The role of miscarriage and sororal birth order in male same-sex orientation:

Theoretical predictions and empirical data

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Abstract

This study explores the proximal and biological mechanisms underlying male same-sex orientation, with a focus on the Fraternal Birth Order Effect (FBOE), a robust phenomenon whereby androphilic men tend to have more older brothers, and its relationship with the Sororal Birth Order Effect (SBOE), whereby older sisters also appear to influence sexual orientation, albeit less consistently. The Maternal Immune Hypothesis (MIH), which posits that maternal immune responses to male-specific antigens accumulate across successive male pregnancies, provides a compelling proximal explanation for the FBOE, but it fails to fully account for the SBOE and other birth order patterns, such as the elevated prevalence of same-sex orientation among only-children compared to firstborns in larger sibships. Through explicit modelling of the MIH, our simulations reveal that the correlation between the number of older brothers and sisters generates a spurious SBOE, which disappears when controlling for older brothers, unless miscarriages are considered, in which case this control becomes insufficient. Additionally, the increased prevalence of same-sex orientation among only-children, relative to firstborns with siblings, only emerges when miscarriages are incorporated into the model. Empirical analyses across eight diverse populations (Indonesia, France, French Polynesia, Greece, Canada, Czech Republic, Samoa, Iran) confirm the presence of an overall significant FBOE and, critically, an overall significant SBOE even after controlling for the number of older brothers. The higher frequency of same-sex orientation men among only-children, compared to firstborns in larger sibships, further supports a possible role of miscarriage. However, the miscarriage rates estimated to explain the observed SBOE (37% - 57%) exceed typical reported rates (10% - 30%), suggesting either that additional mechanisms contribute to a spurious SBOE or that a non-spurious SBOE exists alongside the FBOE. Limitations of this study are discussed, as well as whether the MIH framework can be extended to accommodate these findings, or if alternative explanations are needed to resolve these discrepancies.

Introduction

Male same-sex orientation (or male androphilia), i.e., preferential attraction of male subjects to same-sex partners for sexual intercourse and/or romantic relationships, is an evolutionary enigma. This is because preference for male-male relationships is partially heritable (Bailey et al., 2000; Långström et al., 2010) and is associated with a fertility cost with a 30-100% decrease in offspring number (Iemmola & Camperio-Ciani, 2009; Rieger et al., 2012; Vasey et al., 2014; Nila et al., 2018). Also, male androphilia is surprisingly common in many societies (2%–6% in Western countries) for such a costly trait (Berman, 2003; Apostolou, 2020a; Rahman et al., 2020).

A solid empirical observation is that androphilic males have on average more older brothers compared to heterosexual men: this is referred to as the fraternal birth order effect, or FBOE (Blanchard & Bogaert, 1996). The FBOE has been found independently in Western (e.g., Blanchard & Bogaert, 2004; Bogaert & Skorska, 2011; Blanchard, 2018a; Blanchard, 2018b; Apostolou, 2020b; Ablaza et al., 2022; Fořt et al., 2024a) and non-Western countries such as Turkey, Iran, Hong Kong, Samoa, Mexico, and Indonesia (Blanchard, 2018a; Li & Wong, 2018; Nila et al., 2019; Gómez Jiménez et al., 2020; Semenyna et al., 2023; Sadr-Bazzaz & Vasey, 2025) The only exceptions to this empirical rule appear to come from studies with small sample sizes or populations where the average fertility rate is low, e.g., France (Raymond et al., 2023), China (Xu & Zheng, 2017), Thailand (Skorska et al., 2020). The FBOE thus remains a well-established proximal determinant of male androphilia.

The FBOE has not revealed any statistical association with potential confounders such as sibling size, birth year, age, socio-economic status (Blanchard & Bogaert, 1996; Bogaert, 2003) or parental age (e.g., Bogaert, 2006; Bogaert & Liu, 2006). Most importantly, it seems to be present even when the biological brothers were raised in different households, suggesting that it operates only during prenatal life (Bogaert, 2006). The FBOE thus seems to be caused by lasting effects from previous male gestations. The first proposed candidate for such "memory" across the successive pregnancies has been the maternal immune system: under the maternal immune hypothesis (MIH), mothers would develop antibodies against proteins involved in male brain development such as Y-linked proteins, with increasingly stronger effects with each male pregnancy, affecting the brain structures underlying sexual partner preference in later-born sons (Blanchard et al., 2001; Bogaert & Skorska, 2011). A recent study provided empirical support to this hypothesis by showing that mothers of gay sons with older brothers had significantly higher circulating levels of anti-neuroligin 4 Y-linked (NLGN4Y, a Y-linked protein) antibodies than the control samples including mothers of only gynephilic sons (Bogaert et al., 2018). In spite of this apparent empirical support for the MIH, three lines of evidence are challenging the validity of this hypothesis to explain the FBOE. Recently, three additional birth order effects on sexual orientation have been identified, suggesting that the MIH is either inadequate or needs to be supplemented with other hypotheses to proximally explain all birth order effects on sexual orientation.

First, a sororal birth order effect (SBOE) has been described, which is not predicted by MIH. It has been described in several studies, e.g., in UK (King et al., 2005), Finland (Kangassalo et al., 2011), Samoa (Semenyna et al., 2023), Canada (Swift-Gallant et al., 2018), Iran (Sadr-Bazzaz & Vasey, 2025), and confirmed in a meta-analysis (Blanchard et al., 2021) and in a nation-wide study (Ablaza et al., 2022). This SBOE has always been found in association with a FBOE and has usually been found to be weaker than the FBOE, with some exceptions (Semenyna et al., 2023; Fořt et al., 2024a; Sadr-Bazzaz & Vasey, 2025). Part of this SBOE may be spurious, due to a trivial sampling effect: in a population with an even sex-ratio, sampling individuals with more older brothers also means sampling individuals with correlatively more older sisters. This spurious SBOE has been suggested several times (e.g., Blanchard, 1997; Blanchard & Lippa, 2007), and has been formally supported by Raymond et al. (2023). However, recent evidence suggests that a real (non-spurious) SBOE also contributes to male androphilia: the number of older sisters, independent of the number of older brothers, influences the likelihood of androphilia in later-born males. This has been demonstrated by controlling for the FBOE, either experimentally by considering only specific birth ranks (Khovanova, 2020; Blanchard & Lippa, 2021), or statistically by considering large national-wide samples (Ablaza et al., 2022). This real SBOE is presently not predicted by the MIH, although it has been claimed that this SBOE is still spurious, thus still compatible with the MIH (Blanchard, 2022). The verbal argument for this claim is based on the presence of differential miscarriage: if male embryos are more often miscarried than female embryos, the correlation between older brothers and older sisters is different whether all older brothers are considered (miscarried or not), or only those not miscarried. In other words, the verbal argument suggests that there is a remaining spurious SBOE after controlling for the number of older brothers that were born, due to the number of older brothers that were not born. Whether the SBOE observed is real or spurious thus remains unclear.

Second, the presence of male androphilia in male only-children, firstborn, or with only older sisters is not directly predicted by the MIH. These three categories of males do not have older brothers; thus their mother could not have developed an immune response against specific male antigens. However, there may be a natural variability in the initial maternal immune response in a population, so that firstborn androphilic males could emerge at a low rate. Alternatively, it has been hypothesized that miscarried male embryos contribute to the maternal immune response: the firstborn male is thus not necessarily the first male embryo present in the maternal womb (Bogaert & Skorska, 2011). The relatively high estimate of miscarriage, ca. 10-30% (Wilcox et al., 1988; Andersen et al., 2000; Buss et al., 2006), is consistent with this hypothesis, reinforced by the fact that miscarried male embryos are more likely to lead to immunization (Bianchi et al., 2001). However, not all male discontinued embryos have the potential to trigger such specific maternal immune response: a minimum developmental time is probably required for the brain to be sufficiently developed to display the relevant antigens, thus decreasing (to an unknown value) the effective rate of miscarriage involved in the maternal immune response. Thus, it remains to be seen if the minimum miscarriage rate required to generate the observed frequency of same-sex orientation in men without older brothers is quantitatively compatible with actual data on miscarriage rate.

Third, it has been observed that there is a higher prevalence of male same-sex orientation in only-children than in firstborn of larger sibships (Blanchard & Lippa, 2021), a result also found in a large sample from the Netherlands (Ablaza et al., 2022). This could be explained if there is a heterogeneity of maternal conditions: mothers who produce an androphilic son at their first delivery could belong to a biologically distinct subpopulation of mothers with a decreased probability of carrying subsequent foetuses to term (Blanchard, 2012). To explain this observation in the framework of the MIH, a different type of immune response has been hypothesized in these women, specifically affecting foetuses in first pregnancies and reducing subsequent fertility (Skorska et al., 2017; Blanchard & Lippa, 2021). However, birth weights of firstborn androphilic and gynephilic men (including only-children) are not different (Blanchard & Ellis, 2001, but see Skorska et al., 2017), a result which indirectly suggests nothing unusual about the gestation of firstborn androphilic men (Blanchard, 2012). Thus, whether an additional type of immune response, thus an extended MIH, is required, or another type of explanation, remains unclear.

Taken together, these observations and theoretical considerations highlight that the MIH provides a plausible biological mechanism for the FBOE, but its inability to fully account for the other birth order effects suggests that the hypothesis may need refinement, or that additional mechanisms are at play. To systematically evaluate these possibilities, a quantitative approach is required. By modelling the MIH and its predictions, we can explicitly test whether the observed patterns in real-world data align with its theoretical framework. This allows us to assess the necessity of extending the MIH or incorporating alternative explanations.

In this study, we addressed the following key questions. First, we developed a formal model of the MIH to: a) derive explicit functions for both the FBOE and SBOE, b) quantitatively evaluate the relative contributions of spurious and non-spurious SBOE by manipulating the correlation between the number of older brothers and older sisters, c) assess the impact of miscarriage on the SBOE and on the prevalence of same-sex orientation in firstborn males, and d) compare the prevalence of male same-sex orientation between only-children and firstborns from larger sibships. This modelling approach, based on simulated data, allowed us to clarify the specific predictions generated by the MIH, and quantitatively estimate the possible importance of miscarriage for the various birth order effects. Second, using individual-level datasets from real populations, we empirically tested whether birth order effects beyond the FBOE, such as spurious or non-spurious SBOE, are consistent with the MIH when accounting for miscarriage.

Material and methods

Simulating random population samples

In order to evaluate the properties of family data under the MIH hypothesis, population samples of male individuals were generated, and the following sampling process was applied for each focal individual. A birth rank was drawn from the rank sampling distribution R(λ) (Raymond et al., 2023, Eq. 1), where λ is the parameter of a Poisson distribution. Alternatively, when the number of younger siblings was also considered, the total number of siblings was drawn from a displaced Poisson distribution of parameter $r = -1$, with mean $\lambda + 1$ and variance λ (Staff, 1967), see Appendix 2 of Raymond et al. (2023) for details. The rank of the focal individual was randomly assigned within the sibship. When the rank of the focal individual was > 1, the sex of each older sibling was randomly assigned with equal chance of being male or female, and the birth order was recorded. For the mother of the sibship, an initial level of immune response (*imr*) was attributed, drawn from a Gamma distribution of parameters mean = *imr_mean*, and sd = *imr_sd*. Each male birth increased *imr* by a fixed quantity (*b*): each increase of *imr* thus corresponds to an increase of the maternal immune response against male antigens. A female birth did not affect *imr* (Fig. 1). Sexual orientation for each male was determined by a logistic function of *imr:* $1/\left(1+e^{-slope\cdot imr}\right)$, with *slope* > 0. Thus, as *imr* increased, the probability of a same-sex orientation increased. This process was run until the sample reached 300 gynephilic and 300 androphilic men (thus matching most empirical data sets where balanced numbers of gynephilic and androphilic male subjects are sampled from the populations), before performing the various tests and storing the corresponding estimates and *P*-values. This was replicated at least 100 times for a given set of parameters. Unless otherwise indicated, the following parameter values were considered throughout. The initial amount of immune response refers to a relative quantity and was set to an arbitrary value of *imr_mean = -5* and *imr_sd = 0.2.* The increase of *imr* for each male birth was *b* =1, and the slope of the logistic curve determining the probability of a same-sex orientation according to the amount of *imr* was set to *slope* = 1. Thus, the frequency of same-sex orientation for a firstborn male was ~1.84 % (SEM = 1.1×10^{-2}) using these standard parameters values. The mean fecundity was set at $\lambda = 5$, in order to study FBOE and SBOE over a large range of birth ranks.

In order to generate a population sample without a correlation between the number of older brothers (*ob*) and older sisters (*os*), for each individual, a male birth rank (r_m) and a female birth rank (r_f) were independently drawn from the rank sampling distribution R(λ/2) (see Eq A1b.1 of Raymond et al., 2023). The resulting number of older brothers (r_m - *1*) and older sisters (r_f - *1*) were added, and their birth order was randomly assigned before calculating *imr* levels, and sexual orientation, as above.

In models that incorporate the effect of miscarriage, siblings were assumed to be subject to a miscarriage with probability *fm* (ranging from 0 to 0.7) affecting both male and female embryos (*fm,* or frequency of miscarriage, represents the probability of miscarriage for each pregnancy). Each miscarried older sib increased the level of *imr* by $b(1-\alpha)$ for a boy (no change for miscarried girls), where $\alpha \in [0,1]$.

Statistical analysis of simulated data

The birth order effect, i.e. the increase in the probability p of displaying a same-sex orientation with the number of older siblings was modelled as $p = f(X)$ where X is the number of older brothers (for modelling FBOE), or the number of older sisters (for modelling SBOE). The function f was inferred from modelling (a logistic function for FBOE, see below) or, when such inference was not possible (for SBOE), various continuous forms of the function f were considered, notably logistic, logistic with a polynomial effect, saturating exponential, or geometric (Table S1). These functions describing the SBOE effect were compared by fitting models to the simulated data using MCMC, then comparing the various SBOE functions using WAIC (Watanabe-Akaike Information Criterion), a generalized version of AIC onto singular statistical models, see Gelman et al. (2014) and Watanabe (2013; de Valpine et al., 2020): the mean of ten independent chains was used, each with a length of 50,000 samples and a burn-in phase of 20,000. To avoid the effects of small sample sizes for the number of older sisters, we restricted the data to categories of birth rank including at least 50 individuals.

The presence of an SBOE was assessed using two different approaches for controlling for a FBOE. First, a generalized linear model with the sexual orientation as the response variable, the number of older sisters (*os*, quantitative) as the variable of interest, and the number of older brothers (*ob,* quantitative), and the number of sibs (*sib*, quantitative) as control variables, as in (Blanchard et al. 2025). Second, by considering only individuals with a specific male birth rank (here male birth rank = 1, i.e. $ob = 0$) and performing a generalized linear model with the sexual orientation as a response variable, and *os* and *sib* as independent variables. In both cases, the significance of the variable of interest (*os*) was calculated by removing it and comparing the resulting variation in deviance using the $\chi 2$ test, as done by the function Anova from the R package *car* (Fox & Weisberg, 2019). The frequency of significant SBOE was calculated on the results of at least 400 independent samples. Significant *P*-values indicative of a SBOE corresponded to cases where more older sisters were associated with a same-sex orientation, relatively to heterosexual men (i.e., a positive slope estimate of the variable of interest), so the expected false discovery rate was 2.5% (one-sided test).

Estimating the miscarriage frequency from simulated data

To estimate the miscarriage frequency from the observed SBOE, a population sample was generated with a specific frequency of miscarriage *fm*, a mean observed fertility $\lambda_{obs} = 3$ (thus a real mean fecundity of $\lambda_{obs}/(1- fm)$), and composed of the same number of androphilic or gynephilic men, with the total size (androphilic plus gynephilic) being $N_{obs} = 2{,}400$. The effect of the number of older sisters (*os*) on sexual orientation was tested with a logistic regression, with the number of older brothers and the number of sibs as independent variables, and the estimated slope associated with *os* (*slope_obs*) was used to estimate *fm*. This was done using *fm_estim(freq_mis)*, a function with a parametric value of frequency of miscarriage *freq_mis*, generating a population sample with the same observed fertility as in the sample, the same proportion of androphilic or gynephilic men, with a total size of $n.N_{obs}$ (with $n = 20$, n being an amplification parameter reducing the variance of the estimates; lower values of n, including $n = 1$, provided quantitatively similar mean estimates), and returning the absolute difference between the calculated slope of SBOE and *slope_obs*. The value of *freq_mis* generating the minimum of the function was calculated using *optimize()* from the stats R package. This process was replicated at least 200 times for each *fm* value, for *fm* value from 0.1 to 0.7.

Empirical individual family data

Sampling in French Polynesia was conducted in January and October 2023, and May 2024, using a snowball sampling approach. Participants were recruited in public areas (e.g., markets, malls, parks) and private locations (e.g., hotels, shops) on the islands of Tahiti, Moorea, and Bora-Bora. Prior to participation, each individual received a document outlining the study's purpose and the contact details of the principal investigator (M.R.). This document explicitly states that personal data will only be used for research purposes and that only global results –not individual data– will be published. Written informed consent was obtained from all participants. This project was approved by the ethical committee of the University of Montpellier (n°UM 2023-008bis), and protocols used to recruit individuals and to collect data were approved by the French National Committee of Information and Liberty (CNIL) through the CNRS (approval #1226659). Each participant was interviewed confidentially and anonymously at a convenient location near the point of contact. They were asked to report their sex assigned at birth (male or female), gender identity (male, female, or third gender such as Rae rae or Mahu), date of birth, self-declared sexual orientation (attraction to males, females, both, or other), and the island or country of birth of their four grandparents. Individuals under the age of 18 (the legal age of majority in France) were excluded from the study. Individuals below 18 years of age (legal age of majority in France) were not considered. To reduce cultural heterogeneity, individuals with three or more grandparent(s) born outside Polynesia were not further considered. Individuals from multiple births, or with brothers of sisters from multiple births, were also not considered. In each sibship, full-sibs or half-sibs with the same mother as the focal individual were kept. Usable data were obtained from *N* = 380 men of mean age (M +/-SEM) = 34.8 +/- 0.60, including *N* = 149 androphilic (mean age = 31.6 +/-0.78, mean date of birth = 1992.2), and *N* = 231 gynephilic (mean age = 37.0 +/- 0.82, mean date of birth = 1986.8). Seven other individual available datasets were also considered: 1) the Indonesian sample used in Nila et al. (2019), and fully described in Nila et al. (2018), and restricted to men with either a homosexual or heterosexual orientation (thus removing the “Bisexuals” category) 3) the French sample described in Raymond et al. (2023), restricted to men with either a homosexual or heterosexual orientation (thus removing the “Bisexuals” category), 4) the Canadian sample from Blanchard and Bogaert (1996), 5) the Samoa sample from Semenyna et al. (2023), 6) The Greek sample described by Apostolou (2020b), restricted to men with either a homosexual or heterosexual orientation (thus removing “Bisexuals” and "Heterosexual with same-sex attractions"), 7) the Czech sample from Fořt et al. (2024b), restricted to men, and used without imputing missing values, and 8) the Iranian sample from Sadr-Bazzaz and Vasey (2025), restricted to individuals whose sex assigned at birth was male (thus including transgender males), and whose sexual orientation was either androphilic or gynephilic (thus removing the ambiphilic category). The basic sibship data for these eight datasets are detailed in Table S3.

Statistical analysis of empirical individual family data

The presence of an FBOE and SBOE in the population samples was assessed using an ABZ regression (Zdaniuk et al., 2025; Blanchard et al., 2025), a generalized linear model with the sexual orientation as the response variables, the number of older sisters (*os*, quantitative), the number of older brothers (*ob*, quantitative), and the number of sibs (*sib*, quantitative) as independent variables. When the slope of *os* (*slope_os*) was positive (corresponding to a SBOE), the amount of miscarriage (*fm*) required to generate it was estimated using the following procedure, for each population sample *i*. First, the demographic parameters potentially influencing the correlation between *ob* and *os*, i.e. the mean and variance of the observed fertility, were calculated: the mean fertility λ_i was estimated from the heterosexual sample only (as the mean fertility observed in samples of same-sex males is slightly inflated when there is a FBOE due to their higher mean birth rank), using the mean number of brothers and sisters, see Raymond et al. (2023) for details; the variance in fertility was modelled as λ_i/v_i, with v_i measuring over- or under-dispersion relatively to a Poisson distribution ($v_i < 1$, or $v_i > 1$, respectively), and v_i was estimated using the COMPoissonReg R package (Sellers & Shmueli, 2010). Second, fm_i was estimated using *fm_estim2(freq_mis)*, a function with a parametric value of frequency of miscarriage *freq_mis*, generating a population sample with the same parameters λ_i, and v_i, the same proportion of androphilic and gynephilic men as observed in population sample *i*, with a total size of $n.N_{\text{obs}}$, (with $n = 50$, n being an amplification parameter reducing the variance of the estimates; lower values of n, including $n = 1$, provided quantitatively similar mean estimates, see Fig. S4) and calculating the slope of *os* from an ABZ regression, and returning the absolute difference between this calculated slope and $slope\_os_i$. The value of *freq_mis* generating the minimum of the function was calculated using *optimize()* from the stats R package. This process was replicated at least 200 times, and the mean of the replicates was used as the estimated fm_i.

All analyses were run in R version 4.5.2 (R Core Team, 2025)

Results

Modelling the FBOE generated by MIH

Let's consider an initial immunological maternal response level of x_0. We assume that, under MIH, only sons increase the level of *imr* (*i.e.,* increase the specific immune response), with each son increasing this *imr* by a quantity *b*, with $b > 0$ (Fig. 1). The level of *imr* is $x_1 = x_0 + b$ for a firstborn male. Successive brothers have an additive effect on the amount of *imr*: $x_n = x_0 + b.n$, or $x_n = x_0 + b + b.ob$, where *n* is the male birth rank and *ob* the number of older brothers ($ob = n - 1$). The probability of a same-sex orientation as a function of the number of older brothers is given by $p_n = f(x_n)$, where *f* is a logistic function with a positive slope (so that p_n increases as x_n increases, see Fig. 1).

Simulations were conducted by varying two key parameters: *b* (the additional immune response triggered by a male gestation) and the slope of the logistic curve (which determines the probability of a same-sex orientation based on the immune response level). This generated a FBOE described by a logistic regression: when the effect on the immune response of each older brother was relatively large (e.g., $b > 2$), the proportion of androphilic men p_n reached a plateau at $p_n \approx 1$ for three or four older brothers. For relatively smaller effects of each older brother (e.g., $b < 2$), p_n displayed a continuous and sigmoid increase over the common range of 0-4 older brothers (Fig. 2A). The same effect was observed when *slope* varied (i.e. the slope of the logistic function determining sexual orientation from the level of the immunological response), with higher values decreasing the proportion of androphilia in individuals with a low number of older brothers and increasing those with higher numbers of older brothers (Fig. 2B).

Spurious SBOE

In addition to a FBOE, a SBOE was apparent when analysing simulated data under the MIH (Fig 3). The theoretical shape of this spurious SBOE was not readily identifiable; various functions (Table S1) describing the variation of probability of a same-sex orientation according to the number of older sisters were thus compared using WAIC. This SBOE was best described by a saturating exponential with 2 or 3 parameters, particularly when the shape of the curve can be estimated over a large range of number of older sisters (e.g., up to 6 older sisters). When a more restricted range of number of older sisters are available (for example when having a limited sample size from a population with a low mean fertility), a larger number of possible functions could describe this SBOE, including a logistic function (Table S2).

This SBOE is necessarily spurious as, under our simulation of the MIH, older sisters have no influence on the sexual orientation of their younger brothers since they have no direct effect on the maternal immune response. When data were generated without a correlation between the number of older brother and older sisters (by generating independently the number of older brothers and older sisters), the FBOE was not significantly affected: the slope decreased from 0.986 (linear unit) to 0.981, and this change was not significant (X^2 = 1.6 10^{-3}, df = 1, P = 0.968). However, the SBOE became not significantly different from a line of slope = 0 (X^2 = 0.26, df = 1, P = 0.61), suggesting that this spurious SBOE is the result of the correlation between the number of older brothers and older sisters (Fig. 3). Indeed, when this correlation is taken into account in a logistic regression, i.e., when *ob* is introduced as a control variable, the proportion of significant SBOE was not different from the false rejection rate of 2.5%, for all sample sizes (Binomial test, P = 0.074, 0.074, and 0.333, for sample sizes N = 600, 1,200, and 2,400, respectively).

However, when miscarriage was present and increased in frequency, the rate of false rejection increased, and became significantly above the false rejection rate of 2.5 % (Binomial test, $P < 10^{-4}$) from a miscarriage rate of 15%, 10%, or 5%, for respectively sample sizes N = 600, 1,200, and 2,400 (Fig. 4A). This increase of false rejection rate was more pronounced for higher sample size values. To better understand this result, three additional analyses were performed. 1) The logistic regression was performed on a restricted data containing only the firstborn among the males (i.e., $ob = 0$, and $os \geq 0$), and with only the number of sibs as a control variable: the results were similar but less pronounced (Fig. 4B). 2) Samples were generated without a correlation between the number of older brothers and the number of older sisters, and in presence of miscarriage: the rate of false rejection was not different from 2.5%, for all sample sizes (across all miscarriage frequencies, Fisher's method, $P = 0.930$, 0.852, or 0.946, for N = 600, 1,200, or 2,400, respectively). 3) When the number of older brothers was replaced, in the regression, by the initial number of older brothers (before miscarriage), the proportion of significant SBOE was not different from the false rejection rate of 2.5%, for all sample sizes (across all miscarriage frequencies, Fisher's method, $P = 0.118$, 0.166, or 0.927, for N = 600, 1,200, or 2,400, respectively).

In presence of miscarriage, the slope of the regression corresponding to SBOE was used to estimate the frequency of miscarriage *fm*. Negative slopes were not considered. The mean estimated values of *fm* were linearly related to the true *fm* values (Fig. S1), with the slope of the regression line (slope = 0.88, SEM = 0.052) marginally not significantly different from 1 ($t = -2.338$, $P = 0.067$). When the point corresponding to $fm = 0.1$ was omitted, the slope was not significantly different from 1 ($t = -1.632$, $P = 0.178$) and was closer to 1 (slope = 0.96, SEM = 0.022), suggesting that *fm* is slightly overestimated for low values of *fm*, probably due to the impossibility to estimate *fm* when the observed SBOE slope is negative.

Firstborn androphilic men and miscarriage

On simulated data, the percentage of firstborn male individuals displaying same-sex orientation (including only-children) was not constant when the frequency of miscarriage increased. For a given mean fecundity λ, increasing the frequency of miscarriage *fm*, thus with a decreasing observed mean fertility λ(1-*fm)*, increased the frequency of male same-sex orientation among firstborn individuals (Fig. S2, A). For the given observed mean fertility λ, increasing the frequency of miscarriage *fm*, thus with an increasing mean fecundity λ/(1-*fm)*, significantly decreased ($\beta = -0.028$, $F_{1,7} = 8.95$, $P = 0.020$) the frequency of male same-sex orientation among firstborn individuals (Fig. S2, B).

In the absence of miscarriage, the prevalence of male same-sex orientation in only-children and firstborn of larger sibship was not statistically different (Fisher exact test on 2x2 contingency table, $P = 0.323$). When the frequency of miscarriage increased, the prevalence of male same-sex orientation became significantly higher in only-children relatively to firstborn of larger sibship (10% miscarriage: $P = 0.034$; 20% miscarriage or above: $P < 10^{-10}$). This effect was observed for a large range of lambda values, except when lambda was very low (Fig. 5).

Empirical population data

For the various empirical population datasets, the correlation between *ob* and *os* ($\tau_{ob\text{-}os}$) varied from 0.007 to 0.385, with an overall mean of 0.295, significantly different from zero ($z = 24.9$, $P < 10^{-10}$). All sample values were significantly higher than 0, except the French dataset (Table S3). The variability of $\tau_{ob\text{-}os}$ values was well explained by the mean fecundity λ and the under/over-dispersion v parameter: a linear regression model using λ and v to predict $\tau_{ob\ os}$ explained 95.7% of the deviance, and the higher the mean fertility (higher λ), and the more over-dispersed the fertility distribution (lower v), the higher the value of $\tau_{ob\text{-}os}$ (mean fertility λ: $\beta = 0.059$, SEM = 0.013, $X^2 = 21.7$, $df = 1$, $P = 3.2{\times}10^{-6}$; under/over-dispersion v parameter: $\beta = -0.127$, SEM = 0.039, $X^2 = 10.6$, $df = 1$, $P = 1.1{\times}10^{-3}$).

Overall, the number of older sisters (*os*) had a significant effect on the sexual orientation, when the number of older brothers, and the sib size, were statistically controlled for ($X^2 = 32.1$, $df = 1$, $P = 1.5{\times}10^{-8}$), Table 1. With the full model incorporating also intercept and slope variation across populations (i.e. *pop* and *pop:os*), *os* was significant ($X^2 = 19.5$, $df = 1$, $P < 1.02{\times}10^{-5}$), as well as the intercept *pop* ($X^2 = 309.9$, $df = 7$, $P < 10^{-10}$) reflecting different frequencies of androphilic men across the dataset, and the interaction *os:pop* ($X^2 = 14.1$, $df = 7$, $P = 0.049$), marginally suggesting distinct slopes for *os* across the datasets. To remove directly the correlation between older brothers and older sisters, data were restricted to individuals with a fixed number of older brothers, the largest category being individuals without older brothers (*ob* = 0). The number of older sisters still had a significant effect on the sexual orientation ($X^2 = 11.8$, $df = 1$, $P = 5.9{\times}10^{-4}$). The slope of *os* was statistically not different across the datasets (interaction *os:data* : $X^2 = 5.75$, $df = 7$, $P = 0.569$).

Seven population samples displayed a positive slope associated to *os*, indicating either a spurious SBOE resulting from miscarriage, or (non-exclusively) a true SBOE resulting from a distinct mechanism than MIH. Assuming the absence of the latter, the miscarriage frequency *fm* required to explain the apparent SBOE was estimated, except when slopes were low (Indonesia, slope = 0.015), in order to avoid overestimation for *fm* (Fig. S1). The resulting *fm* estimates (Table 1) were between 0.367 (SEM = 0.001) for the Canada sample, and 0.573 (SEM = 0.002) for the Czech sample, displaying unimodal distributions (Fig. 6), with a decreased variance when the amplification parameter *n* increased (Fig. S3).

In all population samples, the frequency of same-sex orientation was higher in only-children than in firstborn with younger siblings, except the Indonesian sample displaying a low number of only-children (N = 4). This difference was significant (Fisher's test on 2×2 contingency table, onetailed, $P < 0.05$) for three population samples, and marginally non-significant ($0.05 < P < 0.10$) for two population samples (Table S4). Over all population samples, the frequency of same-sex orientation was higher in only-children ($f_H = 0.459$) than in firstborn with younger siblings ($f_H = 0.363$), the difference being significant (combined P-values using Fisher's method: $P = 0.002$). This difference suggests an impact of miscarriage.

Discussion

The aim was to evaluate if the various birth order effects other than the FBOE can be accounted for by the MIH, or if additional mechanisms are to be considered. To that aim, we modelled the MIH and derived explicit functions for the FBOE and SBOE to identify their predicted shapes, and we showed that the spurious SBOE does not manifest when data are generated without the correlation between older brothers and older sisters, or when this correlation is controlled for in statistical analyses. However, in the presence of miscarriage, the statistical control of this correlation is insufficient and a significant spurious SBOE is apparent in a regression, with or without restricting the data to a specific birth order. Additionally, and counter-intuitively, miscarriage increases the prevalence of male same-sex orientation in only-children compared to firstborn of larger sibships. Analysing empirical data from different populations data showed the presence of a significant SBOE, and an overall higher frequency of same-sex orientation in only-children relatively to firstborn of larger sibships, compatible with the effect of miscarriage. However, the estimated level of miscarriage required to explain the SBOE observed in real population data seems relatively high compared to the published rates of miscarriage, suggesting that some parameters were not taken into account, or that additional hypotheses, beyond the MIH, are required to explain these observations.

The classical Maternal Immune Hypothesis was initially proposed to account for the observation that the presence of older brothers increases the odds of same-sex orientation, while the presence of older sisters or younger sibs does not (Blanchard & Bogaert, 1996). Under this hypothesis, older brothers have a cumulative influence on the neuro-development of their younger brothers through long-lasting effects on the immune system of their mother as it reacts to specific male antigens. This "older brothers effect" has long been suspected to generate an apparent older sister effect, due to the correlation between the number of older brothers and the number of older sisters in population data (Blanchard, 1997). It is surprising to note that, to our knowledge, this correlation has never been reported in the ca. 3 decades of studies addressing the FBOE or SBOE.

Here, we could verify that the number of older brothers and older sisters are positively correlated by simulating virtual population samples with fertility values similar to those of human population and assuming a balanced sex-ratio at birth; we also found this correlation in most empirical human population samples analysed. In spite of this correlation, for a given number of older sibs, the numbers of older sisters and older brothers are negatively correlated (more older brothers means fewer older sisters). The variance in sibship size generates a variance in number of older sibs, with a resulting positive correlation between *ob* and *os*, this correlation increasing with the mean fertility (and thus the variance), and also with the overdispersion of the variance relatively to a Poisson distribution. Any spurious SBOE due to a correlation with FBOE can thus be expected to be stronger when the fertility of the population is larger.

Several solutions can be employed in analysis of empirical population data to protect from the correlation between *ob* and *os* and examine the SBOE independently of the effects of older brothers. The first one is to evaluate the SBOE while controlling for the number of older brothers, thus statistically controlling for the correlation between older brothers and older sisters, as suggested by e.g., Blanchard (1997). Another option is to restrict the data to a specific male birth rank, which allows also to control for the correlation (Blanchard & Lippa, 2021). The first report of an SBOE, despite such a control, was published in 2005 (King et al., 2005). Since then, various studies from distinct populations reported also a significant SBOE while controlling for SBOE (e.g., Vasey & VanderLaan, 2007; VanderLaan & Vasey, 2011; Blanchard & Lippa, 2021; Ablaza et al., 2022; Kabátek & Blanchard, 2024; Sadr-Bazzaz & Vasey, 2025). To reconcile this apparently genuine SBOE with the MIH, it has been proposed that miscarried male foetuses, contributing to the building up of maternal antibodies and thus to FBOE, were not properly taken into account and thus that the resulting significant SBOE, controlling for the born older brothers, was still spurious.

To examine this hypothesis, we simulated data with various frequencies of miscarriage and confirmed that miscarriage can generate a spurious SBOE in a regression model when the number of older brothers is controlled for. Interestingly, this spurious SBOE vanishes if the total number of older brothers (miscarried or not) are used, instead of the live-born ones, in the regression, or if the data are generated without a correlation between the number of older brothers and older sisters. This suggests that removing randomly sibs, including older sibs, affects the correlation between older brothers and older sisters, rendering the use of the live-born older brothers as a control variable insufficient to control for the spurious SBOE. Similarly, restricting the dataset to a specific male birth rank (and considering only live-born sibs) is also insufficient to control for the spurious SBOE. This phenomenon would apply to population samples if miscarriage were present, suggesting that when a significant SBOE is observed, it is not possible to disentangle the effect of miscarriage from a putative real SBOE, even when male birth rank is controlled for.

In simulated data, the percentage of androphilic men among the firstborn (including only-children) did not vary clearly with the miscarriage rate (Fig. S2). The theoretical sample frequency of firstborn individuals ($f_i = (1 - e^{-\lambda}) / \lambda$, see Raymond *et al.* 2023) decreases when the mean fertility λ increases, and this f_i frequency increases when the miscarriage rate increases, for a given λ, due to the subsequent reduction of older sibs. However, the frequency of androphilic men among the firstborn individuals is more difficult to predict, and generated data show that it varies with λ, the miscarriage rate, and the interaction between both.

In simulated data, in the absence of miscarriage, the frequency of androphilic men is the same in only-children and in firstborn of larger sibships. This is because, at least in simulated data, latter events such as the occurrence of younger sibs have no effect on the sexual orientation of the firstborn. This equality is true despite the fact that these two categories have different sampling probabilities (only-children: $e^{-\lambda}$; firstborn of larger sibship: $f_i - e^{-\lambda}$), because the frequency of androphilic men is calculated within each category. However, in presence of miscarriage, the frequency of androphilic men is higher in only-children than in firstborn of larger sibship. To understand this counter-intuitive phenomenon, let's consider a situation with two simplified categories: the category “only-children” being composed of real only-children (no sibs miscarried, represented as O), plus children with one older miscarried brother (represented as .O), and the category “firstborn with one younger sib” being composed of real firstborn children with one younger sib (Oo), plus children with an older miscarried brother and one younger sib (.Oo). The frequency of androphilic men is the same in the O and Oo categories, as well as in the .O and .Oo categories. However, the frequency of androphilic men is different in O and .O categories (and in Oo and .Oo), because a miscarried brother, under the MIH, contributes to increase the maternal immune response. Importantly, the sampling probabilities of O and .O are different because their population frequencies are not the same, and similarly the sampling probabilities of Oo and .Oo are different, resulting in different frequency of androphilic men in the O + .O category, compared to the Oo + .Oo category. This reasoning extends to less simplified situation, where the categories “only-children” and “firstborn of larger sibships” are in fact composed of many subcategories having different sampling frequencies. In conclusion, miscarriage generates a difference in the frequency of androphilic men in only-children, compared to firstborn of larger sibships. In real population samples, the frequency of androphilic men in only-children was overall higher than in firstborn of larger sibship (0.45 vs 0.36, respectively, Table S4). This suggests the presence of substantial miscarriage, unless other unknown mechanisms are shown to also generate this phenomenon.

In human populations, miscarriage frequency is around 10-20% (e.g., Buss et al., 2006; Blohm et al., 2008; Strumpf et al., 2021), although values around 30% have been reported when finely measured with sensitive methods (e.g., Wilcox et al., 1988; Ellish et al., 1996), or much higher for women over 40-year-old (Andersen et al. 2000; Magnus et al. 2019). The values estimated here to account of the observed SBOE (between 37% and 57%, Table 1) seem higher than the usually reported miscarriage frequency. For example, miscarriage frequency is reported to be around 19% in Iran (Hojati et al., 2025), and around 11% in Canada (Strumpf et al., 2021), although the miscarriage frequency explaining the SBOE is ~57% and ~37% for respectively, the Iranian and Canadian samples. Moreover, when considering male embryos, the estimated miscarriage frequencies triggering a maternal immune response against male-specific antigens exclude early miscarriages occurring before the expression of these antigens. These findings suggest that miscarriage rates, even at their highest realistic estimates, may be insufficient to fully explain the observed SBOE if only a spurious effect is assumed. In other words, mechanisms beyond those proposed by the original maternal immune hypothesis (MIH) may be at play, potentially generating a non-spurious SBOE.

It has been previously suggested an extension of the classical MIH, by considering that the maternal immune response could be triggered primarily by autosomal antigens rather than by specific male antigens, thus female pregnancies contributing also to the maternal immune response, and generating a true SBOE along the FBOE (Kabátek & Blanchard, 2024). However, this hypothesis does not explain why such non-spurious SBOE is not apparent in most studies, particularly those showing a FBOE from populations displaying a low maternal fertility, thus a low spurious SBOE.

However, it is possible that other mechanisms outside the explanatory field of the MIH are operating, and they remain to be identified and evaluated.

This study has several limitations, although none fundamentally undermine our results. First, only eight population samples were analysed, covering a limited portion of the global geographic diversity. This restricts the generality of the conclusions drawn from the empirical data. Second, some populations had relatively small sample sizes, which may limit the robustness of certain inferences. However, while individual sample values were reported, the primary results are derived from overall analyses across all samples, thereby mitigating the influence of any single sample. Third, our model assumed that miscarriage affects male and female embryos equally, despite possible evidence that male embryos are more susceptible (Ellis & Blanchard, 2001, but see Del Fabro et al., 2011). Nevertheless, even under an extreme scenario where only male embryos were affected by miscarriage, the results remained qualitatively unchanged (data not shown). This suggests that incorporating more realistic differential miscarriage parameters would not alter our conclusions. Finally, the MIH was modelled using four independent parameters: *b*, *slope*, *imr_sd*, and α. Variations in *b* and *slope* were considered, while variations in *imr_sd* could account for the importance of variance in the initial immune response among mothers, and variations in α could reflect the effect of miscarriage on the maternal immune response, respectively. Additionally, not all parameter combinations were explored in the simulations. Therefore, it remains possible that further phenomena could emerge under different parameter sets or alternative parametrizations of the MIH.

In conclusion, the presence of a FBOE induces a spurious SBOE, driven by the inherent correlation between the number of older brothers and older sisters in population samples. This phenomenon holds true regardless of the underlying mechanism generating the FBOE, including the Maternal Immune Hypothesis (MIH). To mitigate this bias, statistical control for male birth rank, or restricting analyses to a specific birth rank, effectively reduces the occurrence of significant spurious SBOEs to levels consistent with the expected type-I error rate. However, in the presence of miscarriages, the frequency of significant spurious SBOEs may far exceed this baseline. Another consequence of miscarriages is the elevated proportion of androphilic men among only-children, relative to firstborns in larger sibships. Analyses of real-world population data reveal two key findings: first, a significant SBOE persists even after controlling for the FBOE; second, the higher frequency of androphilic men among only-children, compared to firstborns in larger families, strongly suggests a substantial role for miscarriages. Yet, quantitative estimates of the miscarriage rates required to account for the observed SBOE appear unrealistically high, suggesting either that additional mechanisms are generating a spurious SBOE, or that a non-spurious SBOE is also present. Should the presence of a genuine SBOE be confirmed, its proximal mechanism remains unidentified, presenting a critical avenue for future research.

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Declaration of AI use

During the preparation of this work, the authors used Emmy in order to improve grammar and style. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

References

Ablaza C, Kabátek J, Perales F (2022) Are sibship characteristics predictive of same sex marriage? An examination of fraternal birth order and female fecundity effects in population-level administrative data from the Netherlands. *Journal of Sex Research*, **59**, 671–683. https://doi.org/10.1080/00224499.2021.1974330

Andersen A-MN, Wohlfahrt J, Christens P, Olsen J, Melbye M (2000) Maternal age and fetal loss: population based register linkage study. *General practice*, **320**.

Apostolou M (2020a) *The evolution of same-sex attraction*. Springer, Switzerland.

Apostolou M (2020b) Does fraternal birth order predict male homosexuality, bisexuality, and heterosexual orientation with same-sex attraction? Evidence from a greek-speaking sample from Greece. *Archives of Sexual Behavior*, **49**, 575–579. https://doi.org/10.1007/s10508-019-01466-3

Bailey JM, Dunne MP, Martin NG (2000) Genetic and environmental influences on sexual orientation and its correlates in an Australian twin sample. *Journal of Personality and Social Psychology*, **78**, 524–536. https://doi.org/10.1037/0022-3514.78.3.524

Berman LA (2003) *The puzzle: exploring the evolutionary puzzle of male homosexuality*. Godot press, Wilmette, Illinois.

Bianchi DW, Farina A, Weber W, Delli-Bovi LC, DeRiso M, Williams JM, Klinger KW (2001) Significant fetal-maternal hemorrhage after termination of pregnancy: Implications for development of fetal cell microchimerism. *Am J Obstet Gynecol*.

Blanchard R (1997) Birth order and sibling sex ratio in homosexual versus heterosexual males and females. *Annual review of sex research*, **8**, 27–67.

Blanchard R (2012) Fertility in the mothers of firstborn homosexual and heterosexual men. *Archives of Sexual Behavior*, **41**, 551–556. https://doi.org/10.1007/s10508-011-9888-0

Blanchard R (2018a) Fraternal birth order, family size, and male homosexuality: meta-analysis of studies spanning 25 years. *Archives of Sexual Behavior*, **47**, 1–15. https://doi.org/10.1007/s10508-017-1007-4

Blanchard R (2018b) Response to commentaries: meta-analysis of probability samples and other new evidence. *Archives of Sexual Behavior*, **47**, 49–57. https://doi.org/10.1007/s10508-017-1134-y

Blanchard R (2022) A novel method for studying the effect of older brothers on sexual orientation and its robustness to stopping rule distortions. *The Journal of Sex Research*, **0**, 1–6. https://doi.org/10.1080/00224499.2021.1984379

Blanchard R, Beier KM, Gómez Jiménez FR, Grundmann D, Krupp J, Semenyna SW, Vasey PL (2021) Meta-analyses of fraternal and sororal birth order effects in homosexual pedophiles, hebephiles, and teleiophiles. *Archives of Sexual Behavior*, **50**, 779–796. https://doi.org/10.1007/s10508-020-01819-3

Blanchard R, Bogaert AF (1996) Homosexuality in men and number of older brothers. *American Journal of Psychiatry*, **153**, 27–31.

Blanchard R, Bogaert AF (2004) Proportion of homosexual men who owe their sexual orientation to fraternal birth order: An estimate based on two national probability samples. *American Journal of Human Biology*, **16**, 151–157.

Blanchard R, Cantor JM, Bogaert AF, Breedlove M, Ellis L (2001) Fraternal birth order and the maternal immune hypothesis of male homosexuality. *Hormones and Behavior*, **40**, 105–114.

Blanchard R, Ellis L (2001) Birth weight, sexual orientation and the sex of the preceding siblings. *Journal of Biosocial Science*, **33**, 451–467. https://doi.org/10.1017/S0021932001004515

Blanchard R, Kabátek J, Zdaniuk B (2025) A current approach to logistic regression analysis of birth order and sexual orientation. *Archives of Sexual Behavior*, 1–10. https://doi.org/10.1007/s10508-025-03275-3

Blanchard R, Lippa RA (2007) Birth order, sibling sex ratio, handedness, and sexual orientation of male and female participants in a BBC internet research project. *Archives of Sexual Behavior*, **36**, 163–176. https://doi.org/10.1007/s10508-006-9159-7

Blanchard R, Lippa RA (2021) Reassessing the effect of older sisters on sexual orientation in men. *Archives of Sexual Behavior*, **50**, 797–805. https://doi.org/10.1007/s10508-020-01840-6

Blohm F, Fridén B, Milsom I (2008) A prospective longitudinal population-based study of clinical miscarriage in an urban Swedish population. *BJOG: An International Journal of Obstetrics & Gynaecology*, **115**, 176–183. https://doi.org/10.1111/j.1471-0528.2007.01426.x

Bogaert AF (2003) The interaction of fraternal birth order and body size in male sexual orientation. *Behavioral Neuroscience*, **117**, 381–384. https://doi.org/10.1037/0735-7044.117.2.381

Bogaert AF (2006) Biological versus nonbiological older brothers and men's sexual orientation. *Proceedings of the National Academy of Sciences*, **103**, 10771–10774. https://doi.org/10.1073/pnas.0511152103

Bogaert AF, Liu J (2006) Birth order and sexual orientation in men: evidence for two independent interactions. *Journal of Biosocial Science*, **38**, 811–819. https://doi.org/10.1017/S0021932005001033

Bogaert AF, Skorska M (2011) Sexual orientation, fraternal birth order, and the maternal immune hypothesis: A review. *Frontiers in Neuroendocrinology*, **32**, 247–254.

Bogaert AF, Skorska MN, Wang C, Gabrie J, MacNeil AJ, Hoffarth MR, VanderLaan DP, Zucker KJ, Blanchard R (2018) Male homosexuality and maternal immune responsivity to the Y-linked protein NLGN4Y. *Proceedings of the National Academy of Sciences*, **115**, 302–306. https://doi.org/10.1073/pnas.1705895114

Buss L, Tolstrup J, Munk C, Bergholt T, Ottesen B, Grønb M, Kjaer SK (2006) Spontaneous abortion: A prospective cohort study of younger women from the general population in Denmark. Validation, occurrence and risk determinants. *Acta Obstetricia et Gynecologica*, **85**, 467–475.

Del Fabro A, Driul L, Anis O, Londero AP, Bertozzi S, Bortotto L, Marchesoni D (2011) Fetal gender ratio in recurrent miscarriages. *International Journal of Women's Health*, **3**, 213–217. https://doi.org/10.2147/IJWH.S20557

Ellis L, Blanchard R (2001) Birth order, sibling sex ratio, and maternal miscarriages in homosexual and heterosexual men and women. *Personality and Individual Differences*, **30**, 543–552. https://doi.org/10.1016/S0191-8869(00)00051-9

Ellish NJ, Saboda K, O'Connor J, Nasca PC, Stanek EJ, Boyle C (1996) A prospective study of early pregnancy loss. *Human Reproduction*, **11**, 406–412. https://doi.org/10.1093/HUMREP/11.2.406

Fořt J, Flegr J, Kuba R, Kaňková Š (2024a) Fertility of Czech gay and straight men, women, and their relatives: testing the sexually antagonistic gene hypothesis. *Archives of Sexual Behavior*. https://doi.org/10.1007/s10508-024-02827-3

Fořt J, Kunc B, Valentova JV, Bártová K, Hudáčová K (2024b) Examining the fraternal birth order effect and sexual orientation: insights from an East European population. *Archives of Sexual Behavior*. https://doi.org/10.1007/s10508-024-02892-8

Fox J, Weisberg S (2019) *An R companion to applied regression*. Sage Publications, Thousand Oaks CA.

Gelman A, Hwang J, Vehtari A (2014) Understanding predictive information criteria for Bayesian models. *Statistics and Computing*, **24**, 997–1016. https://doi.org/10.1007/s11222-013-9416-2

Gómez Jiménez FR, Semenyna SW, Vasey PL (2020) The relationship between fraternal birth order and childhood sex-atypical behavior among the Istmo Zapotec *muxes*. *Developmental Psychobiology*, **62**, 792–803. https://doi.org/10.1002/dev.21987

Hojati M, Izadi S, Mansourian M (2025) Epidemiology of Spontaneous Abortion in Iran: A Comprehensive Analysis of Demographic, Socioeconomic, Fertility, Clinical Characteristics, and Lifestyle Factors. https://doi.org/10.21203/rs.3.rs-6461180/v1

Iemmola F, Camperio-Ciani A (2009) New evidence of genetic factors Influencing sexual orientation in men: female fecundity increase in the maternal line. *Archives of Sexual Behavior*, **38**, 393–399.

Kabátek J, Blanchard R (2024) Birth order and family size of UK Biobank subjects identified as asexual, cisexual, heterosexual, or homosexual according to self-reported sexual histories. *Archives of Sexual Behavior*. https://doi.org/10.1007/s10508-024-03004-2

Kangassalo K, Pölkki M, Rantala MJ (2011) Prenatal influences on sexual orientation: digit ratio (2D:4D) and number of older siblings. *Evolutionary Psychology*, **9**, 147470491100900402. https://doi.org/10.1177/147470491100900402

Khovanova T (2020) On the mathematics of fraternal birth order effect and the genetics of homosexuality. *Archives of Sexual Behavior*, **49**, 551–555. https://doi.org/doi.org/10.1016/j.jtbi.2004.04.021

King M, Green J, Osborn DPJ, Arkell J, Hetherton J, Pereira E (2005) Family size in white gay and heterosexual men. *Archives of Sexual Behavior,* **34**, 117–122. https://doi.org/10.1007/s10508-005-1006-8

Långström N, Rahman Q, Carlström E, Lichtenstein P (2010) Genetic and environmental effects on same-sex sexual behavior: A population study of twins in sweden. *Archives of Sexual Behavior,* **39**, 75–80.

Li G, Wong WI (2018) Single-sex schooling: friendships, dating, and sexual orientation. *Archives of Sexual Behavior*, **47**, 1025–1039. https://doi.org/10.1007/s10508-018-1187-6

Magnus MC, Wilcox AJ, Morken N-H, Weinberg CR, Håberg SE (2019) Role of maternal age and pregnancy history in risk of miscarriage: prospective register based study. *BMJ*, **364**, l869. https://doi.org/10.1136/bmj.l869

Nila S, Barthes J, Crochet P-A, Suryobroto B, Raymond M (2018) Kin selection and male homosexual preference in Indonesia. *Archives of Sexual Behavior*, **47**, 2455–2465. https://doi.org/10.1007/s10508-018-1202-y

Nila S, Crochet P-A, Barthes J, Rianti P, Juliandi B, Suryobroto B, Raymond M (2019) Male homosexual preference: femininity and the older brother effect in Indonesia. *Evolutionary Psychology*. https://doi.org/doi.org/10.1177/1474704919880701

R Core Team (2025) *R: A language and environment for statistical computing*. URL: https://www.R-project.org/.

Rahman Q, Xu Y, Lippa RA, Vasey PL (2020) Prevalence of sexual orientation across 28 nations and its association with gender equality, economic development, and individualism. *Archives of Sexual Behavior*, **49**, 595–606. https://doi.org/10.1007/s10508-019-01590-0

Raymond M, Turek D, Durand V, Nila S, Suryobroto B, Vadez J, Barthes J, Apostolou M, Crochet P-A (2023) Increased birth rank of homosexual males: disentangling the older brother effect and sexual antagonism hypothesis. *Peer Community Journal*, **3**, e22. https://doi.org/10.24072/pcjournal.247

Rieger G, Blanchard R, Schwartz G, Bailey JM, Sanders AR (2012) Further data concerning Blanchard’s (2011) ‘‘fertility in the mothers of firstborn homosexual and heterosexual men" [Letter to the Editor]. *Archives of Sexual Behavior*, **41**, 529–531.

Sadr-Bazzaz M, Vasey PL (2025) Birth order and sibling sex ratio predict same-sex sexual attraction in Iranian cisgender and transgender adult males and females. *Archives of Sexual Behavior*. https://doi.org/10.1007/s10508-025-03249-5

Sellers KF, Shmueli G (2010) A flexible regression model for count data. *The Annals of Applied Statistics*, **4**, 943–961.

Semenyna SW, Gómez Jiménez FR, VanderLaan DP, Vasey PL (2023) Male androphilia, fraternal birth order, and female fecundity in Samoa: A 10-y retrospective. *Proceedings of the National Academy of Sciences*, **120**, e2313284120. https://doi.org/10.1073/pnas.2313284120

Skorska MN, Blanchard R, VanderLaan DP, Zucker KJ, Bogaert AF (2017) Gay male only-children: evidence for low birth weight and high maternal miscarriage rates. *Archives of Sexual Behavior*, **46**, 205–215. https://doi.org/10.1007/s10508-016-0829-9

Skorska MN, Coome LA, Saokhieo P, Kaewthip O, Chariyalertsak S, VanderLaan DP (2020) Handedness and birth order among heterosexual men, gay men, and Sao Praphet Song in northern Thailand. *Archives of Sexual Behavior*, **49**, 2431–2448. https://doi.org/10.1007/s10508-020-01774-z

Staff PJ (1967) The displaced Poisson distribution. Region B. *Journal of the American Statistical Association*, **62**, 643–654. https://doi.org/10.2307/2283992

Strumpf E, Lang A, Austin N, Derksen SA, Bolton JM, Brownell MD, Chateau D, Gregory P, Heaman MI (2021) Prevalence and clinical, social, and health care predictors of miscarriage. *BMC Pregnancy and Childbirth*, **21**, 185. https://doi.org/10.1186/s12884-021-03682-z

Swift-Gallant A, Coome LA, Monks DA, VanderLaan DP (2018) Gender nonconformity and birth order in relation to anal sex role among gay men. *Archives of Sexual Behavior*, **47**, 1041–1052. https://doi.org/10.1007/s10508-017-0980-y

de Valpine P, Paciorek C, Turek D, Michaud N, Anderson-Bergman C, Obermeyer F, Wehrhahn C, Rodrìguez A, Temple Lang D, Zhang W, Paganin S, Hug J (2020) *Nimble: MCMC, particle filtering, and programmable hierarchical modeling* (version 0.10.1). URL: https://CRAN.R-project.org/package=nimble. Accessed 19 February 2021.

VanderLaan DP, Vasey PL (2011) Male sexual orientation in independent Samoa: Evidence for fraternal birth order and maternal fecundity effects. *Archives of Sexual Behavior*, **40**, 495–503.

Vasey PL, Parker JL, VanderLaan DP (2014) Comparative reproductive output of androphilic and gynephilic males in Samoa. *Arch Sex Behav*, 5.

Vasey PL, VanderLaan DP (2007) Birth order and male androphilia in Samoan fa’afafine. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1437–1442.

Watanabe S (2013) A widely applicable Bayesian information criterion. *Journal of Machine Learning Research*, **14**, 867–897.

Wilcox AJ, Weinberg CR, O’Connor JF, Baird DD, Schlatterer JP, Canfield RE, Armstrong EG, Nisula BC (1988) Incidence of early loss of pregnancy. *New England Journal of Medicine*, **319**, 189–194. https://doi.org/10.1056/NEJM198807283190401

Xu Y, Zheng Y (2017) Fraternal birth order, handedness, and sexual orientation in a Chinese population. *The Journal of Sex Research*, **54**, 10–18. https://doi.org/10.1080/00224499.2015.1104530

Zdaniuk B, Milani S, Makarenko B, Marriott N, Bogaert AF, Brotto LA (2025) Asexuality: its relationship to sibling sex composition and birth order. *Archives of Sexual Behavior*, **54**, 51–64. https://doi.org/10.1007/s10508-024-03043-9

Table 1. Slopes of the binomial ABZ regression from population data. The slope (β) of *ob* (for FBOE) and *os* (for SBOE) are given, with their corresponding SEM and *P*-value, for each sample. For positive slope of SBOE, the frequency *fm* of miscarriage required to generate the SBOE slope is given (distribution of *fm* in Fig. 6). 'All' refers to values generated when all population samples were pooled. Significant ($P < 0.05$) *P*-values are in bold.

	FBOE			SBOE			Miscarriage	
Sample	β	(SEM)	P-value	β	(SEM)	P-value	*fm*	(SEM)
Canada	0.324	(0.103)	**0.001**	0.134	(0.098)	0.172	0.367	(0.001)
Czech	0.405	(0.093)	**$<10^{-4}$**	0.195	(0.091)	**0.032**	0.573	(0.002)
France	0.390	(0.157)	**0.012**	0.163	(0.146)	0.261	0.466	(0.003)
Greece	0.364	(0.141)	**0.010**	0.213	(0.149)	0.156	0.579	(0.001)
Indonesia	0.164	(0.174)	0.336	0.015	(0.158)	0.926	-	-
Iran	0.303	(0.125)	**0.013**	0.263	(0.122)	**0.030**	0.572	(0.001)
Polynesia	0.200	(0.101)	**0.047**	-0.003	(0.107)	0.975	-	-
Samoa	0.177	(0.054)	**0.001**	0.182	(0.057)	**0.001**	0.409	(0.001)
All	0.263	(0.033)	**$<10^{-10}$**	0.189	(0.034)	**$<10^{-7}$**	0.480	(0.001)

Figure 1. Evolution of the maternal immunological response during successive pregnancies of a mother, under MIH. Initial immune response is set at an arbitrary value (-5) before the first pregnancy. The amount of immune response increase for each male child, and is associated to the probability of a same-sex orientation (P), according to a logistic curve (right panel). The sex of each successive child (M or F) is indicated. Parameter values: increase of the *Immune response* for each son is b = 1. The logistic curve of sexual orientation assignation has *slope* = 1 and is centred on *Immune response* = 0 (dotted line).

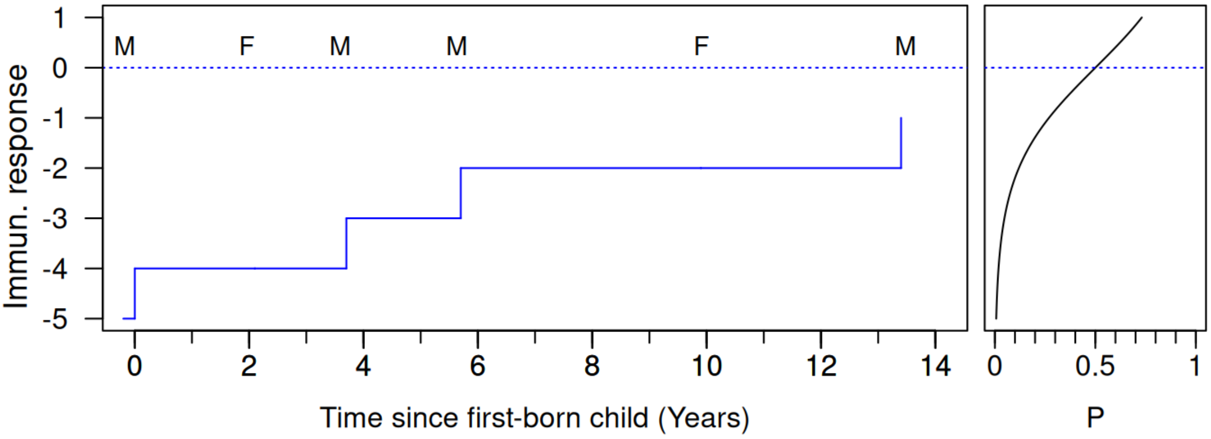

Figure 2. FBOE generated by the MIH. Simulating random population samples of gynephilic and androphilic men with a variable value of *b* (A), or *slope* (B), and computing the proportion of androphilic men for each number of older brothers. The increase of *imr* for each son is *b* = 1/4, 1, or 2, with *slope* = 1 (A), and the slope takes the values 0.5, 1, or 2, with *b* = 1 (B). The mean of 100 replicates, for each number of older brother, is depicted as a circle. Lines are the expected curve from a logistic regression. Absence of FBOE is indicated by a dotted line, corresponding to *b* = 0 (A), or *slope* = 0 (B), at the level (0.5) corresponding to the sample frequency of androphilic men.

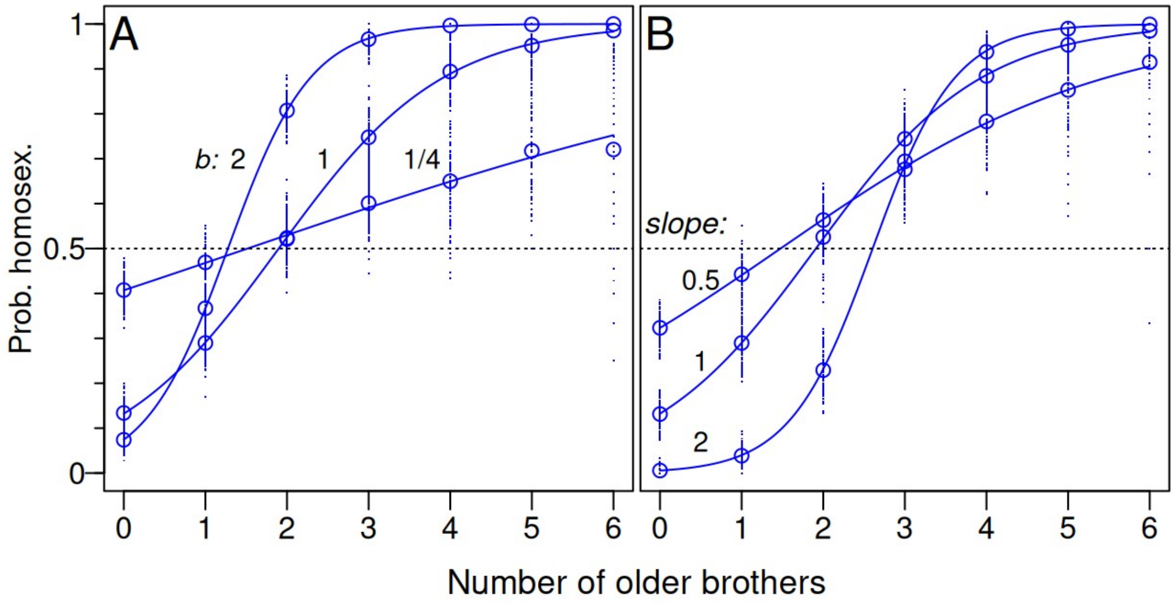

Figure 3. Effect of the correlation between the number of older brothers and older sisters on FBOE and SBOE. The curves depict the predicted proportion of androphilic men according to the number of older brother (FBOE, in blue), or older sisters (SBOE, in red). Data contained the same number of androphilic or gynephilic men (thus a frequency of androphilic men of 0.5), and a total size being N ≈ 600, from a population with mean fertility λ = 5. They were generated with (plain line) or without (dotted line) a correlation between older brothers and older sisters. The coloured circles represent the mean of up to 100 replicates, with the same colour code as above. For clarity, these replicates are depicted as coloured dots only for the data generated with uncorrelated *ob* and *os*.

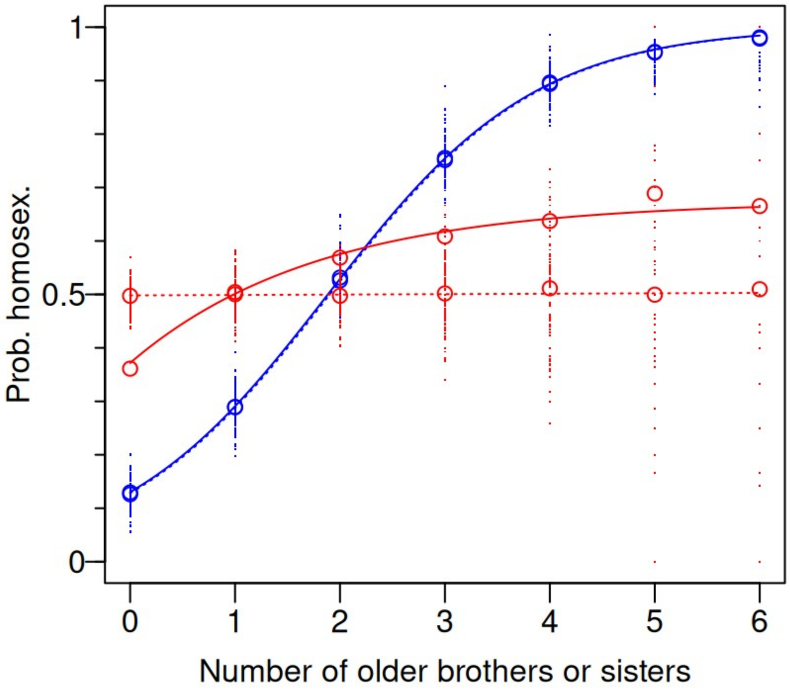

Figure 4. Effect of miscarriage frequency on type-I error for detecting an SBOE. Data were generated under the MIH for various values of miscarriage affecting both male and female embryos, and SBOE was detected using a logistic regression, controlling for the number of older brothers statistically (A), or by restricting the data to firstborn males (B). Each point depicts the proportion of significant SBOE over 400 independent replicate samples, with the corresponding 95% confidence interval. Each sample is composed of the same number of androphilic or gynephilic men, with the total size being N = 600 (empty circles), N = 1,200 (empty squares), or N = 2,400 (empty rhombus). The proportion of significant SBOE when controlling for the initial number of older brother (before miscarriage), or by restricting the data to firstborn among all males (before miscarriage), is depicted by full small rhombus, in A, and B, respectively (only N = 2,400 is shown). The dotted horizontal line indicates the false rejection rate of 2.5%.

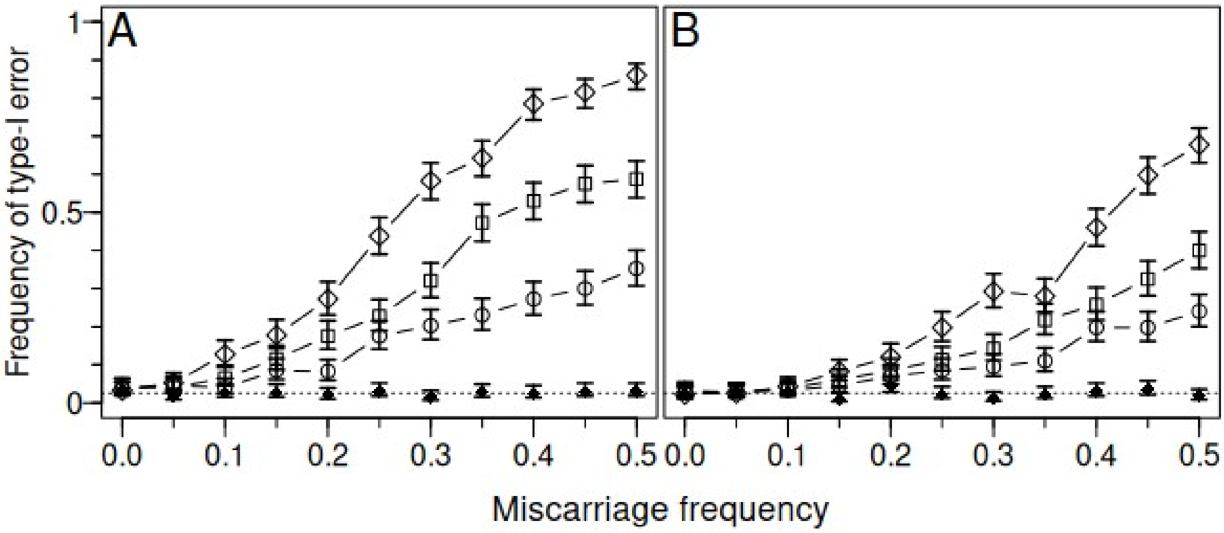

Figure 5. Effect of the mean population fertility on the frequency of androphilic men in only-children and firstborn with younger siblings. Data are generated using a mean fertility of $\lambda = 5$, and a rate of miscarriage *fm*= ½, thus with an observed fertility of $\lambda(1 - fm)$, and with a miscarriage cost $\alpha = 25\%$. Each sample is composed of the same number of androphilic or gynephilic men, with the total size being N = 2,400. The frequency of androphilic men in only-children and in firstborn with younger siblings are depicted in red and blue dots, respectively. The coloured circles, with the same colour code, represent the mean of at least 200 replicates for each value of lambda.

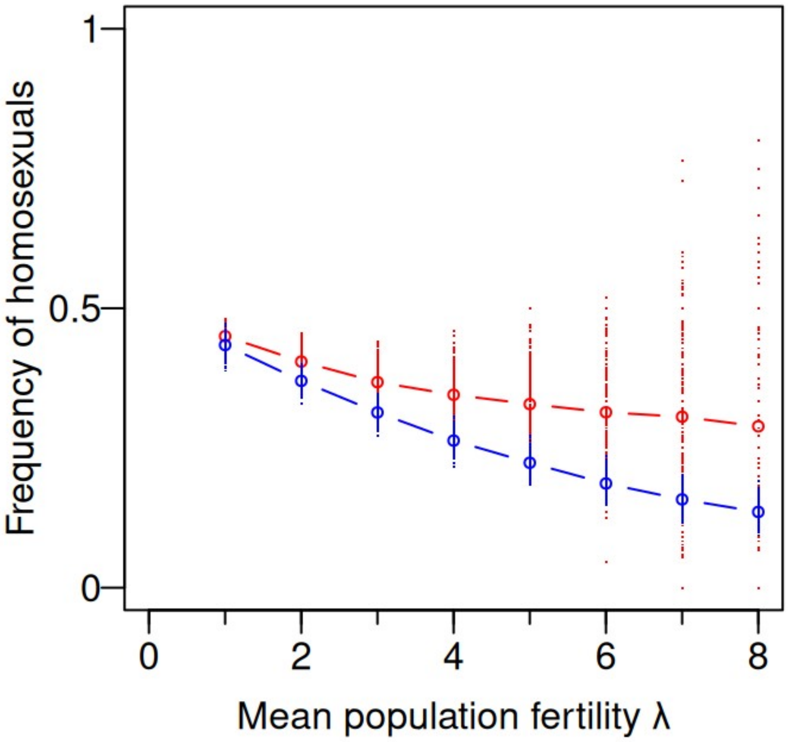

Figure 6. Estimating the frequency of miscarriage (*fm*) from the slope of SBOE, for each population sample. The effect of the number of older sisters on sexual orientation was tested with a logistic ABZ regression, with the number of older brothers and the number of sibs as control variables, and the corresponding slope was used to estimate *fm* by minimizing the function *fm_estim2()*, for each population sample, or for all population samples pooled ("All"). Amplification parameter: *n* = 50 (see Figure S3 for other values). The distribution of at least 200 replicates is shown. See Table 1 for mean values.