, survival and health of children of both sexes who might result from the marriage*" (Shenk, 2007, p. 260) and "*I have argued in this paper that one important reason why Indians*

resist dowry prohibition is that many of them benefit from dowry through its positive effects on their daughters and grandchildren" (page 257–258). This conclusion does not concern all of India, and Shenk writes: "*I have argued in this paper that dowry has a positive, functional role in the lives of many South Indians, and that at least in Bangalore dowry is not necessarily associated with violence and significant discrimination against women*" (p 260). Clearly, quantitative data are needed to justify the claim that hypergynous women suffer a reproductive cost compared to non-hypergynous ones. In addition, marrying up is only one form of hypergyny. Harems in ancient, highly stratified societies were used as an efficient reproductive engine by their wealthy owners (Betzig, 1986, 1992, 1993). Nevertheless, we acknowledge that a formal fitness analysis of hypergynous and non-hypergynous women remains to be done.

F. VanderLaan et al. suggest that our mathematical models rely on postulates. We grant that this is the case for our model and, however, every other model. Our models are based on explicit postulates that are detailed in the original article (and in the Supplementary Online Materials of the original paper). They provide interesting results and predictions on the evolution of a sex antagonistic gene in the context of human stratification. Not every parameter of our model has been quantified in the literature, but they are strongly grounded in previous research, at least qualitatively.

G. Contrary to Boswell (1982/1983), our goal was not to discourse on the impossibility to transpose the dichotomous concept of "homosexuality"/"heterosexuality" to non-western societies. The aim was not to find western-like categories of homosexuality in non-western societies, and we did not conclude that there was no MHP in cultures that do not name the western concept of homosexuality. However, the absence of a word to indicate a sexual variant such as MHP, whatever form it takes, seems to be a good proxy of the absence of MHP. We present the strong example of the Aka in our original paper. Hewlett and Hewlett (2010) state that "*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*". In this example and in similar reports, the absence of a word is linked to the absence of a concept to describe MHP. The most parsimonious conclusion, based on this information, is that MHP is absent from this society. We did consider some possible limitations concerning the reliability of the anthropological data. The additional limitation proposed by VanderLaan et al. is interesting and should be kept in mind while analyzing any work of comparative anthropology about MHP. Because this type of bias is most likely independent from the level of stratification, not considering this bias introduces noise to the analysis, which only serves to render the significant conclusions more conservative. When we rerun our analysis without considering the societies in which there was a discrepancy between our MHP codes and those of VanderLaan et al., the results are not qualitatively changed for the level of stratification $\chi^2 = 15.316$, df = 1, P = <0.0001; geographical area, $\chi^2 = 20.89$, df = 1, P = 0.0008; population density, $\chi^2 = 0.238$, df = 1, P = 0.625; or Belief in a "moralizing god", $\chi^2 = 0.835$, df = 1, P = 0.361. A corrected table of the original A1 Table is provided in the Supplementary Online Materials (Table A1C).

H. The SCCS is a useful tool, as it has been designed for comparative anthropology and therefore limits the problem of pseudoreplication (or Galton's problem) (Mace et al., 1994). However, the distinction between MHP and homosexual behaviors is not made in this anthropological sample; thus, the presence/absence of MHP could not be reliably assessed using the SCCS (see Barthes, Godelle, & Raymond, 2013). Direct access to anthropological monographs was thus required, and HRAF is very useful is that case.

I. Our analysis is not directly comparable to the study of VanderLaan et al. (2013). Their "ancestral sociocultural conditions" variable is a composite variable obtained from a PCA, and it includes the variables community size, subsistence dependency, level of sovereignty, and stage of religious evolution. The correlation of social stratification with this composite variable is not presented; thus, no conclusion can be derived from this analysis of the link between social stratification and transgenderism. In conclusion, it is not possible to compare these studies because they are not concerned with the same dependent variable, indeed *transgenderism* is not the same as MHP. While transgenderism is a firm clue of the presence of MHP in some societies, the extent to which MHP without transgenderism is common in traditional societies has not been assessed. Furthermore, these studies are not using the same explanatory variables. In addition, we recently found a study based on HRAF and SCCS that concludes that "homosexuality" is rarer in hunter–gatherer societies than in agricultural and urban economies (Barber, 1998), which is consistent with our results.

The criticisms from VanderLaan et al. are important, and we believe that new hypotheses should always be challenged. Even after these criticisms are given due consideration, the hypergyny hypothesis remains a viable hypothesis of the existence of MHP in humans. Interestingly, we have recently increased the sample size of the cross-cultural sample on MHP and used more refined analysis tools. The results on social stratification are still strongly significant and consistent with our first results (Barthes et al., submitted). Obviously, further work is required, as are empirical data on the various predictions of the hypergyny hypothesis. The Barthes et al. (2013) article was not intended to present the final solution to the complex problem of MHP in humans. Rather, the intention was to offer a new direction on the puzzling case of MHP in humans, with some modeling to support the central argument and some empirical data to test its strongest predictions. More data will come, as will more criticisms; knowledge is going forward.

Supplementary materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2014.06.001.

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