

Possible Balancing Selection in Human Female Homosexuality

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Abstract A growing number of researchers suggest that female homosexuality is at least in part influenced by genetic factors. Unlike for male homosexuality, few familial studies have attempted to explore maintenance of this apparently fitness-detrimental trait in the population. Using multiple recruitment methods, we explored fecundity and sexual orientation within the pedigrees of 1,458 adult female respondents. We compared 487 homosexual and 163 bisexual with 808 heterosexual females and 30,203 of their relatives. Our data suggest that the direct fitness of homosexual females is four times lower than the direct fitness of heterosexual females of corresponding ages. The prevalence of nonheterosexuality within the homosexual female respondents' families (2.83%) appear to be more than four times higher than the basal prevalence in the Italian population (0.63%). Pedigree size and relative fecundity in both the paternal and maternal sides of the homosexual women's families were significantly higher than in the heterosexuals' families. If confirmed, the relative average fecundity increase within the family seems to offset the loss in fitness due to the low direct fitness of homosexual females. Therefore, the balanced fecundity in the homosexual females' families may allow the trait to be maintained at a low-frequency equilibrium in the population.

Keywords Female homosexuality · Fecundity · Fitness · Pedigrees · Balancing selection

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Sexual orientation is variable in humans and includes a proportion of individuals that are sexually attracted to their own sex; this preference can reduce reproductive success and direct fitness. A growing body of evidence suggests that sexual preference is partially influenced by genetic factors in both males and females (Alanko et al. 2010; Bailey et al. 1993, 2000; Burri et al. 2011; Långström et al. 2010). The existence and permanence of genetic factors that influence homosexual orientation in the population requires an adaptive explanation supported by empirical observations (Camperio Ciani et al. 2004, 2008, 2012; Gavrilets and Rice 2006).

Historical cross-cultural documentation and archaeological evidence suggest that homosexuality in humans appears to be universal in modern, large-scale societies but not in small-scale societies, and it appears to have considerable antiquity at least since prehistoric times (Barthes et al. 2013; Crompton 2006; Diamond 1993; Herdt 1997; Mondimore 1996; Nash 2001; VanderLaan et al. 2014).

Genetic Evidence

When influenced by genetic polymorphisms, a trait aggregates in and is inherited within families. Family studies are considered a preliminary and fundamental prerequisite to support more intensive behavioral genetic investigations (Bailey and Bell 1993). Earlier studies showed that homosexuality occurred in families among both male (Bailey and Zucker 1995; Bailey et al. 2000; Camperio Ciani et al. 2004; Kendler et al. 2000; Långström et al. 2010; Pillard and Weinrich 1986; VanderLaan et al. 2012) and female (Bailey and Zucker 1995; Pattatucci and Hamer 1995) family members.

Bailey et al. (1993) pioneered empirical female family studies by comparing pairs of adoptive sisters, biological sisters, and dizygotic and monozygotic twins. The authors showed that the probability of the sisters being homosexual increased if the respondent was homosexual. In a large US national sample, Kendler et al. (2000) found a relatively strong correlation in both male-male and female-female twins and estimated that between 0.28 and 0.65 of the sexual orientation variance could be attributed to genetic heritability. Subsequently, four other large, population-wide twin studies focusing on sexual orientation found consistent evidence of genetic heritability in female subjects, which ranged from 0.18 to 0.45 of the sexual orientation variance (Alanko et al. 2010; Bailey et al. 2000; Burri et al. 2011; Långström et al. 2010). These studies were based on several thousand twin probands, were designed with a low ascertainment bias, and used an adequate standard quantitative genetic model (Plomin et al. 2001; Posthuma et al. 2003). Heritability is population-specific and depends on the prevalence among other members of the population; hence, some discrepancies in heritability estimates should not be surprising (Alanko et al. 2010).

Genetic polymorphisms are not the only determinants of homosexuality and should be interpreted as influencing behavior within the frame of an environmental background that might also strongly contribute to same-sex orientations in individuals. Genetic studies have found that female homosexuality largely has a more flexible response to a shared environment than male homosexuality (Alanko et al. 2010; Bailey et al. 2000; Långström et al. 2010; Lippa 2006; Rahman 2005).

The hypothesized existence of genetic factors that influence sexual orientation contradicts the fundamental evolutionary assumption that natural selection will

progressively eliminate any genetic factors that contribute to a reduction in individual fecundity and fitness (Camperio Ciani et al. 2004). Notably, the presence of even a partial genetic influence poses evolutionary questions concerning the presence of homosexuality within populations. The role of biological factors has been explored both empirically and theoretically, mostly in studies of male homosexuality (Blanchard 2001, 2004, 2012; Blanchard and Klassen 1997; Bogaert 2004; Camperio Ciani et al. 2008; Gavrillets and Rice 2006; Jannini et al. 2010; King et al. 2005; Rieger et al. 2012), whereas in female subjects homosexuality is still a relatively unexplored and puzzling Darwinian paradox (Bailey et al. 1993; Pattatucci and Hamer 1995; Patterson and Riskind 2010).

Most studies suggest that traits influenced by genetic factors that produce a detrimental effect on direct fitness, such as a reduction in fecundity, can be maintained in the population across generations through balancing selection. Fitness costs and benefits are balanced in two related individuals when the effect of a genetic factor increases the fitness of some individuals (regardless of the reason), which compensates for the fitness loss in the related individual(s) due to the effect of that same genetic factor. Then, the trait promoted by that genetic factor(s) can be maintained in the population, such as in the well-known case of altruistic traits in kin selection (Hamilton 1963; Maynard Smith 1998). Balancing selection has also been suggested in specific human cases (VanderLaan et al. 2012; Vasey and VanderLaan 2010; Vasey et al. 2007), or in the case of sexually antagonistic selection (Camperio Ciani and Pellizzari 2012; Camperio Ciani et al. 2008; Sanders et al. 2015).

In the present study, we aim to better understand the effects of putative genetic factors that might influence female homosexuality by exploring female fecundity and sexual orientation through a pedigree analysis. Additionally, we aim to explore the possible effect of these genetic factors on fecundity to maintain the factors at equilibrium in the population from generation to generation. Obtaining answers to these questions is a prerequisite for further discussion of the selective mechanisms (Camperio Ciani et al. 2008, 2015; Gavrillets and Rice 2006) and precedes questions concerning the number of possible genetic factors influencing female homosexuality and their mapping in the human genome. Pedigree analysis and the family distribution of homosexuality in homosexual studies have sometimes anticipated these answers (Camperio Ciani et al. 2004, 2008, 2012), which have subsequently been confirmed using quantitative genetic methods (Hoskins et al. 2015; Sanders et al. 2015).

Methods

Participants and Procedures

Sampling homosexual subjects is a delicate issue in research. Indeed, complying with these elusive subjects who in some cases understandably worry about threats to their privacy and avoid the exhibition of membership as much as possible can be a challenge. In the case of secretive, rare populations, common probabilistic sampling methods are not very efficient and often produce low response rates and unreliable responses (Heckathorn 1997). Thus, special methods are required to access hidden populations (Watters and Biernacki 1989).

To obtain a large sample of Italian homosexual females, a wide variety of homophile groups were actively targeted on the Internet in either formal or informal groups, some of which were homosexually connoted associations or were collective or public networks. Then, the sampling was amplified via a snowball method. In community-based surveys, we cannot directly contact the subjects for privacy reasons. Instead, the subjects received information about the survey from the community administrators, and we contacted only the subjects who were interested in participating, which could introduce sampling bias. To avoid self-selection bias, all of the contacted individuals who agreed to participate were unaware of the specific goals of the research (fecundity, pedigree size, and sexual orientation). The subjects who agreed were subsequently contacted personally by phone or mail to obtain their participation consent.

The control heterosexual sample was actively recruited following identical procedures but replacing *mutatis mutandis* the sexually connoted associations with cultural, social, and informal networks. We ensured that the ages of the homosexual females and heterosexuals were matched, and we were careful to target both homosexual and heterosexual subjects aged 45 or older in similar number to assess the fitness at the end of the respondents' reproductive histories. Education and employment were determined during sampling to ensure that their social backgrounds were diverse but balanced between the groups. Research data were acquired via an anonymous self-administered questionnaire. The survey questionnaire was distributed by paper and pencil to approximately half of the volunteers and then recollected by trained collaborators. Alternatively, the survey was distributed via CAWI (Computer-Assisted Web Interviewing) to the subjects in the other half of the sample who chose to answer the questionnaire over the Internet. This combined technique lasted two years, with subjects ranging from 18 to 93 years of age interviewed between 2013 and 2015.

We informed the participants that the questionnaire could last up to 20 min and that they could withdraw at any time with no restrictions. All of the participants were unknown to the researchers; anonymity was guaranteed, and it was impossible to associate the questionnaire with the respondent once the questionnaire was submitted.

Sample Size and Exclusion Rate

A substantial number of candidates who were approached in the original search refused to participate, which is typical private and sensitive surveys. The total size of the reachable population cannot be estimated when using CAWI with a volunteer community. Similarly, a response rate comparable to studies based on demographic registers, such as twin studies (e.g., Burri et al. 2011; Kendler et al. 2000), cannot be computed for a hidden population. In total, 2078 subjects initially volunteered their participation, including homosexual, bisexual, and heterosexual females. From the original sample, some refused to complete the questionnaire, leaving entire sections blank (451); others were considered unreliable (63) because they reported an unusual or inconsistent number of relatives (see "Measures"). In addition, some respondents (106) did not know exactly how many relatives were of a particular sexual orientation (most often cousins). All partial or incomplete questionnaires were discarded from the subsequent analysis. The resulting valid sample consisted of 1458 subjects, which represented 70.16% of the original volunteer sample. According to an a posteriori classification (see "Statistical Analysis"), 808 subjects were classified as heterosexual and 650 were

classified as nonheterosexual, of which 487 were homosexual and 163 were bisexual. These respondents provided fecundity and sexual orientation information for 30,203 relatives.

The research protocol was approved by the Ethical Committee of the Department of General Psychology, University of Padua, Italy. The research protocol adhered to the Helsinki Declaration concerning the use of human subjects for research.

Measures

The questionnaire was organized into three sections: personal data; data concerning relatives in her pedigree; and consistency checks and comments.

The first section, which concerned personal data, included the seven-point Kinsey scale to self-rate sexual orientation (Kinsey et al. 1948). The respondents rated themselves on four individually administered scales (self-identification, sexual/romantic attraction, sexual/romantic fantasy, and sexual behavior); these values were averaged into a final value (Kinsey et al. 1948, 1953). The responses ranged from 0 for exclusive heterosexuality or opposite-sex romantic/sexual relations to 6 for exclusive homosexuality or same-sex romantic/sexual relations. The subjects were also asked questions concerning the following information: age, origin, education, profession, number of children, and any miscarried pregnancies. We asked them not to include nonbiological adopted sons and daughters.

The second section systematically addressed the respondent's family, beginning randomly from the paternal or the maternal side and requesting information on the number, gender, and sexual orientation of each member in each class of first- (grandparents), second- (parents, uncles and aunts), and third-generation (sisters, brothers, and cousins) relatives. Following Bailey and Pillard (1991), relatives were reported as nonheterosexual only if the respondent was absolutely certain of their sexual orientation (i.e., if the relative had acknowledged his or her sexual orientation either personally to the respondent or publicly in the family such that it was common family knowledge). This procedure was adopted to avoid overestimation and to achieve the most conservative figure for the rate of nonheterosexuality (see "Limitations").

At the end of the questionnaire, the third section consisted of a space for free comments and control questions for consistency, particularly about the total number of nonheterosexual relatives reported in the second section.

Statistical Analysis

Following the preliminary analysis of the Kinsey scale responses, the subjects were reclassified a posteriori into three monotonic classes by grouping the Kinsey scores by similarity (Table 1). We defined heterosexuals as subjects scoring 0 or 1 on the Kinsey scale, bisexuals as subjects scoring 2 or 3, and homosexuals as subjects with Kinsey scores of 4, 5, or 6. Since the research design specifically targeted homosexual communities, female nonheterosexual prevalence in the population was not estimated using the proportion of nonheterosexual respondents within our sample. Following Pattatucci and Hamer (1995), the reference prevalence of female nonheterosexuality in the population was estimated based on the prevalence of nonheterosexuality reported by the heterosexual respondents, who could be considered equivalent to a street sample,

Table 1 Sample description

Sample subsets		Age	<i>N</i> of offspring	Nonhetero* females in the pedigree	Pedigree size		
					Total	Males	Females
Heterosexuals							
Kinsey 0	<i>M</i>	32.37	0.41	0.04	21.20	10.80	10.40
(<i>N</i> = 537)	<i>SE</i>	0.54	0.04	0.01	0.44	0.25	0.23
Kinsey 1	<i>M</i>	28.10	0.17	0.10	19.16	9.71	9.45
(<i>N</i> = 271)	<i>SE</i>	0.49	0.04	0.02	0.52	0.27	0.30
Bisexuals							
Kinsey 2	<i>M</i>	27.26	0.05	0.16	18.13	9.32	8.81
(<i>N</i> = 62)	<i>SE</i>	0.97	0.03	0.06	0.88	0.58	0.43
Kinsey 3	<i>M</i>	27.51	0.10	0.18	18.07	9.42	8.65
(<i>N</i> = 101)	<i>SE</i>	0.77	0.04	0.05	0.86	0.48	0.46
Lesbians							
Kinsey 4	<i>M</i>	30.51	0.11	0.27	22.32	11.68	10.64
(<i>N</i> = 37)	<i>SE</i>	1.71	0.05	0.13	1.80	0.88	0.99
Kinsey 5	<i>M</i>	31.43	0.07	0.27	22.72	11.84	10.88
(<i>N</i> = 177)	<i>SE</i>	0.81	0.02	0.05	0.83	0.47	0.42
Kinsey 6	<i>M</i>	33.20	0.10	0.33	21.42	10.92	10.50
(<i>N</i> = 273)	<i>SE</i>	0.67	0.03	0.04	0.62	0.35	0.32
Full sample							
Kinsey 0–6	<i>M</i>	31.01	0.22	0.16	20.73	10.61	10.12
(<i>N</i> = 1458)	<i>SE</i>	0.29	0.02	0.01	0.26	0.14	0.14

*The pooled number of relatives reported by the respondent as nonheterosexual

as a random subsample of the whole female population. This prevalence was consistent with estimates produced by other street sample investigations that measured sexual orientation in females using different, explicit methods (Barbagli and Colombo 2007; Tafuri et al. 2011). Naturally, these types of data should be treated with caution because the respondents could underestimate nonheterosexual females in their own families (Kirk et al. 1999). However at present, this is the only effective method available to researchers to explore the rate of nonheterosexuality in the population on a large scale (Camperio Ciani and Battaglia 2014).

Raw data on subject fecundity, pedigree size, fecundity of relatives, and the reported sexual preferences of family members are all correlated to the respondent's age (Camperio Ciani and Pellizzari 2012). Age differences are important wherever the population exhibits large variations in fecundity, as in the present case where the average fecundity has halved in past 60 years. The three subsamples showed small but significant age differences (Table 1). Hence, all of the analyses considered the effects of age differences, and each comparison testing heterosexuals vs. homosexual vs. bisexuals was performed by ANCOVA with age serving as a covariate. In the ANCOVA model, we generally considered the linear effect of age. A quadratic effect

was also included when a parabolic effect could be assumed. For each comparison, we reported the estimated difference corrected by age as a measurement of the effect size (B) and its statistical significance corrected for multiple testing.

Comparisons between the paternal and maternal pedigrees were performed with the paired-sample t test; identical tests were used to compare the numbers of male and female family members in the pedigree.

Results

Sample Description

Table 1 shows the demographic characteristics of the final sample reporting total number of respondents for each Kinsey score class, the average (M) and standard error (SE) score for age, number of offspring, number of nonheterosexual female relatives in their pedigree, total pedigree size, and total number of males and females in the pedigree. The seven Kinsey score levels were presented separately and then grouped into the three monotonic categories (heterosexuals, bisexuals, and homosexuals) based on the highest likelihood of producing homogeneous classes. However, according to the three partitions (Table 2), the homosexual respondents were significantly older than the heterosexuals ($B = 1.41$ years, $p = 0.024$), and the bisexuals were significantly younger than the heterosexuals ($B = -3.52$ years, $p < 0.001$) and homosexuals ($B = -4.93$ years, $p < 0.001$).

Direct Fitness

The observed fecundity of the homosexual respondents was four times lower than the fecundity of the corresponding heterosexuals even when considering the subset equal to or over 45 years of age (Table 2). When the effect of age was removed, the ANCOVA

Table 2 Direct fitness comparison

Sample subsets	Full sample			Subset age ≥ 45			
	Age	Offspring	Miscarriages	Age	Offspring	Miscarriages	
Heterosexuals	$N = 808$			$N = 122$			
Kinsey 0–1	M	30.94	0.33	0.05	53.35	1.54	0.05
	SE	0.62	0.03	0.01	0.89	0.13	0.04
Bisexuals	$N = 163$			$N = 8$			
Kinsey 2–3	M	27.42	0.08	0.09	50.25	0.50	0.00
	SE	0.98	0.03	0.03	2.34	0.33	0.10
Lesbians	$N = 487$			$N = 85$			
Kinsey 4–6	M	32.35	0.09	0.02	50.76	0.31	0.04
	SE	0.49	0.02	0.01	0.69	0.51	0.36

Miscarriages: number of miscarriages per female; the miscarriage rate is the fraction of miscarriages based on the number of pregnancies

estimated a significant difference ($B = -0.292, p < 0.001$) in fewer offspring per homosexual respondent and a significant difference ($B = -0.094, p = 0.001$) in fewer offspring per bisexual respondent than those per heterosexual respondent. The ANCOVA showed a significant difference ($B = -1.16, p < 0.001$) with fewer total offspring than for the heterosexuals even in the subset of respondents at the end of the fertile period (age ≥ 45 years). The analysis of direct fitness in this sample suggests that homosexual females produced one-quarter of the offspring of the heterosexuals, whereas the bisexuals had similar fecundity to the homosexual females. Bisexuals had a very high miscarriage rate of 0.09, which was significantly higher than the rate reported for heterosexual respondents ($B = 0.151, p = 0.017$) but not significant compared with the miscarriage rate in the homosexual females ($B = 0.110, p = 0.121$). The miscarriage rate did not differ between heterosexuals and homosexual females ($B = -0.031, p = 0.469$).

Prevalence of Female Nonheterosexuality

The heterosexual subjects reported 51 nonheterosexual female relatives out of 8133 female relatives in their pedigrees (mother, sisters, cousins, aunts, and grandmothers), thereby providing a reference prevalence of 0.63% nonheterosexual females in the population. The homosexual sample reported a total of 147 nonheterosexual females in their pedigree out of 5187 total females, yielding 2.83% nonheterosexual females in the pedigrees of the homosexual females, which was significantly higher than the prevalence observed among the heterosexuals ($\chi^2 = 105.34, 1; p < 0.001$). Bisexuals were intermediate, with a 1.97% prevalence of nonheterosexual females in their pedigrees accounting for 28 out of 1420 female relatives (bisexuals vs. homosexual females, $\chi^2 = 3.06, df = 1; p = 0.08$; bisexuals vs. heterosexuals, $\chi^2 = 25.98, df = 1; p < 0.001$).

The homosexual respondents reported that nonheterosexual females were equally prevalent in the maternal and paternal sides of their family, with 46 of 2179 (2.11%) female paternal and 62 of 2660 (2.33%) female maternal kin (plus 39 of 348 sisters; 11.21%). The prevalence of nonheterosexual females in the homosexual respondents' pedigrees was sufficiently high to warrant exploration of the prevalence in the different kinship types. Table 3 shows that all kin classes had an even distribution that was not significantly different from the overall prevalence (2.83%), with a low prevalence in the paternal cousins (1.45%) and a much higher prevalence among sisters (11.21%). In the heterosexual sample, the prevalence of nonheterosexuality was equivalent, with 22 of 4273 (0.51%) reported for the maternal family and 29 of 4213 (0.69%) for the paternal. Bisexuals reported 7 of 565 (1.24%) paternal and 10 of 756 (1.32%) nonheterosexual maternal relatives, plus 11 nonheterosexual individuals out of 99 sisters (11.11%). Bisexuals and heterosexuals reported insufficient numbers of nonheterosexuals in their families to further explore the prevalence for each kinship type.

Pedigree Size

Table 4 compares the pedigree size (i.e., the average number of three generations of family members for the three groups). Family size was relatively larger among the homosexual respondents, with a mean of 21.93 individuals, than among the heterosexuals, with a mean of 20.53 individuals; after correcting for age, a difference of more than one individual in excess was detected compared with the heterosexuals ($B = 1.07$,

Table 3 Prevalence (%) of reported nonheterosexual females in the pedigree of homosexual females

	Non-hetero females	Total females	Prevalence %
Total	147	5187	2.83
Mother	13	487	2.66
Sister	39	348	11.21
Paternal family			
Uncles' offspring	7	484	1.45
Aunts' offspring	24	599	4.01
Aunts	14	609	2.30
Grandmothers	1	487	0.21
Maternal family			
Uncles' offspring	15	548	2.74
Aunts' offspring	18	508	3.54
Aunts	15	630	2.38
Grandmothers	1	487	0.21

$p = 0.053$). Bisexuals had an average family size of 18.09, which was significantly smaller than that of both heterosexuals ($B = -1.58$, $p = 0.045$) and homosexuals ($B = -2.68$, $p = 0.002$). In terms of the number of individuals in the paternal and maternal sides of the pedigree, homosexual females appeared to have a similar excess compared with the heterosexuals (after correcting for age) with an effect size of $+0.36$ (B) individuals paternally and $+0.53$ (B) individuals maternally. Homosexual females also had a significantly larger number of siblings than the heterosexuals ($B = 0.18$, $p = 0.002$). Bisexuals had significantly smaller pedigrees than the homosexual females, both paternally ($B = -1.20$, $p = 0.036$) and maternally ($B = -1.35$, $p = 0.011$), but their families were not significantly smaller than the heterosexuals' (paternal $B = -0.832$, $p = 0.125$; maternal $B = -0.810$, $p = 0.089$).

Table 4 Comparison of pedigree size

Sample subsets		Number of relatives				p
		Total	Paternal	Maternal	Siblings	
Heterosexuals ($N = 808$)	M	20.53	8.67	8.64	1.22	0.929
	SE	0.55	0.36	0.33	0.03	
Bisexuals ($N = 163$)	M	18.09	7.44	7.45	1.20	0.991
	SE	0.87	0.57	0.53	0.09	
Lesbians ($N = 487$)	M	21.93	9.17	9.33	1.43	0.593
	SE	0.86	0.57	0.52	0.09	

Total: number of relatives in the paternal and the maternal pedigree plus parents and siblings

Paternal: number of relatives in the paternal pedigree excluding the father

Maternal: number of relatives in the maternal pedigree excluding the mother

p value for paired-samples t test comparing the paternal and maternal pedigrees

Pedigree Sex Ratio

The homosexual subsample has significantly more males in their pedigrees (males, $M = 11.31$, $SE = 0.27$; females, $M = 10.65$, $SE = 0.24$, $p > 0.001$) primarily because of the significantly large number of males (exceeding the expected number) in the maternal pedigree (males, $M = 4.89$, $SE = 0.17$; females, $M = 4.46$, $SE = 0.15$, $p > 0.001$). However, for the same homosexual women, brothers did not significantly outnumber sisters. We also found a significant excess of males in the pedigrees of the heterosexuals and bisexuals (heterosexuals: males, $M = 10.44$, and females, $M = 10.08$, $p = 0.010$; bisexuals: males, $M = 9.38$, and females, $M = 8.71$, $p = 0.027$), but unlike in the homosexual female pedigrees, neither exhibited more males in the maternal side alone.

Fecundity of Relatives

To investigate the larger family size of the homosexual respondents more thoroughly, we analyzed the fecundity of the first (grandparents) and second (parents, aunts and uncles) generations separately. Regarding the first generation, we had complete data for only the paternal and maternal grandparents; no data were recorded for the more remote relatives in that generation, such as the grandparent's siblings. However, the data for the second generation (parents, uncles, and aunts) are complete, and they show a significantly higher fecundity in families of homosexual females ($B = 0.12$ age-corrected, $p < 0.001$) than in families of heterosexuals (Table 5). Since the average numbers of relatives in the preceding generation of the homosexual ($M = 6.08$) and heterosexual ($M = 5.88$) respondents were already larger (albeit not significantly: $p = 0.432$) because of the fecundity differences found for their grandparents, more offspring were found in the third generation for these same groups ($B = 0.934$ corrected for age, $p = 0.021$). In other words, a grandparent of a homosexual female in our study has $M = 11.83$

Table 5 Fecundity of the previous generation (parents, uncles, and aunts)

Sample subsets		Previous generation		Previous generation's offspring			<i>p</i>
		Fecundity	Size	Total	Males	Females	
Heterosexuals	<i>M</i>	1.81	5.88	10.65	4.90	4.75	0.170
(<i>N</i> = 5554)	<i>SE</i>	0.02	0.17	0.40	0.14	0.14	
Bisexuals	<i>M</i>	1.61	5.40	8.7	4.10	3.60	0.023
(<i>N</i> = 1043)	<i>SE</i>	0.02	0.27	0.64	0.26	0.25	
Lesbians	<i>M</i>	1.95	6.08	11.83	5.77	5.06	<0.001
(<i>N</i> = 3423)	<i>SE</i>	0.02	0.27	0.64	0.20	0.18	

Size: number of individuals of the previous generation: uncles + aunts + one parent

Offspring total: number of cousins + siblings + the respondent

Offspring males: male cousins and brothers

Offspring females: female cousins and sisters, excluding the respondent

p value for paired-samples *t* test comparing offspring males and females

grandsons and granddaughters, whereas a grandparent of a heterosexual respondent has only $M = 10.65$. Moreover, we again observed more males than expected in the homosexual women's pedigrees. In contrast, the parents' generation in the bisexual respondents' pedigrees had a significantly lower fecundity than in the heterosexual respondents' pedigrees ($B = -0.26$, $p < 0.001$) (and even more for the homosexuals), producing a significantly lower number ($B = -2.22$, $p < 0.001$) of grandsons and granddaughters of grandparents of bisexual respondents than of heterosexuals.

To explore the individual contribution of the higher fecundity of homosexual females further, we analyzed the fecundity of each kinship class, including parents and both maternal and paternal grandparents, uncles, and aunts (Table 6).

The parents show a significantly higher fecundity in the homosexual female group than those in the heterosexual group ($B = 0.174$, $p = 0.002$). The grandparents showed a similar fecundity increase in the homosexual female group; however, the comparison of the homosexual females with the heterosexuals was not significant ($B = 0.067$, $p = 0.266$). Moreover, other fecundity increases in the homosexual female group were significant in our sample, including those of the paternal aunts ($B = 0.15$, $p = 0.009$) and maternal uncles ($B = 0.25$, $p < 0.001$), whereas the paternal uncles ($B = 0.10$, $p = 0.075$) and maternal aunts ($B = -0.05$, $p = 0.934$) showed no significant fecundity differences. Ultimately, the increased fecundity of these portions of the homosexual female pedigrees together contributed to the higher overall fecundity of the second generation and produced significantly larger homosexual female pedigrees.

Discussion

The direct fitness measures reported here suggest that homosexual female fecundity in Italy is approximately four times lower than the corresponding fecundity of heterosexuals, and bisexuals have similar fecundity to that of homosexual females. This finding appears to be true even when the respondents are at least 45 years of age and approaching the end of their reproductive career. To the best of our knowledge,

Table 6 Fecundity of relatives

Sample subsets		Paternal				Maternal		
		Parents	Uncles	Aunts	Grandparents	Uncles	Aunts	Grandparents
Heterosexuals ($N = 808$)	<i>N</i>	1616	1019	934	1616	1033	952	1616
	<i>M</i>	2.22	1.68	1.81	3.42	1.55	1.84	3.46
	<i>SE</i>	0.056	0.058	0.058	0.112	0.053	0.057	0.113
Bisexuals ($N = 163$)	<i>N</i>	326	189	175	326	183	170	326
	<i>M</i>	2.20	1.50	1.35	3.23	1.34	1.60	2.97
	<i>SE</i>	0.089	0.094	0.095	0.177	0.089	0.096	0.179
Lesbians ($N = 487$)	<i>N</i>	974	588	604	974	633	624	974
	<i>M</i>	2.43	1.81	1.99	3.47	1.81	1.79	3.52
	<i>SE</i>	0.088	0.089	0.089	0.175	0.081	0.088	0.177

homosexual female behavior has not been linked in previous studies with past or present reductions in fecundity (Pattatucci and Hamer 1995; Patterson and Riskind 2010), although it has been in males (Camperio Ciani et al. 2004, 2009, 2012; Iemmola and Camperio Ciani 2009; Moran 1972; Rieger et al. 2012). If confirmed, the present data do not support the notion that the maternal instinct to procreate is a substitute for lack of erotic attraction to the opposite sex as a means of increasing homosexual female fecundity later in life (Camperio Ciani et al. 2015; Farr and Patterson 2013). The fecundity reduction observed here seems rather conspicuous and exceeds the 50% decrease previously found by Pattatucci and Hamer (1995) in a US sample. This particularly low fecundity in Italian homosexual females might be partially ascribed to the law and to sociopolitical attitudes in Italy that still sanction artificial insemination and other alternative methods of reproduction (Pacilli et al. 2011).

This nonclinical study reports on natural human variation within a self-described population. However, medical (developmental) factors can influence female sexual orientation, including the effect of prenatal androgens. Females with CAH (congenital adrenal hyperplasia) can exhibit male-typical behavior and interests and may report significantly more homosexual fantasies and attractions than their sisters, who were used as controls (Burri et al. 2011; Hines et al. 2004; Meyer-Bahlburg et al. 2008; Zucker et al. 1996). Studies in nonclinical populations have shown that variation in fetal testosterone levels can also be associated with homosexual and male-typical gender-related behaviors in young females (Auyeung et al. 2009; Hines et al. 2002). However, as with most fitness-reducing pathologies, the incidence of CAH is very low (approximately 1:15,000). Furthermore, only half of these cases affect females (Stout et al. 2010), and even fewer exhibit influence on their sexual orientation. The frequency of homosexual female investigated here (approximately between 0.63:100 for heterosexual pedigrees and 2.83:100 for homosexual pedigrees) is about 150 times higher than that of CAH. The vast majority of homosexual females have no associated developmental disorders, and female homosexuality is now well-recognized as a natural sexual orientation variant in our species (Johnson 1997). With the exception of a few conditions, as clearly assessed from DSM-III onward, homosexuality is not pathological and is not framed as such in the modern medical literature (Spitzer 1981).

The prevalence of nonheterosexuality (0.63%) recorded in the heterosexual female pedigrees seems low compared with that of other studies (Butler 2005; M. Diamond 1993; L. M. Diamond 2008; Sell et al. 1995; Wilson 2004; Wright 2009:314) but is in line with previous sampling in the Italian population (Barbagli and Colombo 2007; Tafuri et al. 2011).

Homosexual females have been consistently reported to have more homosexual female relatives than heterosexuals (Bailey and Benishay 1993). Pattatucci and Hamer (1995) suggested that families exhibit homosexual female clusters. They found elevated rates of nonheterosexuality in several classes of homosexual female relatives in a pedigree study, including sisters, daughters, nieces, and cousins through a paternal uncle. The pedigree analysis reported here suggests that the prevalence of nonheterosexuality in homosexual females' families appears to be four times higher than the prevalence in the remaining sampled population. Despite minor differences, these data converge with Pattatucci and Hamer's (1995) findings. The present study confirms the much higher rate of nonheterosexuality in sisters of homosexual females found in previous studies (Bailey and Bell 1993; Bailey and Benishay 1993; Bailey

et al. 1993; Pattatucci and Hamer 1995) but not in mothers or female paternal cousins as has been reported (Pattatucci and Hamer 1995).

Notably, information on the sexual orientation of relatives obtained from the homosexual female subjects might be biased because of perceptions of sexual orientation different from those of the heterosexual respondents (Alanko et al. 2010; Kirk et al. 1999; Pacilli et al. 2011). Nevertheless, our method of ascertaining the nonheterosexuality rate was particularly conservative and could have resulted in an underestimation of all rates (Bailey and Pillard 1991) (see “Limitations”).

This study is the first to ascertain whether homosexual females’ families showed an increase in fecundity in the maternal and paternal lines or among classes of relatives (Pattatucci and Hamer 1995; Camperio Ciani et al. 2015). The analysis of all relatives in the homosexual respondents’ pedigrees showed with sufficient power (fecundity data for more than 15,000 relatives) that the overall fecundity appeared to be balanced, and no differences between the maternal and paternal sides. The reduction in average fecundity related to the low direct fitness of nonheterosexuals in the pedigree of 1.1 offspring seemed to be offset by the significantly larger overall fecundity in the previous generations of relatives, which produced on average 1.1 additional offspring in the pedigree. If confirmed, these pedigree data suggest that putative genetic factors influencing the phenotype of female homosexuality might occur at a low-frequency balanced equilibrium in the population. The increase in overall fecundity produced by these genetic factors on relatives, could balance the fecundity reduction of lesbians. Hence, sustain this trait in the population at a constant low frequency equilibrium.

Notably, these data should not be influenced by bias on the part of the respondents because the reported numbers of individuals and their fecundity cannot reasonably be argued to be influenced by the proband’s sexual orientation (see “Limitations”). Unfortunately, the detailed analysis of individual fecundity by kinship class had much lower statistical power. Each specific fecundity comparison among pedigree members could still be affected by a type 1 error and should be interpreted cautiously. These data preliminarily suggest that the homosexual females’ parents, maternal uncles, paternal aunts, and, to a minor extent, grandparents, show significantly higher fecundity. Fecundity in the homosexual female pedigrees was lower than in the heterosexual pedigrees only for maternal aunts. In contrast to findings for male homosexuals (Camperio Ciani et al. 2004), the only conspicuous asymmetries between the paternal and maternal sides of the homosexual female pedigree observed in this study were not in nonheterosexual prevalence, number of individuals, or fecundity, but solely in a higher number of males than expected in the maternal pedigree.

Bisexuals

The large number of bisexual respondents in our study supports previous findings that female bisexuals are relatively more common than male bisexuals (Bailey and Pillard 1991; Camperio Ciani et al. 2009; Diamond 2008; Hamer et al. 1993; Pattatucci and Hamer 1995). The effect of a shared environment (culture and family education) has been suggested to be partially responsible for female sexual fluidity into adulthood, which is unequalled in men (Bailey and Benishay 1993; Bailey et al. 1993; Baumeister 2000; Blumstein and Schwartz 1977; Hershberger et al. 1997; Pattatucci and Hamer 1995; Rust 1992). Hence, bisexuality seems to be more common in women than in men

(Bailey and Pillard 1991; Camperio Ciani et al. 2009; Diamond 2008; Hamer et al. 1993; Hu et al. 1995). Notably, women might become affectively involved with another woman not only because of an inborn sexual attraction but also for feminist, political, egalitarian, or emotional reasons (Blumstein and Schwartz 1977; Rosenbluth 1997; Stein 1997; Whisman 1996). Environmental influences that interact with genetic components might influence the phenotypic expression captured by demographic empirical studies (Plomin et al. 2001). This interaction contributes to make the bisexual interpretation of the present data challenging. We did not have sufficient statistical power for most of the analyses owing to the relatively small sample sizes; thus, few conclusions could be drawn.

Female bisexuals in the present study do not appear to be intermediate between heterosexuals and homosexuals, defying our expectations. They appear to be intermediate only in their fecundity rate and the prevalence of familial nonheterosexuality. Despite their low statistical power, the data on fecundity in bisexual families suggests that grandparents, uncles, aunts, and parents are less fecund in the families of this group of respondents. With the present data, we cannot suggest any balanced selection for bisexuals. The lower fecundity in most classes of relatives, the reduced size of the entire pedigree, and the significant reduction in the direct fitness of bisexual respondents seem consistent with an unbalanced condition possibly associated with instability and familial distress (Cloninger and Guze 1970, 1973; Pillard et al. 1981; Taylor and Abrams 1973). The significantly higher miscarriage rate in bisexuals than in heterosexuals and homosexual females is puzzling. More data and further studies are required before any conclusions can be made to assess whether the hypothesized instability is a cause or a consequence of the bisexual orientation in females.

Limitations

Two sources of bias in this study have to be addressed: (1) biased inclusion of individuals with larger families and (2) the differential estimation of nonheterosexuality in relatives.

We are well aware of the potential biases introduced by our sampling and data collection methods. Individuals with larger families are more likely to be targeted by this type of research; hence, larger families are likely overrepresented (Spren 1992; Watters and Biernacki 1989). This type of bias is not found in investigations conducted with complete samples, such as national census surveys. This bias is intrinsic and can be addressed only a posteriori by appropriate weighting to provide corrected estimates. However, comparisons between samples collected using similar methods resolve most of this bias. Here, as in previous studies on male homosexuality performed with identical techniques, weighting is not required because the control and homosexual/bisexual samples are equally affected (Camperio Ciani et al. 2004; Iemmola and Camperio Ciani 2009).

When sampling elusive populations and asking sensitive questions of respondents whose sexual orientation, memory, or personal acquaintance with family members might influence their responses, researchers must be cautious in interpreting results (Kirk et al. 1999). The respondents' assessment of relatives' sexual orientations might be less reliable than previously reported (Bailey and Benishay 1993; Bailey and Pillard 1991; Pattatucci and Hamer 1995). Nonheterosexuals might overestimate the rate of

nonheterosexuality in their relatives (Bailey and Bell 1993; Clinard and Meier 1979; Kirk et al. 1999; Schur 1965), and differences in levels of social acceptance (and homophobia) might influence the attribution of sexual orientation by the respondents (Savin-Williams 2006). This type of bias could seriously affect prevalence estimates and twin concordance estimates of sexual orientation and could influence measures of genetic heritability (Bailey and Bell 1993; Clinard and Meier 1979; Kirk et al. 1999; Schur 1965). In the current study, this bias affects only the rate of nonheterosexuality reported by homosexual versus heterosexual respondents. The similarity of these rates to those from the previous study (e.g., Bailey and Benishay 1993; Pattatucci and Hamer 1995) confirms that the bias is consistent across studies. The other crucial variables collected from the respondents focused on family size, fecundity estimates, and the number of paternal and maternal relatives. This information has no relationship to the respondents' sexual orientation, and there is no evidence that it is affected by the previously described biases (Camperio Ciani et al. 2004, 2012; Pattatucci 1998; Pattatucci and Hamer 1995). There is also no evidence in family history studies of any systematic overestimation in one kinship class versus another (e.g., number of maternal vs. paternal cousins or uncles vs. brothers).

In future studies, sample size will hopefully be sufficient to allow for a class-by-class analysis in the heterosexual and bisexual pedigrees. In addition, the possible interaction between and reciprocal influence of male and female homosexuality on fecundity within the pedigree should be ascertained (e.g., Bailey and Bell 1993).

Conclusion

In conclusion, and notwithstanding the limitations of the present research, female homosexuality does not appear to result in overall decrease in fecundity within families. In fact, a fecundity increase among both the paternal and maternal relatives of either sex offsets the reduced fecundity of nonheterosexual females. These pedigree data suggest that putative genetic factors influencing the phenotype of female homosexuality might occur at a low-frequency balanced equilibrium in the population. The balanced equilibrium is due to the fecundity reduction in homosexual females on one hand and the overall fecundity increase in their relatives that these genetic factors entail, on the other. These results suggest attention should be paid to the mechanism through which these genetic factors are expressed in the pedigrees of nonheterosexual females.

Acknowledgements This research was partly funded by a BIRD 2017 research grant from the University of Padova, Italy, assigned to Andrea Camperio Ciani.

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