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ORIGINAL PAPER

Femininity and Kin-Directed Altruism in Androphilic Men: A Test of an Evolutionary Developmental Model

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Abstract *Androphilia* refers to sexual attraction and arousal toward males whereas *gynephilia* refers to sexual attraction and arousal toward females. This study tested the *adaptive feminine phenotype model* of the evolution of male androphilia via kin selection, which posits that the development of an evolved disposition toward elevated kin-directed altruism among androphilic males is contingent on the behavioral expression of femininity. Gynephilic men, androphilic women, and androphilic men ($N =$ 387) completed measures of childhood and adulthood gender expression and concern for kin's well-being. Adulthood femininity correlated positively with uncle/aunt-like tendencies among androphilic men and women. Although androphilic women reported greater willingness to invest in nieces and nephews than gynephilic and androphilic men, mediation analyses indicated that adult femininity completely mediated these group differences. In addition, changes in the expression of femininity between childhood and adulthood were associated with parallel changes in concern for the well-being of kin among androphilic men. Thus, these findings suggest that femininity is key to the expression of kin-directed altruism among androphilic males and may have been important in the evolution of male androphilia.

Keywords Sexual orientation · Male androphilia · Evolution · Kin selection · Femininity

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Introduction

Androphilia refers to sexual attraction and arousal toward males whereas *gynephilia* refers to sexual attraction and arousal toward females. Male androphilia has a familial component (Bailey et al., 1999; Schwartz, Kim, Kolundzija, Rieger, & Sanders, 2010; VanderLaan, Forrester, Petterson, & Vasey, 2013a; VanderLaan, Vokey, & Vasey, 2013c) and is at least partially influenced by genetic factors (Alanko et al., 2010; Bailey, Dunne, & Martin, 2000; Kendler, Thornton, Gilman, & Kessler, 2000; Långström, Rahman, Carlström, & Lichtenstein, 2008). Yet, the manner by which genetic factors underlying male androphilia persist from one generation to the next is unclear because androphilic males have significantly lower rates of reproduction than their gynephilic counterparts (e.g., King et al., 2005; Schwartz et al., 2010; Vasey, Parker, & VanderLaan, 2014). The kin selection hypothesis (Wilson, 1975) suggests that androphilic males offset the cost of not reproducing directly by facilitating the reproduction of kin, who share genes in common by virtue of descent. In essence, androphilic males could increase their *indirect fitness* (a measure of an individual's impact on the reproduction of genetic relatives weighted by the degree of relatedness; Hamilton, 1963) via kin-directed altruism and thereby facilitate the maintenance of genetic factors underlying male same-sex sexual partner preference in the gene pool.

To date, a number of studies have examined the kin selection hypothesis by testing the prediction that males who exhibit same-sex sexual partner preference should show greater willingness to invest in close kin than individuals who exhibit opposite-sex sexual partner preference. Research focusing on transgender same-

sex attracted natal males known as *fa'afafine*[1] in the Polynesian island nation of Samoa have repeatedly supported this prediction, finding that such males are significantly more willing to perform avuncular (uncle-like) behavior compared to opposite-sex attracted Samoan males (VanderLaan & Vasey, 2012; Vasey, Pocock, & VanderLaan, 2007; Vasey & VanderLaan, 2010) and opposite-sex attracted Samoan females (Vasey & VanderLaan, 2009). In contrast, research focusing on cisgender androphilic men (i.e., gay men) has repeatedly failed to support this prediction in a number of countries, including the United States (Bobrow & Bailey, 2001), United Kingdom (Rahman & Hull, 2005), Canada (Abild, VanderLaan, & Vasey, 2014; Forrester, VanderLaan, Parker, & Vasey, 2011), and Japan (Vasey & VanderLaan, 2012). Understanding why these cross-cultural discrepancies exist may help identify the proximate factors underlying the development and expression of elevated avuncularity among transgender same-sex attracted males and elucidate the evolutionary basis of male androphilia.

Vasey et al. (2007) highlighted a number of circumstances unique to Samoa that might account for the observed cross-cultural discrepancies. First, they noted that Samoan *fa'afafine* experience relatively greater social tolerance compared to their non-transgender counterparts in other cultures (Bartlett & Vasey, 2006; Mageo, 1996). In Canada, a Western culture characterized by relatively less homophobia (Anderson & Fetner, 2008), Forrester et al. (2011) did not find a male sexual orientation difference in avuncular tendencies. As such, Forrester et al.'s findings were not consistent with the hypothesis that elevated avuncular tendencies among androphilic males are contingent solely on sociocultural environments in which same-sex attracted males experience greater social acceptance.

Second, Samoans often reside in the same village as their relatives or maintain contact with family members via frequent visits (Mageo, 1998). Vasey et al. (2007) proposed, therefore, that geographic proximity might facilitate elevated avuncularity among same-sex attracted males in Samoa. To test this idea, in a Canadian sample, Abild et al. (2014) assessed willingness to engage in avuncular activities that could be performed regardless of distance (e.g., provide advice about dating) and those that required close proximity to be performed (e.g., babysitting nieces and nephews). Compared to gynephilic men and androphilic women, androphilic men did not show elevated avuncularity regardless of the degree of geographic proximity required to perform avuncular acts. Hence, geographic proximity to kin does not seem to be the key factor in the expression of elevated avuncularity among same-sex attracted males.

Third, Vasey et al. (2007) proposed that the collectivistic culture found in Samoa could have been the key to the expression of elevated avuncularity. To test this idea, Vasey and VanderLaan (2012) examined avuncularity in Japan. Like Samoan culture, Japanese culture is characterized by vertical collectivism, which entails a hierarchical social structure in which group well-being is emphasized over individual well-being (Shore, 1981; Triandis, 1995). Compared to Japanese gynephilic men, Japanese androphilic men did not show elevated avuncularity. Thus, it appears that collectivism, in and of itself, cannot account for elevated avuncularity among same-sex attracted males.

Fourth, Vasey et al. (2007) proposed that Samoans might hold special (trans)gender role expectations that *fa'afafine* should exhibit elevated avuncularity. However, VanderLaan, Petterson, Mallard, and Vasey (2015a) found no evidence to support this hypothesis. Samoans do not expect *fa'afafine* to be any more altruistic toward nieces and nephews than men and women nor do *fa'afafine* hold such expectations for themselves.

Social tolerance toward same-sex attracted males, geographic proximity to kin, collectivism, and (trans)gender role expectations are not necessarily irrelevant to the expression of elevated avuncular tendencies. Rather, based on these studies, they simply appear to be insufficient on their own to account for elevated avuncularity among Samoan *fa'afafine*.

The Adaptive Feminine Phenotype Model

An alternate explanation yet to be tested is that the development of an evolved disposition toward elevated kin-directed altruism among androphilic males is contingent on the behavioral expression of marked femininity. If so, cross-cultural differences regarding male sexual orientation and avuncularity may be understood as a consequence of cross-cultural differences in the manner in which gender is expressed among males who exhibit same-sex sexual orientation. We refer to this explanation here as the *adaptive feminine phenotype model*.[2] This model is founded on an evolutionary developmental approach that integrates cross-cultural research findings on male sexual orientation, gender atypicality across the lifespan, and psychological domains relevant to childhood and adulthood relationships with kin.

[1] Translated literally, *fa'afafine* means "in the manner of a woman."

[2] Miller (2000) hypothesized that genes underlying male androphilia increase femininity among gynephilic male carriers and that such femininity is perceived by women as attractive because it provides a cue that a man would make a good long-term partner and father to her offspring. As such, Miller's hypothesis views femininity in gynephilic male carriers of androphilic genes as adaptive and fitness-enhancing while regarding androphilic partner preference and androphilic male femininity as evolutionary by-products of these genes (sensu Buss, Haselton, Shakelford, Bleske, & Wakefield, 1998). Also, it views femininity among androphilic males as being of no reproductive value because it would not enhance reproduction as it does in gynephilic male carriers. In contrast, the adaptive feminine phenotype model proposed here argues that femininity is adaptive and fitness-enhancing among androphilic males because it facilitates the behavioral expression of kin-directed altruism. Importantly, Miller's hypothesis and the adaptive feminine phenotype model are not mutually exclusive. It is possible that both hypotheses describe processes that account for some portion of the evolutionary maintenance of genes underlying male androphilia.

The basic premise of the adaptive feminine phenotype model is supported by ethnological research. A study of 192 non-industrial societies indicated an association between the presence of ancestral sociocultural characteristics typical of early human tribal societies (e.g., dependence of hunting and foraging, animistic religious beliefs, relatively less complex sociopolitical systems) and the presence of transgenderism within a society (VanderLaan, Ren, & Vasey, 2013b). Thus, it appears likely that ancestral human sociocultural environments would have facilitated the expression of marked lifelong feminine, transgender gender expression among same-sex attracted males similar to that seen among contemporary Samoan *fa'afafine*. As a likely aspect of the developmental pattern associated with male androphilia over evolutionary history, it is plausible that sufficient opportunity existed for such gender expression and a disposition toward kin-directed altruism to become linked by evolutionary selection pressure such that their expression covaried.

The majority of empirical support for the idea that gender expression might be key to understanding cross-cultural variation in avuncularity among same-sex attracted males comes from cross-cultural psychological studies. In attempting to account for why their Samoan findings differed from other studies in Western countries, Vasey et al. (2007) noted that Samoan *fa'afafine* are markedly feminine relative to their Western counterparts. *Fa'afafine* identify as such, not as men or women, and tend to be feminine in appearance and mannerisms beginning in early childhood (Bartlett & Vasey, 2006). From a Western cultural perspective, some *fa'afafine* would be described as effeminate males while many would be described as transgender. Indeed, *fa'afafine* range from extremely feminine to unremarkably masculine, although instances of the latter are quite rare (Bartlett & Vasey, 2006; Schmidt, 2003; Vasey & Bartlett, 2007). In contrast, same-sex attracted males in the other cultures in which the kin selection hypothesis was tested (i.e., U.S., UK, Canada, and Japan), although more gender-atypical than their heterosexual counterparts (Lippa, 2005), are relatively more gender-typical in that they identify and express themselves publically as men. Thus, it is possible that the pronounced gender atypicality of Samoan *fa'afafine*, relative to gay men in other cultures, is responsible for the cross-cultural discrepancies in the expression of elevated avuncularity.

From a developmental perspective, gender-atypical behavior is a cross-culturally consistent correlate of male sexual orientation beginning in childhood. Retrospective and prospective studies have shown that androphilic males in Western cultures exhibit elevated gender-atypical behavior during childhood (Bailey & Zucker, 1995; Green, 1987; Rieger, Linsenmeier, Gygax, & Bailey, 2008; Steensma, van der Ende, Verhulst, & Cohen-Kettenis, 2013). Retrospective studies conducted in Brazil, Guatemala, Samoa, Thailand, Turkey, and the Philippines have shown that the childhood behavior of male androphiles raised in these non-Western cultures also tends to be gender-atypical regardless of whether such males are transgender as adults (Bartlett & Vasey, 2006; Cardoso, 2005, 2009; Whitam & Zent, 1984; Winter, 2006). Hence, increased childhood gender atypicality is a cross-culturally stable characteristic of males who exhibit same-sex sexual partner preference as adults.

Critically, the idea that gender expression and a disposition toward kin-directed altruism are linked is supported by an additional cross-culturally consistent pattern: gender atypicality is associated with elevated kin-attachment during childhood among (pre)androphilic males. VanderLaan, Gothreau, Bartlett, and Vasey (2011a) argued this to be the case based on research examining childhood separation anxiety (i.e., elevated anxiety due to separation from major attachment figures such as parents). In one study, Canadian boys diagnosed with Gender Dysphoria (GD; formerly Gender Identity Disorder) due to persistent cross-gender behavior and identity exhibited elevated traits of separation anxiety compared to boys who were sub-threshold for such a diagnosis (Zucker, Bradley, & Lowry Sullivan, 1996). Likewise, retrospective studies found elevated traits of recalled childhood separation anxiety among Canadian cisgender androphilic men who recalled being gender-atypical as children (VanderLaan, Gothreau, Bartlett, & Vasey, 2011b) and Samoan *fa'afafine* (Vasey, VanderLaan, Gothreau, & Bartlett, 2011).

VanderLaan et al. (2011a) speculated that elevated traits of separation anxiety in (pre)androphilic males were motivated by concern for the well-being of close kin. In support of this idea, they noted that GD boys, Canadian gay men, and Samoan *fa'afafine* all scored highest on the separation anxiety item related to worrying about some ill fate befalling their parents (VanderLaan et al., 2011b; Vasey et al., 2011; Zucker et al., 1996). Moreover, in a retrospective study examining Canadian gynephilic and androphilic men and women, there were no significant group differences for items related to anxiety resulting simply from prolonged separation from parents (e.g., "I did not want to sleep alone"); however, androphilic men and women scored significantly higher than gynephilic men for a set of items related to worrying about the well-being of parents (e.g., "I worried that something terrible would happen to my parents"), and these group differences were entirely contingent on recalled female-(a)typical, but not male-(a)typical, behavior (Vander Laan, Petterson, & Vasey, 2015b). Given that elevated childhood traits of separation anxiety due to worrying about the well-being of parents and elevated adulthood avuncularity are both conceptually related to securing the well-being of kin, Vander Laan et al. (2011a) posited that the former represents a developmental precursor of the latter.

The adaptive feminine phenotype model draws on and integrates these empirical observations to suggest that transgender androphilic males such as the Samoan *fa'afafine* exhibit elevated traits of separation anxiety and elevated avuncularity because they maintain a high level of feminine gender expression across childhood and adulthood. In contrast, the model suggests that cisgender androphilic males show elevated traits of separation

anxiety during childhood when they are gender atypical, but lack elevated avuncularity in adulthood due to a decrease in the intensity of gender atypicality between childhood and adulthood. Although the literature reviewed here provides a considerable amount of circumstantial evidence in support of this model, there have yet to be any direct tests of it. Specifically, it remains uncertain whether this model provides a useful framework for explaining associations among gender expression across the lifespan, childhood separation anxiety, and adulthood disposition toward kin-directed altruism among androphilic males relative to opposite-sex attracted males and females.

The Present Study

The present study tested the adaptive feminine phenotype model directly by examining recalled childhood and adulthood gender (a)typicality, recalled childhood traits of separation anxiety, and adulthood avuncularity/materterality in a Canadian sample of gynephilic men, androphilic women, and androphilic men. In previous Canadian studies, androphilic men and women recalled elevated traits of childhood separation anxiety relative to gynephilic men (VanderLaan et al., 2011b, 2015b). Such anxiety was positively correlated with childhood feminine, but not masculine, behavior in androphilic men and women; among gynephilic men, such anxiety did not correlate with gender expression (VanderLaan et al., 2015b). Meanwhile, studies of avuncularity/materterality reported that androphilic women's materteral tendencies exceeded the avuncular tendencies of both gynephilic and androphilic men while the avuncular tendencies of these men did not differ (Abild et al., 2014; Forrester et al., 2011). One goal of the present study was to verify whether similar patterns existed within the current sample.

The primary purpose of the present study, however, was to evaluate the tenability of the adaptive feminine phenotype model by testing a number of novel hypotheses and predictions derived from the model. These hypotheses and predictions were as follows:

Hypothesis 1 Childhood traits of separation anxiety due to concern about the well-being of parents is a developmental precursor of adulthood avuncularity/materterality.

Prediction 1 Childhood traits of separation anxiety due to concern about the well-being of parents, but not other sources of childhood separation anxiety, should be positively correlated with avuncularity/materterality.

Hypothesis 2 Feminine gender expressions are associated with avuncularity/materterality, and group differences in the latter are owing to parallel differences in the former.

Prediction 2 Femininity, but not masculinity, should correlate positively with avuncularity/materterality in androphilic men and women, but—similar to previous research on recalled childhood separation anxiety—not gynephilic men.

Prediction 3 Accounting for femininity by statistically controlling for its association with avuncularity/materterality should eliminate group differences in avuncularity/materterality.

Hypothesis 3 As androphilic males progress from childhood to adulthood, their level of concern about the well-being of kin decreases as a consequence of a concomitant decrease in femininity.

Prediction 4 Relative to opposite-sex attracted males and females, androphilic males should show a significant decrease in their concern about the well-being of kin from childhood to adulthood.

Prediction 5 If femininity underlies the expression of concern for the well-being of kin for androphilic males, then the discrepancy between childhood and adulthood concern for kin should correlate positively with the discrepancy between childhood and adulthood femininity.

Method

Participants

An institutional research ethics committee approved this research. Participants were required to provide informed consent prior to taking part in the study. This study was conducted via an online survey that was advertised to 757 university distribution lists and community organizations throughout Canada, and through the social networking site, Facebook. The survey was advertised to Canadian men and women who were 18 years of age and older. Individuals were informed that the survey would contain questions pertaining to human sexuality, personality, and social relationships. A total of 107 gynephilic men, 147 androphilic women, and 133 androphilic men participated in the study ($N = 387$).

Measures

Survey items regarding participants' biographic information, sexual orientation, recalled childhood gendered behavior, recalled childhood traits of separation anxiety, adult gendered behavior, and adulthood avuncularity were included. Biographic information (Table 1) included the participant's age (in years), childhood socioeconomic status, annual income, level of education completed, religious affiliation, religiosity, ethnicity, region of residence, and number of children parented. Additionally, participants were asked to report how they heard about the study (method of recruitment).

A *Kinsey scale* was used to assess participant sexual orientation (Kinsey, Pomeroy, & Martin, 1948). This measure

Table 1 Descriptive statistics for biographic information

Biographic variable	Gynephilic men ($n = 107$)	Androphilic women ($n = 147$)	Androphilic men ($n = 133$)
Age (years): *M* (*SD*)	31.30 (13.54)	28.67 (12.37)	37.20 (17.05)
Socioeconomic status during childhood			
Upper/upper-middle class (%)	27.10	29.25	20.30
Middle (%)	39.25	51.02	45.86
Lower/lower-middle class (%)	33.64	19.73	33.83
Years of education: *M* (*SD*)	14.77 (3.11)	15.40 (2.78)	15.40 (3.16)
Religious affiliation			
Christian (%)	55.14	64.63	54.89
Jewish/Muslim/Buddhist (%)	1.87	2.04	3.76
None (%)	34.58	26.53	30.83
Other (%)	8.41	6.80	10.53
Religiosity[a]: *M* (*SD*)	2.00 (1.35)	2.11 (1.21)	1.62 (1.06)
Ethnicity			
Caucasian (%)	87.85	89.80	94.74
Non-Caucasian (%)	12.15	10.20	5.26
Region			
Western Canada (%)	42.06	45.58	36.84
Ontario (%)	33.64	43.54	42.11
Quebec (%)	11.21	6.80	10.53
Eastern Canada (%)	13.08	4.08	10.53
Recruitment			
Word of mouth (%)	21.50	44.90	19.55
Facebook/online (%)	78.50	55.10	80.45
Annual income ($): *M* (*SD*)	39,700.93 (47,133.99)	25,707.48 (21,941.64)	36,259.84 (37,495.02)
Number of children parented: *M* (*SD*)	.65 (1.32)	.48 (1.03)	.19 (.72)

[a] Absolute range: 1 (not religious) to 5 (very religious)

asked participants to describe their sexual feelings over the last year. Participants were given the response range from 0-"Sexual feelings toward the opposite sex only" to 6-"Sexual feelings toward the same sex only," as well as the option of "No sexual feelings." This scale, therefore, allowed participants to identify whether they experienced same-sex, opposite-sex, bisexual, or no sexual attraction. Male and female participants who reported Kinsey scores of 0 and 1 (opposite-sex attracted men and women) and male participants who reported Kinsey scores of 5 and 6 (androphilic men) were included in the current study. All others were excluded.

The *Childhood Gender Identity Scale* (CGIS; 9 items) was used to measure participants' childhood gendered behavior (from age 6 to age 12). The CGIS has been previously validated as an appropriate measure of childhood gendered behavior (Johnson et al., 2004) and has shown appreciable inter-item reliability in retrospective studies (Bartlett & Vasey, 2006; VanderLaan et al., 2011b). It consists of a Female-Typical Behavior subscale (5 items) with items such as "How often did you play with girls?" and a Male-Typical Behavior subscale (4 items) with items such as "How often did you engage in rough-and-tumble play?" Participants responded using a 5-point Likert-type scale that ranged from 1-"Never" to 5-"Always/everyday." For each participant, mean scores were calculated for the Female-Typical Behavior and Male-Typical Behavior subscales.

The *Gender Diagnosticity Scale* (GDS; Lippa, 2000; Lippa & Sharon, 1990; 22 items) was used to measure participants' gendered behavior during adulthood. This scale assesses gendered behavior via hobby preferences, which have been shown to be an accurate measure of gender (non)conformity (Lippa, 2000). The GDS consists of a Female-Typical subscale (11 items) with items such as "How interested are you in clothes shopping?" and a Male-Typical subscale (11 items) with items such as "How interested are you in working on cars?" Participants responded using a 5-point Likert-type scale that ranged from 1-"Strongly dislike" to 5-"Strongly like." For each participant, mean scores were calculated for the Female-Typical and Male-Typical subscales.

The *Separation Anxiety Scale-Revised* (SAS-R; 13 items) was used to measure participants' recalled traits of separation anxiety between the ages of 6–12 years. The SAS-R was used previously by VanderLaan et al. (2015b) and includes a Worry subscale (8 items) consisting of items pertaining to worry

regarding the well-being of parents (e.g., "I worried a lot about something terrible happening to my parents") and a Separation subscale (5 items) consisting of items pertaining to anxiety regarding extended separation from parents (e.g., "I worried a lot about getting separated from my parents [getting kidnapped, lost]"). Participants responded using a 5-point Likert-type scale that ranged from 1-"Not true" to 5-"Very true." For each participant, mean scores were calculated for the Worry and Separation subscales.

The *Avuncular/Materteral Tendencies subscale* (9 items) was used to determine participants' willingness to care for siblings' children. Previous studies have used the Avuncular/Materteral Tendencies subscale as a measure of uncle/aunt-like behavior (Bobrow & Bailey, 2001; Rahman & Hull, 2005; Vasey et al., 2007; Vasey & VanderLaan, 2009). Participants were asked to imagine that a sibling they were close to asked for help with various childcare activities (e.g., babysitting for an evening, helping pay for the child's medical expenses) and to indicate their willingness to perform each activity. Participants responded using a 7-point Likert-type scale that ranged from 1-"Very unwilling" to 7-"Very willing." For each participant, mean scores were calculated for the Avuncular/Materteral Tendencies subscale.

For all scales, scores were standardized across the entire sample. Specifically, each scale was arbitrarily given a mean of five and a SD of one. Doing so facilitated calculating four discrepancy scores. With respect to discrepancies between adulthood and childhood gender expression, discrepancy scores were calculated for female-typical gender expression (GDS Female-Typical Behavior subscale score minus CGIS Female-Typical Behavior subscale score) and male-typical gender expression (GDS Male-Typical Behavior subscale score minus CGIS Male-Typical Behavior subscale score). With respect to discrepancies between adulthood and childhood concern about the well-being of kin, a discrepancy score was calculated for concern for kin (Avuncularity/Materterality subscale score minus Worry subscale score). As a control, we also calculated a discrepancy score for adulthood concern for kin compared to other bases of childhood anxiety related to separation from parents (Avuncularity/Materterality subscale score minus Separation subscale score). Thus, positive and negative scores indicate increases and decreases in femininity, masculinity, or concern for kin between childhood and adulthood, respectively.

Statistical Analysis

Unless otherwise stated, between-group analyses were conducted using one-way analysis of variance (ANOVA) or covariance (ANCOVA). Post hoc analyses were conducted using Fisher's Protected Test, which entails limiting Type I error by performing direct pair-wise group comparisons using Fisher's Least Significant Difference (LSD) only when a statistically significant omnibus effect was detected. This analytical approach is reasonable when assessing a priori predictions (Saville, 1990), as was the case here. Within-group analyses were conducted using two-tailed Pearson's *r* correlation or partial correlation tests. An alpha value of .05 was used for making decisions about the statistical significance of all inferential tests.

Prior to running the focal analyses, a number of procedures were performed. First, for all scales, inter-item reliability was assessed using standardized inter-item reliabilities (alphas). Second, a series of between-group and within-group analyses were conducted to evaluate whether any biographic variables should be included as covariates in analyses pertaining to the study's focal variables (i.e., gender expression, separation anxiety, avuncularity/materterality).

The remaining analyses addressed the main study aims: (1) evaluating whether previous findings were replicated in the present sample and, more importantly, (2) testing the novel predictions derived from the adaptive feminine phenotype model. Several tests were used to examine whether the present sample showed similar response patterns on measures of focal variables relative to previous samples. First, to verify similar patterns of group differences, between-group analyses of these variables were conducted using one-way ANCOVA (see "Between-Group Comparisons of Scale Scores" section). Second, within-group partial correlations between gender expression and childhood separation anxiety were performed to verify previously documented positive correlations between childhood femininity, but not masculinity, and recalled childhood separation anxiety for androphilic men and women (VanderLaan et al., 2015a) (see "Correlation Analyses of Scale Scores"). Additional statistical analyses were conducted to test the predictions derived from the adaptive feminine phenotype model as follows:

Prediction 1 Within-group partial correlations were used to examine possible associations between childhood measures of separation anxiety and adulthood avuncularity/materterality (see "Correlation Analyses of Scale Scores" section).

Prediction 2 Within-group partial correlations were used to examine associations between adulthood avuncularity/materterality and adulthood gender expression (see "Correlation Analyses of Scale Scores" section).

Prediction 3 A series of hierarchical multiple linear regressions were conducted to determine whether group differences in avuncularity/materterality were mediated by adulthood femininity (see "Mediation Analyses" section).

Prediction 4 Analyses of between-group differences in discrepancy scores were used to examine whether androphilic men exhibited a greater decrease in concern for kin between childhood and adulthood compared to others (see "Discrepancy Scores Analyses" section).

Prediction 5 Within-group partial correlations between discrepancy scores were conducted to examine whether changes in concern for kin between childhood and adulthood were associated with concomitant changes in gender expression (see "Discrepancy Scores Analyses" section).

Table 2 Subscale standardized inter-item reliabilities (alphas)

	Gynephilic men ($n = 107$)	Androphilic women ($n = 147$)	Androphilic men ($n = 133$)	Combined ($N = 387$)
Worry Subscale	.82	.83	.80	.82
Separation Subscale	.85	.81	.83	.83
Female-Typical Childhood Behavior Subscale	.68	.82	.82	.92
Male-Typical Childhood Behavior Subscale	.59	.68	.70	.80
Female-Typical Adulthood Behavior Subscale	.73	.65	.69	.76
Male-Typical Adulthood Behavior Subscale	.70	.63	.62	.69
Avuncular/Materteral Tendencies Subscale	.89	.83	.91	.89

Results

Scale Reliabilities

For each of the four subscales, alphas were computed within each group as well as for all groups combined. These reliabilities were appreciable (Table 2).

Covariates

Descriptive statistics for each of the biographic variables are shown in Table 1 as a function of group. Inferential statistics showed that participant groups did not differ significantly for years of education completed $F(2, 386) = 1.68, p = .19$, religious affiliation, $\chi^2(6) = 5.16$, $p = .52$, region of residency, $\chi^2(6) = 10.99$, $p = .089$, or ethnicity $\chi^2(2) = 3.81$, $p = .15$. Inferential statistics showed that participant groups differed significantly for age, $F(2, 386) = 12.56$, $p < .001$, religiosity, $F(2, 386) = 6.29$, $p = .002$, annual income, $F(2, 386) = 5.48$, $p = .005$, childhood socioeconomic status, $\chi^2(4) = 10.49$, $p = .033$, and method of recruitment, $\chi^2(2) = 26.27$, $p < .001$. As such, biographic items for which group differences existed were controlled in subsequent inferential analyses.

Also, because having to parent one's own children could be considered germane to one's willingness to invest in siblings' children, we examined the potential impact of number of children parented on avuncularity/materterality. A one-way ANOVA showed there was a significant effect of group for number of children parented, $F(2, 385) = 6.40$, $p = .002$. Number of children parented was significantly correlated with Materteral Tendencies scores for androphilic women ($r = -.16$, $p = .048$), but was not significantly correlated with Avuncular Tendencies scores for gynephilic men ($r = -.18$, $p = .065$) or androphilic men ($r = -.019$). As such, the influence of number of children parented on androphilic women's materteral tendencies was controlled in subsequent inferential analyses involving their materterality.

Between-Group Comparisons of Scale Scores

Descriptive statistics for each subscale are shown in Table 3 by group. Between-group analysis on the Female-Typical

Table 3 Group comparisons for the subscales

	Gynephilic men ($n = 107$)		Androphilic women ($n = 147$)		Androphilic men ($n = 133$)	
	M	*SE*	*M*	*SE*	*M*	*SE*
Worry Subscale[a,c]	4.74	.09	5.13	.08	5.07	.09
Separation Subscale	4.89	.09	5.03	.08	5.06	.09
Child Female-Typical Behavior Subscale[a,b,c]	4.15	.05	6.00	.05	4.57	.05
Child Male-Typical Behavior Subscale[a,b,c]	5.94	.07	4.19	.06	5.14	.06
Adult Female-Typical Behavior Subscale[a,b,c]	4.41	.08	5.59	.07	4.82	.08
Adult Male-Typical Behavior Subscale[a,c]	5.66	.09	4.83	.08	4.66	.08
Avuncular/Materteral Tendencies Subscale[b,c]	4.87	.09	5.27	.09	4.81	.09

[a] Androphilic men differ significantly from gynephilic men ($p < .05$)

[b] Androphilic men differ significantly from androphilic women ($p < .05$)

[c] Gynephilic men differ significantly from androphilic women ($p < .05$)

For all scales, the absolute range of the original scale was 1–5 with the exception of the Avuncular/Materteral Tendences subscale, which had a range of 1–7; however, for all scales, scores were standardized across the entire sample and arbitrarily given a mean of five and a standard deviation of one. This table reports the standardized scores

Behavior subscale of the CGIS yielded significance, $F(2, 379) = 382.25$, $p < .001$, $\eta_p^2 = .67$. Androphilic women scored significantly higher than gynephilic men ($p < .001$, Cohen's $d = 3.28$) and androphilic men ($p < .001$, Cohen's $d = 2.55$). Androphilic men scored significantly higher than gynephilic men ($p < .001$, Cohen's $d = .76$). Between-group analysis conducted on the Male-Typical Behavior subscale of the CGIS yielded significance, $F(2, 379) = 180.64$, $p < .001$, $\eta_p^2 = 49$. Gynephilic men scored significantly higher than androphilic women ($p < .001$, Cohen's $d = 2.42$) and androphilic men ($p < .001$, Cohen's $d = 1.11$). Androphilic men scored significantly higher than androphilic women ($p < .001$, Cohen's $d = 1.30$).

Between-group analysis on the Female-Typical Behavior subscale of the GDS yielded significance, $F(2, 379) = 56.59$, $p < .001$, $\eta_p^2 = .23$. Androphilic women scored significantly higher than gynephilic men ($p < .001$, Cohen's $d = 1.34$) and androphilic men ($p < .001$, Cohen's $d = .86$). Androphilic men scored significantly higher than gynephilic men ($p < .001$, Cohen's $d = .47$). Between-group analysis conducted on the Male-Typical Behavior subscale of the GDS yielded significance, $F(2, 379) = 39.66$, $p < .001$, $\eta_p^2 = .17$. Gynephilic men scored significantly higher than androphilic women ($p < .001$, Cohen's $d = .90$) and androphilic men ($p < .001$, Cohen's $d = 1.08$). Androphilic men did not differ significantly from androphilic women ($p = .16$, Cohen's $d = -.18$).

Between-group analysis on the Worry subscale yielded significance, $F(2, 379) = 5.78$, $p = .003$, $\eta_p^2 = .03$. Gynephilic men scored significantly lower than androphilic women ($p = .002$, Cohen's $d = -.41$) and androphilic men ($p = .008$, Cohen's $d = -.35$). Androphilic women did not differ significantly from androphilic men ($p = .62$, Cohen's $d = .06$). Between-group analysis conducted on the Separation subscale did not yield significance, $F(2, 379) = 1.06$, $p = .35$, $\eta_p^2 = .01$.

Between-group analysis on the Avuncular/Materteral Tendencies subscale yielded significance, $F(2, 378) = 6.80$, $p = .001$, $\eta_p^2 = .04$. Androphilic women scored significantly higher than gynephilic men ($p = .003$ Cohen's $d = .40$) and androphilic men ($p = .001$, Cohen's $d = .45$). Gynephilic and androphilic men did not differ significantly ($p = .63$, Cohen's $d = .06$).

Correlation Analyses of Scale Scores

Partial correlations between the subscales are shown in Table 4. Consistent with previous studies, for androphilic men, CGIS Female-Typical Behavior subscale scores were significantly positively correlated with Worry subscale scores ($p = .027$) and

Table 4 Partial correlations between subscales

	1	2	3	4	5	6
Gynephilic men ($n = 107$)						
1. Worry Subscale						
2. Separation Subscale	.67***					
3. Child Female-Typical Behavior Subscale	−.04	.12				
4. Child Male-Typical Behavior Subscale	.17	−.06	−.32***			
5. Adult Female-Typical Behavior Subscale	.04	.09	.22*	−.05		
6. Adult Male-Typical Behavior Subscale	.03	−.15	−.13	.29**	.34***	
7. Avuncular/Materteral Tendencies Subscale	.03	.03	<−.01	−.02	.04	−.04
Androphilic women ($n = 147$)						
1. Worry Subscale						
2. Separation Subscale	.57***					
3. Child Female-Typical Behavior Subscale	.12	.18*				
4. Child Male-Typical Behavior Subscale	−.07	−.14	−.48***			
5. Adult Female-Typical Behavior Subscale	.06	.07	.29***	−.16		
6. Adult Male-Typical Behavior Subscale	.17*	.12	−.16	.29***	.21*	
7. Avuncular/Materteral Tendencies Subscale	.16	.07	.14	.02	.20*	.16
Androphilic men ($n = 133$)						
1. Worry Subscale						
2. Separation Subscale	.65***					
3. Child Female-Typical Behavior Subscale	.20*	.23**				
4. Child Male-Typical Behavior Subscale	−.14	−.14	−.69***			
5. Adult Female-Typical Behavior Subscale	.06	.13	.30***	−.20*		
6. Adult Male-Typical Behavior Subscale	−.07	−.05	−.22*	.39***	.26**	
7. Avuncular/Materteral Tendencies Subscale	−.05	−.07	.06	.03	.25**	.19*

* $p \leq .05$; ** $p \leq .01$; *** $p \leq .001$

Separation subscale scores ($p = .01$). For androphilic women, CGIS Female-Typical Behavior subscale scores were significantly positively correlated with Separation subscale scores ($p = .037$). Worry and Avuncular/Materteral Tendencies subscale scores were not significantly correlated for any groups, although there was some limited support for Prediction 1 in that there was a marginally significant positive association among these variables for androphilic women ($p = .058$). Avuncular/Materteral Tendencies subscale scores were significantly positively correlated with GDS Female-Typical Behavior subscale scores for androphilic women ($p = .015$) and androphilic men ($p = .005$), which was consistent with Prediction 2. Unexpectedly, however, Avuncular Tendencies scores were also significantly positively correlated with GDS Male-Typical Behavior subscale scores for androphilic men ($p = .035$).

Mediation Analyses

The patterns of between-group differences and within-group correlations for the GDS Female-Typical Behavior subscale and Avuncular/Materteral Tendencies subscale fit the criteria for mediation (Frazier, Tix, & Barron, 2004; Preacher, Rucker, & Hayes, 2007). Specifically, it is possible that the difference in avuncularity/materterality between androphilic women and gynephilic men may be due to a combination of: (1) a parallel group difference in female-typical behavior and (2) the positive correlation between materterality and female-typical behavior among androphilic women. Meanwhile, the avuncularity/materterality difference between androphilic women and androphilic men may be due to a combination of: (1) a parallel group difference in female-typical behavior and (2) the positive correlation between avuncularity/materterality and female-typical behavior among androphilic men and women.

To evaluate whether this was the case, a series of hierarchical multiple linear regressions controlling for the relevant biographic variables were conducted based on the guidelines of Fraizer et al. (2004) and Preacher et al. (2007). Three steps were involved in these analyses. First, we verified the GDS Female-Typical Behavior subscale difference between opposite-sex attracted men and women ($B = -1.22$, $SE = .12$, $\beta = -.55$, $p < .001$, $sr_i^2 = .21$) as well as that between androphilic men and women ($B = -.80$, $SE = .12$, $\beta = -.38$, $p < .001$, $sr_i^2 = .10$) ($B = -.768$, $SE = .112$, $p < .001$).[3] Second, we verified that Avuncular/Materteral Tendencies scores were significantly predicted by GDS Female-Typical Behavior in androphilic men and women ($B = .08$, $SE = .03$, $\beta = .13$, $p = .009$, $sr_i^2 = .02$).[4] Third, we examined the possible mediation effects by assessing group differences in Avuncular/Materteral Tendencies scores while controlling for the Female-Typical Behavior scores of androphilic men and women.[5] When controlling for GDS Female-Typical Behavior, gynephilic men were significantly higher than androphilic women for Avuncular/Materteral Tendencies subscale scores ($B = 1.21$, $SE = .43$, $\beta = .54$, $p = .005$, $sr_i^2 = .02$) due to a significant complete moderated mediation effect (Sobel's test: $z = -2.54$, $p = .011$). Meanwhile, the difference between androphilic men and women in Avuncular/Materteral Tendencies subscale scores was no longer significant ($B = -.26$, $SE = .14$, $\beta = -.13$, $p = .066$, $sr_i^2 = .01$), and the disappearance of this effect was due to a significant complete mediation effect (Sobel's test: $z = -2.44$, $p = .015$). Thus, these mediation analyses provided support for Prediction 3.

Discrepancy Scores Analyses

The descriptive statistics for the discrepancy scores are shown in Table 5 by group. For the discrepancy in adulthood and childhood female-typical gender expression, there was a significant effect of group, $F(2, 379) = 22.48$, $p < .001$, $\eta_p^2 = .11$. Between childhood and adulthood, androphilic women's Female-Typical Behavior decreased significantly more compared to gynephilic men ($p < .001$, Cohen's $d = -.74$) and androphilic men ($p < .001$, Cohen's $d = -.69$). Gynephilic men did not differ significantly from androphilic men (Cohen's $d < .01$). For the discrepancy in adulthood and childhood male-typical gender expression, there was a significant effect of group, $F(2, 379) = 47.07$, $p < .001$, $\eta_p^2 = .20$. Between childhood and adulthood, androphilic women's Male-Typical Behavior increased significantly more compared to gynephilic men ($p < .001$, Cohen's $d = .94$) and androphilic men ($p < .001$, Cohen's $d = 1.13$). Gynephilic men did not differ significantly from androphilic men ($p = .098$, Cohen's $d = .22$).

For the discrepancy in adulthood and childhood concern for kin, there was a significant effect of group, $F(2, 378) = 3.64$, $p = .027$, $\eta_p^2 = .02$. Between childhood and adulthood, androphilic men exhibited a significantly greater decrease in concern for kin compared to gynephilic men ($p = .023$, Cohen's $d = -.29$) and androphilic women ($p = .02$, Cohen's $d = -.30$). Discrepancies in concern for kin did not differ significantly between gynephilic men and androphilic women (Cohen's $d =$

[3] This step is necessary to obtain coefficients associated with the regression of Female-Typical Behavior scores on group that were used in the calculation of a mediation effect. Two dummy coded predictor variables were used to compare androphilic women to the two groups of men (androphilic women were coded as 0 for both predictor variables).

[4] Given that significant positive correlations between Avuncularity/Materterality and GDS Female-Typical Behavior Scores existed for only androphilic men and women, an interaction term was used for this analysis. Creating the interaction term entailed multiplying the GDS Female-Typical Behavior subscale scores with a dummy coded variable for which androphilic men and women were coded as 1 and gynephilic men were coded as 0.

[5] This analysis controlled for Female-Typical Behavior scores in androphilic men and women, but not gynephilic men, because these scores were correlated with Avuncularity/Materterality scores for the former two groups only.

Table 5 Group comparisons for discrepancy scores

	Gynephilic men ($n = 107$)		Androphilic women ($n = 147$)		Androphilic men ($n = 133$)	
	M	*SE*	*M*	*SE*	*M*	*SE*
Avuncular/Materteral Tendencies Subscale minus Worry Subscale[a,b]	.12	.13	.16	.12	−.28	.12
Avuncular/Materteral Tendencies Subscale minus Separation Subscale[b]	−.01	.13	.22	.13	−.24	.13
Adult Female-Typical Behavior Subscale minus Child Female-Typical Behavior Subscale[b,c]	.26	.09	−.41	.08	.25	.08
Adult Male-Typical Behavior Subscale minus Child Male-Typical Behavior Subscale[b,c]	−.28	.09	.64	.08	−.48	.09

[a] Androphilic men differ significantly from gynephilic men ($p < .05$)

[b] Androphilic men differ significantly from androphilic women ($p < .05$)

[c] Gynephilic men differ significantly from androphilic women ($p < .05$)

−.03). For the discrepancy in adulthood concern for kin and anxiety unrelated to concern about parental well-being during periods of separation from parents, there was not a significant effect of group, $F(2, 378) = 2.86$, $p = .059$, $\eta_p^2 = .02$; however, androphilic men exhibited a significantly greater decrease than androphilic women ($p = .018$, Cohen's $d = -.26$) whereas gynephilic men did not differ from androphilic women ($p = .24$, Cohen's $d = -.10$) or androphilic men ($p = .20$, Cohen's $d = .16$). These patterns of group differences were consistent with Prediction 4.

Within-group partial correlations between the Avuncular/Materteral Tendencies and SAS-R subscales discrepancy scores and gender expression discrepancy scores are shown in Table 6. For androphilic men, there was a significant positive correlation between the change in femininity and the change in concern for kin between childhood and adulthood ($p = .028$), indicating that increases in femininity were associated with increases in concern for kin while decreases in femininity were associated with decreases in concern for kin. No other correlations obtained significance. This pattern of results confirmed Prediction 5.

Discussion

The present study tested several underlying tenets of the adaptive feminine phenotype model, which posits that a disposition toward elevated kin-directed altruism among androphilic males is contingent on the behavioral expression of femininity. As detailed below, most, but not all, of the predictions were well supported by the data presented here. Thus, the adaptive feminine phenotype model appears to be a tenable explanation for the cross-cultural discrepancies regarding same-sex attracted males' avuncular tendencies.

Importantly, a number of patterns observed in previous studies were confirmed in the current sample. First, for both childhood

Table 6 Partial correlations between discrepancy scores

	1	2	3
Gynephilic men ($n = 107$)			
1. Avuncular/Materteral Tendencies Subscale minus Worry Subscale			
2. Avuncular/Materteral Tendencies Subscale minus Separation Subscale	.83***		
3. Adult Female-Typical Behavior Subscale minus Child Female-Typical Behavior Subscale	−.01	<.01	
4. Adult Male-Typical Behavior Subscale minus Child Male-Typical Behavior Subscale	.03	.06	.34***
Androphilic women ($n = 147$)			
1. Avuncular/Materteral Tendencies Subscale minus Worry Subscale			
2. Avuncular/Materteral Tendencies Subscale minus Separation Subscale	.69***		
3. Adult Female-Typical Behavior Subscale minus Child Female-Typical Behavior Subscale	.08	.11	
4. Adult Male-Typical Behavior Subscale minus Child Male-Typical Behavior Subscale	−.09	−.08	.16
Androphilic men ($n = 133$)			
1. Avuncular/Materteral Tendencies Subscale minus Worry Subscale			
2. Avuncular/Materteral Tendencies Subscale minus Separation Subscale	.86***		
3. Adult Female-Typical Behavior Subscale minus Child Female-Typical Behavior Subscale	.19*	.16	
4. Adult Male-Typical Behavior Subscale minus Child Male-Typical Behavior Subscale	.08	.06	.18*

* $p \leq .05$; ** $p \leq .01$; *** $p \leq .001$

and adulthood measures of gender expression, gynephilic men were more masculine than androphilic women, androphilic women were more feminine than gynephilic men, and androphilic men were intermediate. Second, gynephilic men reported significantly lower levels of childhood concern for parents than androphilic men and women, whereas these latter two groups did not differ significantly for this measure. Third, Female-Typical Behavior scores were positively correlated with the separation anxiety measures among androphilic men and women. Fourth, the materteral tendencies of androphilic women were greater than the avuncular tendencies of gynephilic and androphilic men.

Hypothesis 1 predicted that childhood traits of separation anxiety due to concern about the well-being of parents are a developmental precursor of adulthood avuncularity/materterality. Support for this hypothesis was limited because, inconsistent with Prediction 1, concern about the well-being of parents in childhood and avuncular/materteral tendencies in adulthood were not positively correlated among any of the groups, although there was a trend toward significance for androphilic women.

VanderLaan et al. (2011a) argued that the association between childhood concern for parental well-being and adulthood avuncularity/materterality should be strong for androphilic females because elevated concern for the well-being of kin would facilitate effective caring of young, dependent offspring. As such, the lack of an association between these variables among gynephilic men is not particularly surprising given that fathers are less critical than mothers to the survival of offspring (Sear & Mace, 2008). VanderLaan et al.'s (2011a) model argued that, unlike gynephilic males, androphilic males would be similar to androphilic females in this regard given that their indirect fitness critically depends on kin. That being said, it also argued that elevated adulthood femininity was important to the expression of the evolved avuncular androphilic male phenotype. It is, therefore, also not particularly surprising that these domains were not correlated among the current sample of Canadian cisgender androphilic men. Consequently, our Canadian sample of cisgender androphilic men may not have been appropriate for testing this specific aspect of the adaptive feminine phenotype model (Prediction 1). Future research may consider testing Prediction 1 in a sample of transgender same-sex attracted males such as the Samoan *fa'afafine* given that they might be a more relevant group for testing this particular prediction.

Hypothesis 2 argued that gender expression, particularly femininity, is associated with avuncularity/materterality, and that group differences in avuncularity/materterality are due to parallel differences in gender expression. Predictions 2 and 3 were derived from this hypothesis. In line with Prediction 2, adulthood femininity was significantly positively correlated with materterality among androphilic women and avuncularity among androphilic men, whereas no such significant correlation existed for gynephilic men.

Unexpectedly, however, adulthood masculinity was also significantly positively correlated with avuncular tendencies among androphilic men. One possible explanation for this unexpected correlation draws on the fact that interest in masculine vs. feminine occupations and hobbies are positively correlated (see Table 4). As such, individuals who have high scores for femininity on the GDS also tend to have high scores for masculinity on the GDS, which renders this measurement instrument less than ideal in contexts such as the present one where differing response patterns are predicted for femininity vs. masculinity. An alternate scale for measuring adult feminine vs. masculine gender expression that would produce scale scores that are relatively more independent and non-overlapping may, therefore, be more optimal for studies similar to the present one.

An alternative explanation for the positive correlation between adulthood masculinity and avuncular tendencies among androphilic men stems from gay men's sexual and romantic relationship partner preferences. Gay men tend to favor masculine, as opposed to feminine, male sexual partners (Bailey, Kim, Hills, & Linsenmeier, 1997). It is possible, then, that androphilic men who are avuncular and exhibit interests considered feminine on the GDS (e.g., shopping) compensate for these putatively less attractive qualities by simultaneously showing interest in putatively more attractive, masculine activities found in the GDS (e.g., sports).

In any case, future replications of this research will be necessary to determine whether this unexpected correlation is genuine or spurious (i.e., Type I error) in nature. Importantly, given the possible limits of the GDS, other measures of adult masculinity and femininity should also be employed. If this unexpected correlation does prove to be genuine, then additional research should aim to detail the manner in which masculine gender expression contributes toward avuncular tendencies and behavior among androphilic males.

Consistent with Prediction 3, when the positive association between avuncular/materteral tendencies and adulthood femininity among androphilic men and women was controlled, the androphilic women no longer scored significantly higher than gynephilic and androphilic men.[6] These changes in significance were due to significant complete mediation effects of feminine behavioral expression toward willingness

[6] When comparing gynephilic men and androphilic women for Avuncular/Materteral Tendencies scores while controlling for GDS Female-Typical Behavior scores, the direction of the group difference reversed; however, we caution the reader against interpreting this change in the direction of the effect as an indication that gynephilic men are more willing to invest in nieces and nephews once femininity is taken into account. The reversal in the heterosexual sex difference observed in this analysis is likely a statistical artifact (commonly referred to as a "suppression effect") that occurred because degree of feminine behavioral expression, compared to sex of heterosexual participant, was substantially more predictive of willingness to invest in nieces and nephews in the regression model (for further discussion of this statistical artifact, see Giles, 1989).

to invest in nieces and nephews. These findings indicate that femininity is a key factor influencing group differences in willingness to invest in nieces and nephews.

Hypothesis 3 argued that as androphilic males progress from childhood to adulthood, their level of concern about the well-being of kin decreases as a consequence of a concomitant decrease in femininity. Predictions 4 and 5 were derived from this hypothesis. Consistent with Prediction 4, relative to opposite-sex attracted men and women, androphilic men showed a significant decrease in their concern about the well-being of kin from childhood to adulthood. This pattern was found when comparing androphilic men to both other groups using the Avuncular/Materteral tendencies subscale minus the Worry subscale and when comparing androphilic men to androphilic women using the Avuncular/Materteral tendencies subscale minus the Separation subscale. It is noteworthy that the more robust between-group findings in support of Prediction 4 were those based on avuncularity/materterality and childhood concern for the well-being of parents, rather than the anxiety related to separation from parents, which would be expected according to the adaptive feminine phenotype model.

Consistent with Prediction 5, the discrepancy between childhood and adulthood concern for the well-being of kin correlated positively with the discrepancy between childhood and adulthood femininity among androphilic men. In other words, androphilic men who increased in femininity also tended to show an increase in concern about the well-being of kin; androphilic men who decreased in femininity also tended to show a decrease in concern about the well-being of kin. These findings further implicate femininity as being of proximal importance to androphilic males' concern for the well-being of kin.

The question remains as to why femininity has such proximal importance. Female kin such as mothers and grandmothers appear to have greater influence on offspring survival than male kin such as fathers and grandfathers (Sear & Mace, 2008). As such, VanderLaan et al. (2011a) suggested that being a female-like individual and having a disposition toward securing the well-being of kin might be part of the same psychological/behavioral complex. If so, given the putative relevance of avuncularity to enhancing indirect fitness in androphilic males and the fact that femininity mediates the expression of avuncularity in this group, it follows that selection would favor a close association between these traits and male androphilia over evolutionary time.

Following this logic, because selection creates phenotypes by acting on genes, one might predict that the links among these characteristics are based on common genetic factors. Twin studies have indicated that common genetic factors underlie same-sex attraction and gender-atypical behavior (Alanko et al., 2010) as well as neuroticism, which is conceptually similar to anxiety (Zietsch, Verweij, Bailey, Wright, & Martin, 2011). Furthermore, findings from a mouse model showed that Xq28, a region of the X-chromosome linked to human male sexual orientation (Hu et al., 1995; Sanders et al., 2015), is associated with anxious behavioral patterns (i.e., less exploratory behavior) using open field, elevated maze, and light–dark box paradigms (Samaco et al., 2012). Thus, there appears to be some cursory evidence to suggest that common genetic factors underlie the psychological characteristics investigated in the current study.

An additional important question that needs to be addressed by future research pertains to the role of kin selection in the evolutionary maintenance of genes underlying male androphilia, if any such role does exist. Here, we focused on testing for associations among childhood separation anxiety, adulthood avuncularity, and gender expression across the lifespan that were hypothesized to exist should the adaptive feminine phenotype model be accurate. This study did not, therefore, provide any data that speak directly to the impact of investment in nieces and nephews on indirect fitness. That said, similar to the present study, several studies have tested evolutionarily minded predictions derived from the kin selection hypothesis and found that androphilic males possess features of avuncular cognition that would, in theory, enable them to maximize indirect fitness (for review, see VanderLaan & Vasey, 2014). If past selection pressure is indeed responsible for the existence of such specialized cognitive features, then the kin selection hypothesis at least partially accounts for past evolutionary maintenance of genes underlying male androphilia ipso facto. Future research measuring the impacts of same-sex attracted males' avuncular investment on the quantity and quality of nieces and nephews will help clarify the extent to which kin selection accounts for the persistence of genes underlying male androphilia, and if additional evolutionary mechanisms are required to provide a complete explanation.

Limitations

The measures employed here were selected because they were the same as those used in previous studies that VanderLaan et al. (2011a) relied on when proposing the adaptive feminine phenotype model. As such, these measures provided a relevant starting point for testing this model. Yet, although these measures have all been psychometrically validated and successfully employed on their own in previous research, in hindsight, they may not have been optimal for the current study. For example, in the present study, the Avuncular/Materteral Tendencies and Worry subscales were employed as measures of an underlying construct posited by VanderLaan et al. Namely, they were both used as measures of level of concern for the well-being of kin. However, the former measure was designed to assess willingness to invest in nieces and nephews (Bobrow & Bailey, 2001) while the latter measure was designed to measure recalled anxiety related to worrying about the well-being of parents in particular (VanderLaan et al., 2015a). These subscales were not designed to be direct measures of general concern for the well-being of kin and this may explain why scores for these

subscales were not strongly correlated in the manner predicted (i.e., Prediction 1). Future research may, therefore, attempt to employ superior measures that directly assess childhood and adulthood concern for the well-being of kin in general as opposed to very specific categories of kin.

Similarly, the scales that were used to assess childhood and adulthood gender expression may not have been sufficiently well matched despite a number of strengths. The CGIS and the GDS have reliably yielded the expected sex and sexual orientation differences (CGIS: Johnson et al., 2004; GDS: Lippa, 2005) and provided results that were consistent with other similar measures of masculinity and femininity in males and females (Lippa, 2005; VanderLaan et al., 2011b). Also, in the present sample, the CGIS and GDS Female-Typical Behavior subscales were positively correlated, as were the CGIS and GDS Male-Typical Behavior subscales. Nonetheless, because the CGIS measures these constructs with items related to childhood behavior, whereas the GDS uses occupational and hobby preferences, these measures may not have been sufficiently similar to provide a clear sense of how masculinity and femininity change, or remain stable, as a function of life stage (i.e., childhood vs. adulthood). As mentioned above, an additional limit of the GDS is that stereotypically masculine vs. feminine occupational and hobby preferences tend to be positively correlated, resulting in overlap between these constructs. Thus, future research might consider using more comparable measures of childhood and adulthood gender expression that produce more independent constructs of masculinity vs. femininity.

Conclusions

The current study informed the adaptive feminine phenotype model and, by extension, our understanding of the evolution of male androphilia. The findings indicated that femininity among androphilic males might have a unique evolutionary significance. Among androphilic men in the present sample, femininity was associated with individual differences in both childhood concern for parental well-being and adulthood avuncularity. Femininity also accounted for why androphilic men reported lower willingness to allocate time and money toward nieces and nephews compared to androphilic women. With respect to developmental patterns, between childhood and adulthood, androphilic men's level of concern for kin's well-being tended to decrease compared to opposite-sex attracted men and women. Such decreases were associated with concomitant decreases in femininity.

Together, these findings suggest that femininity is critical to the expression of elevated kin-directed altruism in same-sex sexually oriented males. If so, this may explain why the kin selection hypothesis has been repeatedly supported among the transgender Samoan *fa'afafine*, but not among relatively more masculine adult androphilic males in other countries who identify as men. Hence, if kin selection contributed to the persistence of genetic factors underlying male androphilia, then a markedly feminine or transgender expression of male same-sex sexuality may have been critical for elevated kin-directed altruism. Ethnological data indicate that ancestral same-sex sexually attracted males were indeed likely to exhibit marked feminine or transgender gender expression in a manner similar to the Samoan *fa'afafine* within the context of early human tribal societies (VanderLaan et al., 2013b). Thus, the present study is part of a growing literature supporting the notion that ancestral same-sex attracted males exhibited elevated kin-directed altruism. Such altruism might then have contributed, at least partially, to the persistence of genetic factors underlying male androphilia.

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