Kin Selection and Male Homosexual Preference in Indonesia

Sarah Nila[1] MS, Julien Barthes[2] PhD, Pierre-Andre Crochet[3] PhD,

Bambang Suryobroto[1] PhD & Michel Raymond[2] PhD

1. Department of Biology, Faculty of Mathematics and Natural Sciences, Bogor Agricultural University, Indonesia.

2. Institute of Evolutionary Sciences, Université de Montpellier, CNRS, IRD, EPHE, France.

3. CEFE, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier - EPHE, France.

Corresponding author: Michel Raymond

Mailing address: Institute of Evolutionary Sciences,, CC065, Université de Montpellier, Place Eugène Bataillon, 34095 Montpellier cedex 05. France.

E-mail: michel.raymond@umontpellier.fr

Fax: +33 4 67 14 36 22

Tel.: +33 4 67 14 46 15

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. It has been proposed that individuals with a MHP counterbalance reproductive costs through the transfer of resources to kin, thereby improving their indirect reproduction through kin's reproductive success. This kin selection hypothesis is not supported in Western countries and Japan, although consistent evidence has been obtained in Samoa. In this study, data from Java (Indonesia) were obtained to assess the avuncular tendencies of men with contrasting sexual orientation to measure possible resource transfer. Consistent with the kin selection hypothesis, males with a homosexual orientation reported an increased willingness to transfer resources toward nephews and nieces and declared having transferred more money to nephews and nieces. We developed a method to quantitatively estimate the contribution of kin selection on inclusive reproduction associated to sexual orientation, taking into account various possible biases. Kin selection reduced the direct reproductive cost of homosexual men by 20%, so suggesting that kin selection alone is insufficient to explain the maintenance of male homosexuality. Other potential factors are discussed, as well as the limitations of the study and the social determinant operating for the expression of increased avuncular tendencies of homosexual men.

Keywords: male homosexual preference; Darwinian paradox; kin selection hypothesis

INTRODUCTION

Human male homosexual preference (MHP), i.e., the preference in males for same sex mates, despite the availability of partners of the opposite sex, has long been considered an evolutionary puzzle. Indeed, reproductive cost is observed among men reporting MHP (Bell & Weinberg, 1978; Iemmola & Camperio-Ciani, 2009; Rieger, Linsenmeier, Gygax, & Bailey, 2008; Vasey, Parker, & VanderLaan, 2014), and MHP is partially heritable (Alanko et al., 2010; Bailey, Dunne, & Martin, 2000; Kendler, Thornton, Gilman, & Kessler, 2000; Kirk, Bailey, Dunne, & Martin, 2000; Långström, Rahman, Carlström, & Lichtenstein, 2010). Thus, from an evolutionary standpoint, the frequency of MHP is expected to decrease. However, MHP has been described at least since antiquity (Crompton, 2003), and it is relatively common in several societies: between 3 and 12 % in South and East Asia (Cáceres, Konda, Pecheny, Chatterjee, & Lyerda, 2006), 2 and 6% in Western countries (review in Table 4.3 of Berman, 2003), and between 1.4–4.7% in Samoa (VanderLaan, Forrester, Petterson, & Vasey, 2013).

From an evolutionary point of view, homosexual preferences can emerge and be maintained if the decrease in fertility associated with MHP is compensated by sufficient increases in fertility among close relatives. This increase may be promoted behaviorally by kin selection, and it has been proposed that individuals displaying MHP could behave as “helpers,” favoring the reproduction of kin and thereby directly compensating for the reproductive cost of their preference for same sex partners (Trivers 1974, Wilson, 1975, Pillard & Bailey 1998). In Western/industrialized societies (Canada, UK, and U.S.) and in Japan, homosexual men do not display increased avuncular tendency (i.e., a willingness to channel resources toward nieces and nephews, including gifts, monetary support, and help with childcare) compared with heterosexuals (Bobrow & Bailey, 2001; Forrester, VanderLaan, Parker, & Vasey, 2011; Rahman & Hull, 2005; Vasey & VanderLaan, 2012). This suggests that, in these societies, kin selection is currently not involved in the reduction of the reproductive cost associated with male homosexuality. However,

in Samoa, individuals reporting a homosexual preference (referred to as fa'afafine) displayed an increased avuncular tendency compared with heterosexuals (VanderLaan & Vasey, 2012; Vasey, Pocock, & VanderLaan, 2007; Vasey & VanderLaan, 2009, 2010b), exhibited higher avuncular altruistic behaviors in reported situations concerning monetary transfers toward nephews and nieces (Vasey & VanderLaan, 2010c), and had a stronger propensity to invest in young female kin in hypothetical investment scenarios (VanderLaan & Vasey, 2014). However, how this higher avuncular tendency translates into inclusive fitness has not been empirically evaluated.

The inclusive fitness of a trait depends on two components: direct fitness and indirect fitness (Hamilton, 1963). Direct fitness refers to copies of the trait passed to future generations via direct offspring, and indirect fitness refers to copies of the trait passed to future generations via the reproduction of relatives. Thus, a trait associated with a loss of direct fitness could increase in frequency if the indirect fitness overcompensates for the loss of direct reproduction. When combined to calculate the inclusive fitness, direct and indirect fitness are weighted by the degree of relatedness (Hamilton, 1964), so that to compensate the loss of one direct offspring (with a relatedness of one-half), two nephews or nieces (with a relatedness of 1/4) are required. In a demographically non-decreasing population, at least two offspring able to reproduce are produced; thus, at least four additional nephews or nieces, also able to reproduce, are required. This threshold is based on the assumption that all direct reproduction is suppressed. This is probably true in Samoa, where fa'afafine do not reproduce at all (Vasey et al., 2014). However, if homosexual men have some direct offspring, then a lower additional number of nephews or nieces is required for kin selection to play a significant role.

In addition to kin selection, the increase in fertility in a close relative could be the result of an antagonistic factor. Sexually antagonistic genetic factors that favors MHP in males and that increases fecundity in females have been proposed (Camperio-Ciani, Corna, & Capiluppi, 2004),

and several studies support this hypothesis or have provided results that are consistent with predictions from this hypothesis (for a review, see Barthes, Crochet, & Raymond, 2015).

The skepticism expressed toward kin selection as an explanation for the maintenance of male homosexuality is based on two points. First, there is the absence of any increased avuncular tendencies in industrialized societies (Abild, VanderLaan, & Vasey, 2014; Bobrow & Bailey, 2001; Rahman & Hull, 2005; Vasey & VanderLaan, 2012), where the partial reproduction of homosexual men decreases the threshold of the additional number of nephews/nieces required. Second, in a non-industrialized society, perhaps closer to the social condition where male homosexuality emerged, it seems unlikely that at least four additional nieces and/or nephew could be produced as a result of an avuncular tendency to compensate for the complete absence of direct reproduction displayed by homosexual men. However, to the best of our knowledge, this question has never been empirically addressed in a non-industrialized society.

In this study, we collected original data from Java (Indonesia). Firstly, we tested whether male subjects reporting MHP have an inherent tendency to increase resource transfer toward their kin. Finding evidence that MHP males have an increased tendency to transfer resources to kin would support the idea that kin selection contributed to the evolution of MHP in this population. To do so, we compared the avuncular tendencies of men with contrasted sexual orientation, taking into account possible confounding factors. Secondly, we tested more directly whether kin selection can explain the maintenance of MHP in this contemporary Indonesian population by comparing inclusive fitness of males with contrasted sexual orientation. In order to measure the fitness consequences of sexual orientation, we developed a method to quantitatively estimate inclusive fitness from a field sample, taking into account control variables such such as age and number of sibs. Because a possible increase in fecundity in female relatives due to a genetic antagonistic factor can interact with the effects of kin selection, we first applied this method to offspring from male relatives only to test if kin selection alone is quantitatively sufficient to counterbalance the

direct-reproductive fitness cost of homosexual men. We then considered the offspring from all relatives together to examine whether kin selection together with genetic antagonist factors can counterbalance the direct reproductive cost displayed by homosexual men, providing a more realistic test for the maintenance of MHP is this population.

METHOD

Social Context and Participants

In Indonesia, male homosexuality has existed for several centuries (Boellstorff, 2004): it is currently not totally accepted socially but is not criminalized (Manalastas et al., 2017; Osira et al., 2017; Pew Research Center, 2013; UNDP & USAID, 2014). There is a traditional third gender social category, the “waria”, consisting of biological men living openly as women (Boellstorff, 2004).

The participants (n = 178) consisted of 62 heterosexual men, 82 homosexual men, and 34 bisexual men. Sampling took place in Western and Central Java, Indonesia (for general ethnographic information, see Wessing, 2006). Male participants were recruited from March 2014 to May 2016 in Jakarta, Bogor, and Yogyakarta. Homosexual and bisexual participants were recruited through a targeted sampling performed in a health-care center in Bogor and Yogyakarta (frequented by members of a local LGBT association), and through a network sampling procedure, which involved contacting initial participants and then obtaining referrals from them for additional participants who, in turn, provided further referrals, etc. Further sampling of heterosexual men was performed randomly in the same areas (e.g., in the streets). All interviews were conducted in Bahasa Indonesian by the same local researcher (S.N.). At the beginning of each interview, the participants were informed of the general aim of the study, the type of data collected, and the fact that the data would only be used anonymously for scientific purposes. A written voluntary

agreement was obtained prior to data collection. A compensation was provided to the subjects for their time spent to participate in the present study (IDR 50,000 in Bogor and IDR 100,000 in Yogyakarta, corresponding to ~4 or ~8 €).

Measures and Procedure

The following data were collected for each participant: birth date, nationality, ethnic group (of the participant, parents, and grandparents), highest level of education (four classes: primary, middle school, high school, college or university; for both public or Islamic schools), self-reported weight and height, net monthly income (in Indonesian rupiah, or IDR), parent (mother and father) income, the quality of their relationship with their parents (on a scale ranging from 1 to 10, with 1 being the worst possible and 10 being the best possible), and whether the parents were aware of the subject's sexual orientation. The following demographic variables were also collected: subject's biological children (number, sex, and age) and siblings or half siblings (number, sex, sexual orientation, birth dates, and number of sons or daughters). Only full siblings were further considered. The participants were asked, for each of their siblings considered one by one, how far away (in km) they live, the quality of their relationship with them (scale 1 to 10, with 1 being the worst possible and 10 being the best possible), the number of visits or phone calls during the last year, and how much money was transferred (directly as money, or indirectly as gifts, etc.) for the corresponding nephews or nieces. Participants were invited to provide an overall amount of money transferred if this was more relevant.

In addition, participants were interviewed using a standardized questionnaire (the Family Relationship Scale) to assess their involvement with family members. The questionnaire employed was from Vasey et al. (2007) and Vasey and VanderLaan (2010b) and was composed of three sections: the Overall Generosity subscale (n = 11 items), measuring participant willingness to provide resources, both financial and emotional, to family members; the General Neediness subscale (n = 6 items), measuring the extent to which participants received financial and

emotional resources from family members; and the Avuncular Tendencies subscale (n = 9 items), measuring the theoretical willingness of participants to channel resources toward nieces and nephews. Responses for each item were based on a seven-point Likert-type scale (“strongly disagree/ disagree/ rather disagree/ neither disagree nor agree/ rather agree/ agree/ strongly agree”), and reliability between items for each subscale was measured using Cronbach's α (Tavakol & Dennick, 2011).

Sexual orientation (three classes: heterosexual, homosexual, bisexual) was self-reported by the participants and was completed by a Kinsey scale questionnaire (Questions 2-5 of Table 1 from Iemmola & Camperio-Ciani, 2009). In some cases (N = 40, 22.2% of the sample), the participant hesitated when providing his sexual orientation or the self-declared sexual orientation contradicted the Kinsey scale. Additional information from these participants or from their social network was sufficient to explain the initial hesitation or contradiction and thus correctly assign the sexual orientation. Hesitation was common for heterosexual sex worker men, who regularly have sexual activity with men for financial reasons, as they were unsure if the orientation questions were concerned with their business or personal interest. Three hesitating self-declared bisexual men turned out to be fully homosexual after further questioning (one was married due to social homophobia, and the two others were insecure about disclosing their homosexuality). Among the 82 men reporting a homosexual preference, 11 were declared to be “waria,”. When they were not considered, none of the following results were qualitatively changed, and thus they were kept in the final sample.

Individuals with different sexual orientations did not differ in age ($F(2, 177) = 1.78$, $p = .17$, M age = 31.2 years, SD = 10.6), education (Fisher’s exact test, $p = .29$), or the number of full sibs ($\chi^2 = 0.95$, df = 2, $p = .62$, M number of full sibs: 3.2, SD = 2.4). Individuals with distinct sexual orientation differed in income (Homosexuals: M = IDR 5,461 x 10^3/month, SD=11,705 x 10^3; Bisexuals: M = 2,853 x 10^3 , SD = 2,447 x 10^3; Heterosexuals: M = 2,561 x 10^3, SD = 3,801 x 10^3).

These differences were not significant between homosexuals and bisexuals (Wald test, $\chi^2 = 2.3$, df = 1, $p = .13$), or between heterosexuals and bisexuals (Wald test, $\chi^2 = 0.027$, df= 1, $p = .87$), but the incomes of homosexuals were significantly higher than the incomes of heterosexuals (Wald test, $\chi^2 = 4.2$, df = 1, $p = .04$). There was a tendency for the number of nieces and nephews to differ according to sexual preference (Homosexuals: M = 5.2, SD = 7.8; Bisexuals: M = 4.8, SD = 6.2; Heterosexuals: M = 4.2, SD = 6.9). This difference was significant between homosexuals and heterosexuals (Wald test, $\chi^2 = 7.1$, df = 1, $p = .008$) but not between homosexuals and bisexuals (Wald test, $\chi^2 = 0.69$, df= 1, $p = .40$) or between heterosexuals and bisexuals (Wald test, $\chi^2 = 1.8$, df = 1, $p = .18$). The ethnic composition of the three groups of men were comparable, as the four most represented grandparent ethnicities were similar: Javanese (33.3% of the heterosexuals, 42.4% of the homosexuals and 30.9% of the bisexuals), Sundanese (29.4%, 25.3%, and 46.3%, respectively), Batak (15.7%, 5.8%, and 5.1%, respectively) and Minangkabau (8.1%, 3.0%, and 3.7%, respectively).

Statistical Analyses

Data from questionnaires based on Likert-type scales, thus with a bounded distribution, were analyzed using censored (left and right) Tobit models (Amemiya, 1984). The censored dependent variable was the note on the Likert-type scale, and the explanatory variable was sexual orientation. Significant differences between factor modalities were tested using the Wald χ^2 test. The R "censReg" (version 0.5-22) and "aod" (version 1.3) packages were used for these computations. The distribution of the money spent (directly or indirectly) by the participants for their nephews/nieces displayed a zero-inflated distribution due to a large portion of the individuals in the sample spending no money (focal individuals without nephews or nieces were not considered). Thus, tests were conducted on two response variables—the first on the probability to give money (yes or no, binary variable) using a logistic regression, and the second on the amount of money spent (quantitative variable) using a linear model—restricting the analysis to individuals who

actually gave money. A quasibinomial error function was used for fitting generalized linear models to binomial responses to control for an eventual over-dispersion. The amount of money given was log-transformed to obtain a normal distribution of the residuals. In all cases, the explanatory variable was the sexual orientation of the focal individual, and the control variables were the income, age, the total number of nephews/nieces from full sibs, and (only when the dependent variable was the amount of money spent) the proportion of money given directly to the nephews/nieces over the total amount of money given (quantitative variable, from 0 [only directly given] to 1 [only indirectly given]). The significance of each independent variable was calculated by removing it from the full model and comparing the resulting variation in deviance using an *F* test. The normality of the residuals was tested using the Shapiro test (Royston, 1995). All the computations were completed using R version 3.3.1 (R Core Team, 2016).

A linear regression was used to assess the difference in direct reproduction according to sexual orientation. Control variables were age (centered on the mean age) and the interaction between age and sexual orientation. A linear regression was used to assess the difference in direct or indirect reproduction according to sexual orientation. To measure only indirect reproduction due to avuncular tendencies and not increased female fertility associated with a sex-antagonistic effect (Camperio-Ciani et al., 2004), nieces and nephews from brothers only were considered. The number of brothers was introduced as a control variable, thus controlling for the confounding effect of a higher number of older brothers in homosexual men (see Blanchard & Bogaert, 1996; Bogaert & Skorska, 2011). The other control variables were age, the number of direct children (it is expected that avuncular effects decrease with the number of direct children), and all interaction terms with sexual orientation.

RESULTS

Homosexual and bisexual men did not differed for the traits studied, and thus the bisexual category was pooled with the homosexual category.

Perception of Relationships with Parents

Individuals reporting a homosexual, compared with heterosexuals, had a significantly worse relationship with their father (M ± SE, homosexuals = 6.35 ± 0.24, heterosexuals = 7.85 ± 0.25, Wald test: $\chi^2 = 14.3$, df = 1, $p < .001$). No significant differences were observed in the relationship with their mother (M ± SE, homosexuals = 8.47 ± 0.16, heterosexuals = 8.60 ± 0.21, Wald test: $\chi^2 = 0.045$, df = 1, $p = .83$). Homosexuals had worse relationships with their siblings compared to heterosexuals (M ± SE, heterosexuals = 7.62 ± 0.22, homosexuals = 7.00 ± 0.22, Wald test: $\chi^2 = 7.6$, df = 1, $p = .006$).

Among the individuals reporting a homosexual, 29.5% declared that their father was aware of their sexual orientation, compared to 95.0% for men reporting a heterosexual orientation, this difference being significant (Fisher exact test, $p < .001$). Similarly, 44.3% men reporting a homosexual declared that their mother was aware of their sexual orientation, compared to 95.2% for men reporting a heterosexual orientation, this difference being significant (Fisher exact test, $p < .001$).

Avuncularity

There were no significant differences between homosexuals and heterosexuals in giving resources, either financial or emotional, to family members (Overall Generosity scale, $p = .81$, Table 1). However, they differed in their perception of receiving financial and emotional resources from family members, with heterosexual men reporting a higher perception than homosexuals (General neediness scale, $p = .001$, Table 1). For all men (individuals without any nephews or nieces were removed), the avuncularity scores were positively and significantly correlated with their number of nephews and nieces (Kendall correlation, $\tau = 0.19$, $z = 3.2$, $p = .0014$), but not with their number of older brothers or older sisters (Kendall correlation, $\tau = 0.05$, $p = .41$, $\tau = 0.10$, $p = .11$). The two groups of men were significantly different in their willingness to assist nephews and nieces, with higher values for homosexuals (Avuncular tendencies scale, $p < .001$, Table 1). For all

measures, the estimate of the reliability (Cronbach's α) was acceptable (above 0.70, see Tavakol & Dennick, 2011), except for heterosexuals on the Overall Generosity scale (0.42) and heterosexuals on the General Neediness scale (0.65).

Resources Transferred

The probability of the participants to give money to nephews or nieces was slightly higher for homosexual men, although this was not significant (p = .18, Table 2). Considering only those individuals (N = 99) who actually spent money on their nephews/nieces, a model was built to explain the amount of money given. This model was not adequately fitted, as the residuals were not normally distributed (Shapiro test: W = 0.97, p = .020). This result was due to two outliers, as normality of the residuals was not rejected when they were removed (Shapiro test: W = 0.99, p = .97). Conservatively, these two outliers were kept for further analyses (removing them provided more significant results). Homosexual participants gave directly to their nephews and nieces, on average, an additional IDR 9,516 x 10^3 compared to heterosexual participants (p = .0015, Table 2), representing an increased transfer of 169% compared to heterosexuals. As control variables, the income of the participants had a significant effect (p = .01), with higher incomes increasing the amount of money transferred, but the total number of nephews/nieces, or the number of older brothers or the number of older sisters did not significantly (p = .15, p = .31, p = .69, respectively) affect the amount of money spent. The type of money transfer to the nephews/nieces had a significant effect (p < .001), with direct transfers associated with higher amounts transferred. The model explained (adjusted R-squared) 28.4% of the variance.

Direct and Indirect Reproduction

The number of direct children increased with age, this increase being different according to sexual orientation (F(1, 174) = 50.06, p < .001): heterosexual men had an average of 0.85 direct child per decade, compared to 0.15 for homosexual men (Table 3, Fig. 1A). The deficit in number of children for homosexual men, compared to heterosexuals, thus increased with age, from -0.21

children at 20 years old to -1.27 children at 40 years old (Table 4). The model explained (adjusted R-squared) 49.0% of the variance.

Indirect reproduction was evaluated through the number of nephews and nieces. Firstly, to measure only the effect of different avuncular tendencies and not of the increased female fertility associated with a potential sex-antagonistic effect, indirect reproduction was compared using only nieces and nephews from brothers (men without at least one brothers were not considered, resulting in a sample of 132 men). The control variables were age, avuncular tendencies, mean amount of money given per nephew/niece, number of brothers, number of direct children, and their interaction with sexual orientation. There was an average of 2.5 nieces and nephews per subject, from an average of 2.0 brothers, with one heterosexual man displaying 25 nieces and nephews from 9 brothers. This outlier was removed (keeping it did not change any of the following qualitative conclusions). The number of nephews and nieces increased with the number of direct children, with a slope not significantly different between heterosexuals and homosexuals (interaction: orientation x number of children, $F(1, 102) = 1.32$, $p = .25$). This interaction term was dropped. The number of nephews and nieces increased with the number of brothers, with a slope not significantly different between heterosexuals and homosexuals (interaction: orientation x number of brothers, $F(1, 102) = 2.80$, $p = .097$). This interaction term was kept in the model. The number of nephews and nieces was not significantly different according to sexual orientation, independently of the number of brothers (at mean age, 0.54 additional nephews or nieces for homosexuals, $p = .58$, Table 3). This result was modulated by interaction terms with age. The number of nephews and nieces increased for each year (for a decade, increase of 0.16 for heterosexuals and increase of 1.59 for homosexuals, $p = .003$ for the difference, Table 3). The model explained (adjusted R-squared) 62.0% of the variance.

Homosexual men displayed a deficit of nephews and nieces when young, and an excess when older, this excess was statistically significant from 40 years old (Table 4). At all ages, the

excess of indirect reproduction did not fully compensate for the deficit of direct reproduction, resulting in an overall deficit of ca. 0.42 inclusive children. Several variables differing between homosexual and heterosexual men where then considered. At 40 years old, when the higher avuncular tendencies and the higher amount of money transfer of homosexual men towards their nephew and nieces was taken into account, this resulted to 0.5 additional indirect children for homosexual men, reducing the overall deficit to 0.17 (SE = 0.34) inclusive children. When the lower number of direct children of homosexual men was taken into account, this resulted to 0.83 less indirect children for homosexual men, increasing the overall deficit to 0.83 (SE = 0.33) inclusive children. When both effect were considered together, homosexuals had an excess of 1.3 (SE = 0.56) indirect children, resulting in a deficit of 0.63 (SE =0.30) inclusive children compared to heterosexuals. Taking into account the reproductive output of half-brother (each half-brother was counted as 0.5 brother, and each of their offspring was counted as 0.5 niece or nephew) did not change qualitatively the results (Table 4, B).

Secondly, in order to evaluate whether kin selection and potential antagonist factors can together counterbalance the direct reproductive cost displayed by homosexual men, inclusive reproduction was also calculated by considering all offspring from all full and half siblings (brothers and sisters). Overall, the indirect reproduction of homosexuals did not fully compensate for their deficit of direct reproduction: at 40 years, 0.52 inclusive offspring were missing compared to heterosexuals, i.e., either 0.52 children or 1.04 nephews or nieces (Table 4).

DISCUSSION

Homosexual Men Exhibit Increased Altruistic Behavior

One of the aim of the present study was to test the kin selection hypothesis for the maintenance of male homosexuality through an examination of the propensity to aid kin, particularly nephews and nieces, and of transfer of resources towards the children of siblings. The data showed that homosexual men, compared with heterosexual men, were more willing to channel

resources towards nephews and nieces and that this effect did not extend to other family members, as they did not differ in their score on the overall generosity scale. The measure of (self-declared) money transferred to nephews and nieces suggested that this willingness possibly translates into actual behavior. To ascertain that this result was consistent with the kin selection hypothesis, potential confounding variables were controlled for: income (as amount of resources could affect financially avuncular behaviors), age (avuncular behaviors could perhaps vary with age), and total number of nephews and nieces (family size and realized fertility could affect avuncular behaviors).

Similar research conducted in industrialized countries (Abild, VanderLaan, & Vasey, 2014; Bobrow & Bailey, 2001; Rahman & Hull, 2005; Vasey & VanderLaan, 2012) has not reported any significant differences in the altruistic tendencies of homosexual and heterosexual males. Thus, support for the basic prediction of the kin selection hypothesis, stating that homosexual men should direct more altruistic behavior toward kin than heterosexual men, has thus far only been demonstrated in Java (this study) and Samoa (VanderLaan & Vasey, 2012; Vasey et al., 2007; Vasey & VanderLaan, 2009, 2010b, 2010a).

Indirect Reproductive Advantage of Homosexual Men

Under the kin selection hypothesis, higher altruistic tendencies increase the indirect fitness of homosexual men through increased reproductive output of relatives. To further evaluate this hypothesis, we compared the inclusive reproductive output of homosexual men, through direct or indirect reproduction, with that of their heterosexual counterparts. For that aim, two potential biases should be considered. Firstly, only indirect reproduction through brothers should be compared, to avoid interference with the potentially increased female fertility associated with a sex-antagonistic effect (Camperio-Ciani et al., 2004). Secondly, older brothers, who are more numerous for homosexual men (e.g., Blanchard & Bogaert, 1996; Bogaert & Skorska, 2011), should also be controlled for, as they have necessarily completed a higher part of their reproductive

lifetime, leading to more nephews and nieces and thus increased inclusive reproduction for their homosexual brothers, independently of any kin selection mechanism.

The indirect reproductive output increased with age, this effect being significantly higher for homosexual men relatively to heterosexual men (Table 4). At 40 years old, taking into account differences concerning avuncular tendencies, money given and number of direct children, homosexuals had 1.3 additional nephew or nieces, or 1.3/2 inclusive children, thus reducing the deficit of direct reproduction by 50 %. Avuncular behaviors (money given and avuncular tendencies) accounted for only 0.5 additional indirect reproduction, thus reducing by itself the deficit of direct reproduction by only 20%. The remaining effect (0.78 additional nephew or nieces, or 30% cost reduction) could still be the result of kin selection not captured by our variables. Alternatively, this could be the result of a higher fertility of homosexual's brothers, as previously proposed by Rieger, Blanchard, Schwartz, Bailey & Sanders (2012). This higher fertility could result from pleiotropic genetic influences increasing their attractiveness, thus (for example) resulting in marriage with more fecund women. Consistent with this effect, a higher mating success of homosexual's brothers has been proposed (Zietch et al., 2008).

Direct and Overall Indirect Reproduction of Homosexual Men

We first confirmed that homosexual men pay a cost in direct reproduction; this direct reproductive cost increased with age, with a deficit of 0.7 children per decade. This corresponds to a difference of 0.21 children for men at an age of 20 years and 1.27 children for men aged 40 (Fig. 1A, Table 4). In order to evaluate whether sexually antagonistic genetic effect increasing fecundity of sisters of homosexuals, as proposed by Camperio-Ciani et al. (2004), could add up to the possible increased fecundity of brothers of homosexuals reported above, inclusive reproduction was also calculated by considering offspring from the brothers and sisters. The overall reproductive deficit of homosexual men was not improved, and the effect of kin selection alone in direct cost reduction was similar (21%), in agreement with an absence of differential avuncular tendencies

towards brother or sisters. This suggests that the pleiotropic factors increasing fecundity in brothers are here comparable in effect with a possible pleiotropic factors increasing fecundity in sisters. In any case, no support was found for a substantial contribution of kin selection to reduce the direct reproductive cost of homosexual men. Overall, homosexual men displayed a cost in inclusive fitness, since their higher indirect reproduction did not fully compensate for their direct reproductive cost and the higher avuncular tendencies displayed by homosexual men from Java marginally affected their number of nephews and nieces.

Direct Reproduction and Avuncular Tendencies

Interestingly, the familial pressure on homosexual men to marry and have children could modulate selection on altruistic behavior by limiting the reproductive cost of male homosexuality. In our sample, 9.4% of homosexual men had children, resulting in a mean of 0.17 direct children (i.e., 21.0% of the direct reproduction of heterosexual men) at 32.8 years, the mean age of the sample. This direct reproduction reduces a potential selection for indirect reproduction and thus avuncular tendencies. In this regard, it would be interesting to establish whether avuncular tendencies are enhanced in populations where the direct reproduction of homosexual is decreased. In Samoa, where homosexual men do not reproduce at all (VanderLaan & Vasey, 2012), the increased avuncular tendencies of homosexual men (Fa'afafine), compared to heterosexual men (+ 8.7% or +11.6%, from Study 1 in Table 1 from VanderLaan & Vasey [2012] and from Table 2 from Vasey & VanderLaan [2010b], respectively), was not higher than the similar increase observed here (+11.7%, from Table 1), although further comparison with other populations are required to settle this point. In any case, an increased avuncular tendency could thus be seen as a mechanism (among others) that only reduces the reproductive cost of male homosexuality. Whether or not these enhanced kin-directed behaviors displayed by homosexual men have been selected for as a cost-reduction mechanism is an open issue.

Avuncular Tendencies of Homosexuals Across Societies

Based on currently available data, the higher avuncular tendency of homosexual men is expressed in two societies, Java and Samoa, and not in industrialized countries, such as Canada, the U.S., the UK, and Japan (Bobrow & Bailey, 2001; Forrester et al., 2011; Rahman & Hull, 2005; Vasey & VanderLaan, 2012). Several cultural traits modulating the expression of help among kin could potentially explain these discrepancies.

The first trait is the social and familial acceptance of homosexual men: the limited acceptance of male homosexuality in Western countries (with the possible exception of Canada) and in Japan contrasts with the fairly complete acceptance of these individuals in Samoa (Forrester et al., 2011; Vasey & VanderLaan, 2012). In Java, male homosexuality is also poorly accepted socially, as revealed through conversations with participants after interviews and in the results of the present study, as homosexual men have a lower perception of receiving financial and emotional resources from family members (Table 1). In addition, homosexual men reported poorer ratings concerning their relationships with their fathers compared with heterosexual individuals. While there was no significant difference in the relationships with their mothers, these individuals rated the quality of the relationship with their siblings lower than the heterosexual individuals. Indeed, the overall acceptance of male homosexuality is limited in Indonesia (Pew Research Center, 2013; UNDP & USAID, 2014). Officially, no national law prohibits homosexual relationships, but several participants reported verbal public bullying, and many individuals did not publicly display their sexual orientation. Within the family, a same-sex preference was not always accepted. For example, among homosexuals and bisexuals participants, only 29.5% declared that their father was aware of their sexual orientation, and 44.3% reported that their mother was aware of their sexual orientation (compared with 95.0% and 95.1% for the father and mother, respectively, of heterosexual individuals). Thus, the social acceptance of male homosexuality is not a critical feature to observe increased avuncular behaviors among homosexual men.

Second, a limited kin network, with kin not necessarily living close to each other, is typical of most industrialized societies with nuclear families, but it is not favorable for the expression of valuable resource transfer toward kin (Bobrow & Bailey, 2001). In contrast, Samoans have extended kin networks, in which related individuals typically live in close proximity and individuals have numerous social contacts (Vasey et al., 2007). Javanese and Sundanese (the main ethnic groups of Java) have a kin network centered on the nuclear family (Mangundjaya, 2010; Schröder-Butterfill, 2006), while the "Preferred Family Form" for the Javanese is coded as "extended" in the Standard Cross Cultural Sample. One of the authors of this article (B.S.), an Indonesian anthropologist, classifies the traditional Javanese and Sundanese family as an extended kin network. A quantitative measure of kin networks is likely required to settle this point and evaluate whether this aspect contributed to the higher avuncular tendencies of homosexual men.

Limits and Perspectives

There were several limitations of the present study. First, as the reproductive gap between homosexual and heterosexual men changes with age, potentially increasing the indirect reproduction of homosexual men even though they sustain avuncular tendencies, a sample with a mean age of only 31.2 years is perhaps limited to fully capture this phenomenon.

Second, the simple quantitative count of additional nieces or nephews to measure indirect reproduction has some limitation, as it represents a single generation estimate. Depending on the quality of these nieces/nephews, their contribution to the following generations could vary, modifying indirect fitness. Thus, if avuncular tendencies affect both the number and the quality of nieces or nephews, a lower number of additional sib's children could be required for indirect reproduction compensating the lower direct reproduction of homosexual men.

Third, Indonesian fertility has reduced since 1968 due to a national family planning program (Hull & Hartanto, 2009), potentially affecting measures of inclusive fitness when

individuals with different ages are compared. However, individuals with distinct sexual orientations did not differ in mean age, and age was also explicitly introduced as a control variable in the estimates of inclusive reproductive output.

Fourth, Indonesians and Samoans are both considered as descendants of the Austronesian expansion, and thus these individuals could be considered as non-independent due to a possible single evolutionary origin of homosexual preference. However, the Javanese settlement occurred circa 2,000 BCE (Taylor, 2003), and the Samoan settlement occurred circa 1,500 BCE (Leach & Green, 1989). Thus, both ethnic groups have diverged for more than 3,500 years. There are no cultural constraints known to persist for these time scales, which are even sufficient for genetic adaptation to occur (Itan et al., 2009; Perry et al., 2007). The maintenance of the presence of homosexual preference in both lines (Javanese and Samoans), even if the expression of the higher avuncular tendency reduces the associated cost, thus probably results from independent selection on both lines. Alternatively, the evolutionary origin of homosexual preference is perhaps not unique between Javanese and Samoans: again, selection to maintain the trait (homosexual preference) and its cost modifier (higher avuncular tendency, necessarily selected after the emergence of homosexual preference) would be independent. In any case, Samoans and Javanese diverged sufficiently long ago to safely consider that the higher avuncular tendencies in both groups result from independent selection.

Last, bisexuals were merged with homosexuals in all statistical analyses because no significant differences were found when men declaring a bisexual preference were compared with homosexuals for all the traits analyzed. This absence of differences is consistent with the common and pervasive social bisexuality experienced by homosexual men in Indonesia: it is notoriously known that for homosexual men “Marriages of convenience are common” due to the “strong cultural pressures to enter a heterosexual marriage and form a family,” leading to the situation where “the pressure to form a heterosexual family is very strong [meaning] that bisexuality is fairly

common, although a bisexual identity is not" (UNDP & USAID, 2014). There are thus no obvious cues in this country suggesting that men declaring a bisexual orientation represent a specific category**.**

Compared with heterosexuals, homosexual men from Java showed an increased willingness to channel resources toward nieces and nephews, and this avuncular tendency was translated into a higher financial support for their siblings' children. However, only marginal support was found for a contribution of kin selection to indirect reproduction, suggesting that kin selection alone is insufficient to explain the maintenance of male homosexuality. The direct reproductive cost of homosexual men is likely decreased through familial and social pressures for conformity (e.g., heterosexual marriage), thus reflecting a specific mechanism of cost reduction. Kin selection could still play a role in the evolution of male homosexuality by increasing the quality of nephews and nieces, although this effect remains to be established.

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Compliance with Ethical Standards

Conflict of Interest: Authors declare that they have no conflict of interest.

Ethical Approval: All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. The

protocols that were used to recruit the study's participants and collect data were approved by the French National Commission on Informatics and Liberties (CNIL declaration #1226659).

Informed Consent: Informed consent was obtained from all individual participants included in the study.

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Table 1

Comparison of homosexual and heterosexual men with the Family Relationship Scales.

Scale	Items	Cronbach's α		M ± SE		Wilcoxon		Cohen's *d*
		Homo	Hetero	Homo	Hetero	W	*p*	
Overall generosity	11	0.72	0.42	4.56 ± 0.08	4.66 ± 0.10	3517	.81	.13
General neediness	6	0.65	0.73	3.36 ± 0.12	4.03 ± 0.15	2474	1.0×10^{-3}	.54
Avuncular tendencies	9	0.84	0.72	4.93 ± 0.10	4.41 ± 0.12	3770	6.5×10^{-5}	.56

W = statistics for Wilcoxon-Mann-Whitney test.

Table 2

Effects of sexual orientation on the probability of giving money to nephews or nieces, and on the amount of money given.

	Variables	β	SE	*F*	*p*
Probability of giving money: (logistic regression)	*Intercept*	1.69	0.60	-	-
	SexOrientation(homosexual)	0.88	0.64	1.83	.18
	Income	-0.54	0.38	3.88	.05
	Number of nephews/niece	-0.01	0.07	0.01	.93
	Number of older brothers	-0.13	0.21	0.38	.54
	Number of older sisters	-0.02	0.25	0.01	.93
	Age	0.11	0.38	0.09	.77
Amount of money given: (linear regression)	*Intercept*	7.98	0.47	-	-
	SexOrientation(Homosexual)	0.99	0.30	10.68	.002
	Income	0.88	0.34	6.64	.012
	Number of nephews/nieces	0.04	0.03	2.12	.15
	Number of older brothers	0.09	0.09	1.02	.31
	Number of older sisters	0.05	0.12	0.16	.69
	Type of money transfer	-2.07	0.49	17.49	< .001
	Age	-0.07	0.17	0.18	.67

β = regression coefficient, SE = Standard Error, *F* = change in *F* when the variable is removed (numerator df = 1).

Table 3

Effects of sexual orientation on direct (number of children) or indirect (number of nephews and nieces from the brothers) reproduction.

Reproduction	Variables	β	SE	*F*	*p*-value
Direct:					
	Intercept	0.81	0.09	-	-
	SexOrientation(homosexual)	-0.64	0.11	31.97	< .001
	Age	0.09	0.01	99.61	< .001
	SexOrientation(homosexual):age	-0.07	0.01	50.06	< .001
Indirect:					
	Intercept	1.90	0.40	-	-
	Sex. orientation(homosexual)	0.54	0.53	0.31	.58
	Number of Brothers	0.93	0.40	63.38	< .001
	Age	0.016	0.04	17.49	< .001
	Number of Direct children	0.66	0.28	5.49	.021
	Money given [scaled]	0.67	0.22	9.19	.003
	Avuncular tendency	0.24	0.26	0.83	.36
	SexOrientation(homosexual):age	0.14	0.05	8.87	.003
	SexOrientation(homosexual):Brothers	0.77	0.46	2.80	.097

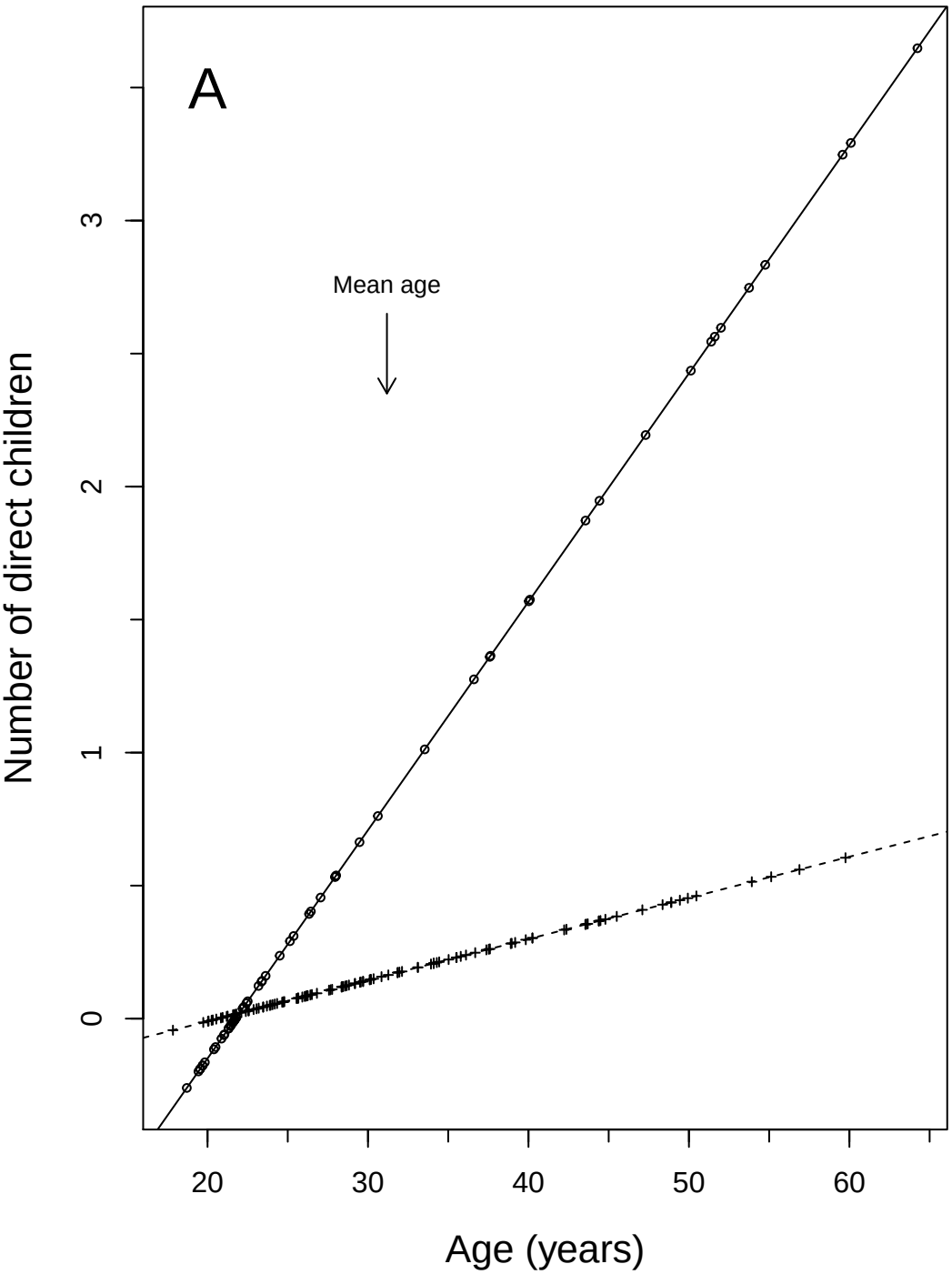
β = regression coefficient, SE = Standard Error, *F* = change in *F* when the variable is removed (numerator df = 1).

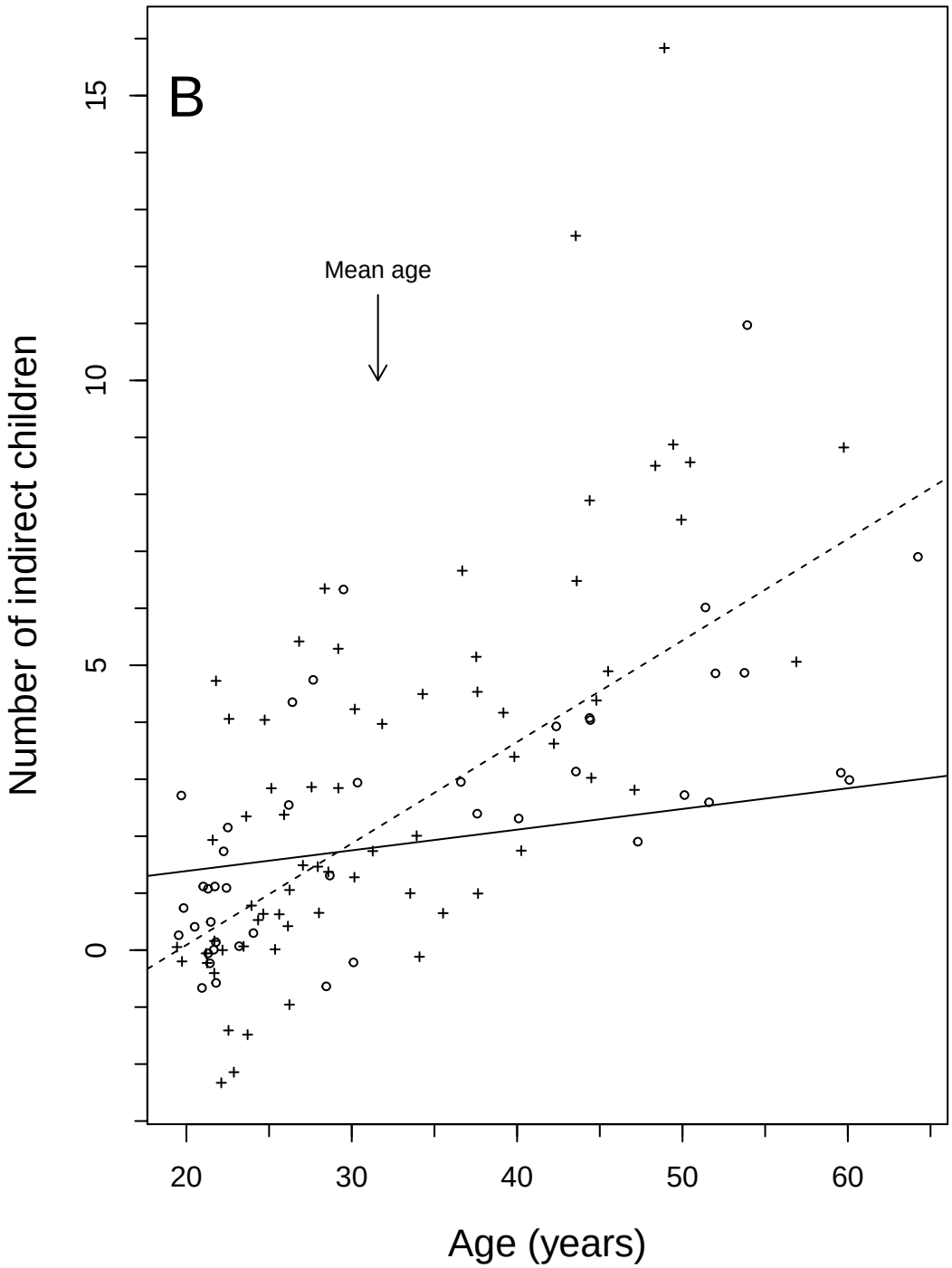
Table 4
Estimates of reproductive output of homosexual men relative to heterosexual men from models of Table 3.

	Reproduction						
	Direct	Indirect:			All:		
		Brothers:		All Sibs:			
Age		A: Full	B: Full & half	C: Full & half	A:	B:	C:
25	-0.21 (0.13)	-0.36 (0.58)	-0.48 (0.62)	**-1.63** (0.80)	-0.39 (0.32)	-0.45 (0.33)	**-1.02** (0.42)
30	**-0.56** (0.11)	+0.33 (0.53)	+0.22 (0.56)	-0.58 (0.73)	-0.40 (0.29)	-0.46 (0.30)	**-0.86** (0.38)
35	**-0.91** (0.12)	+1.02 (0.56)	+0.91 (0.60)	+0.46 (0.77)	-0.40 (0.31)	-0.46 (0.32)	-0.69 (0.41)
40	**-1.27** (0.14)	**+1.71** (0.69)	**+1.61** (0.73)	+1.50 (0.93)	-0.42 (0.37)	-0.46 (0.33)	-0.52 (0.49)

Standard Error in parentheses. Bold $p < .05$

Figure 1. Fitted values for inclusive reproduction according to sexual orientation. A. Direct reproduction (number of children) in function of age. B. Indirect reproduction (number of nephews and nieces) in function of age. Heterosexual or homosexual men are depicted by an empty circle or a cross, respectively. The lines (B) represent the fitted values for the mean number of brothers, the mean number of children, the mean avuncular tendency, and the mean amount of money given to nephews or nieces, for heterosexuals (plain line) and homosexuals (dotted line).


A
Mean age
Number of direct children
0
1
2
3
20
30
40
50
60
Age (years)


B
Mean age
Number of indirect children
0
5
10
15
20
30
40
50
60
Age (years)