Evolutionary Perspectives on Male Androphilia in Humans

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Introduction

Androphilia refers to predominant sexual attraction and arousal to adult males, whereas *gynephilia* refers to predominant sexual attraction and arousal to adult females. Research on the evolution of same-sex sexuality in humans has focused on explaining the origin of exclusive male androphilia and its persistence over time. The evolution of female gynephilia in humans remains under-theorized and researched (but see Diamond, 2006; Zietsch, Morley, Shekar, Verweij, Keller, Macgregor et al., 2008), although a much more substantial body of evolutionary research on female–female sexual behavior exists for non-human primates such as bonobos (Fruth & Hohmann, 2006) and Japanese macaques (Vasey, 2006; Vasey & VanderLaan, 2012).

Until very recently, it would not have been possible to write a book chapter, like this one, which examines the evolution of male androphilia from an evidence-based, quantitative perspective. There simply was not enough information available to justify a review of the literature. In 2004, Andrea Camperio Ciani and his colleagues published what was arguably the first study to gain any traction in relation to understanding the evolutionary paradox that is male androphilia (Camperio-Ciani, Corna, & Capiluppi, 2004). Prior to that, there existed only a single quantitative study on this topic and it reported nonsignificant findings (Bobrow & Bailey, 2001). Apart from that, the literature on the evolution of male androphilia could aptly be characterized up to that point in time as overwhelmingly theoretical and speculative, with no grounding in any quantitative data whatsoever.

Since the publication of the Camperio-Ciani et al. (2004) study, however, significant advances have been made in understanding how a trait like male androphilia, which lowers reproductive success, might persist over evolutionary time. For example, a number of hypotheses that attempt to account for the evolution of male androphilia have been quantitatively examined in different populations including, importantly, nonindustrialized and non-Western ones. Moreover, data relevant to the testing of evolutionary hypotheses has been collected on different cultural forms of male androphilia, thereby extending our knowledge beyond Western "gays." In what follows, we provide a framework for thinking about how to study the evolution of male androphilia and a review of the pertinent literature.

The Expression of Male Androphilia Varies Cross-Culturally

The manner in which male androphilia is publically expressed varies across cultures (Murray, 2000).

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This expression typically takes one of two forms, which are related to gender role enactment. These two forms are *sex-gender congruent* and *transgendered* male androphilia. Sex-gender congruent male androphiles occupy the gender role typical of their sex, behave in a relatively masculine manner, and identify as "men." In contrast, transgendered androphilic males typically behave in an effeminate manner and identify as neither "men" nor "women," but rather as members of some "third" gender category. In some cultures, transgendered male androphilia is linked to particular institutionalized labor practices, which often involve specialized religious activities. For example, on the Indian subcontinent, transgendered male androphiles known as *hijra* bestow blessings from Hindu gods and goddesses for luck and fertility at weddings and at the birth of male babies (Nanda, 1999). Some authors refer to such transgendered male androphilia as "role-structured homosexuality" (Herdt, 1997). Both sex-gender congruent and transgendered male androphilia may occur within a given culture, but typically one or the other tends to predominate (Whitam, 1983). For example, the sex-gender congruent form is more common in many Western cultures, whereas the transgendered form appears to be more common in a number of non-Western cultures (Murray, 2000).

Other authors have referred to sex-gender congruent male androphilia as "egalitarian male homosexuality" (Murray, 2000) and "homophilic homosexuality" (Gorer, 1966). However, the term "sex-gender congruent" androphilia highlights the critical role of gender role enactment in distinguishing the two forms of male androphilia under consideration here. There are several reasons why "androphilia" is the preferential term when undertaking cross-cultural comparisons of male same-sex sexuality. First, the usage and meaning of the term "homosexuality" vary cross-culturally, rendering it a poor construct for the type of cross-cultural research reviewed here. Second, "androphilia" pertains to sexual attraction and arousal, not sexual behavior, which may be constrained by cultural circumstances (e.g., taboos against same-sex sexual behavior) or enacted for ritual purposes. As such, the term "androphilia" makes no assumptions about whether sexual behavior has been expressed. Third, this terminology makes no assumptions about the sexual orientation or the gender role enactment of the *sexual partners* of male androphiles. As such, although transgendered male androphiles routinely engage in sexual activity with masculine males who identify as "men" (Murray, 2000), these men may or may not be androphilic themselves. This may seem perplexing from a Western cultural perspective in which sex-gender congruent male androphiles routinely seek out other sex-gender congruent male androphiles for sexual interactions. However, it is important to note that gynephilic males' willingness to engage in sexual interactions with their less preferred sex varies tremendously across cultures (Whitam & Mathy, 1986). In cultures where transgendered male androphilia predominates, male gynephiles may, for example, experience relatively less sexual aversion to the idea of engaging in certain types of same-sex sexual interactions because, to some extent, transgendered male androphiles represent facsimiles resemble their preferred sex partners (i.e., adult females). The possibility that gynephilic males are cross-culturally invariant in terms of their preference for female sexual partners when given a choice but cross-culturally variable in terms of their aversion to accepting (feminine) male sex partners when they cannot obtain their preferred sex is one that deserves much more research attention.

In addition to these two forms of male androphilia, a third form—transgenerational homosexuality—has also been reported in the literature. Transgenerational homosexuality involves sexual interactions between a sexually immature or younger male and a sexually mature or older male (Murray, 2000). Comparative research on non-human primates suggests that transgenerational homosexuality has a different evolutionary origin than sex-gender congruent and transgendered male androphilia (Dixson, 2010). Furthermore, it is not clear that transgenerational homosexuality is motivated by androphilia on the part of either the older or younger partner. For example, in some instances these same-sex interactions might be enacted for primarily alistic purposes. Moreover, depending on the individual, the older partners in these interactions might be best characterized as either pedophilic (i.e., sexually attracted/aroused to prepubescent individuals), hebephilic (i.e., sexually attracted/aroused to peripubescent individuals), or gynephilic, not androphilic. Similarly, the younger partners might be (pre)gynephilic, not (pre) androphilic. Given these reasons, we do not consider transgenerational homosexuality here. For a discussion of unique properties of transgenerational homosexuality from an ethnological perspective, see Crapo (1995).

Cross-Culturally Invariant Correlates of Male Androphilia

Attempts to draw comparisons between sex-gender congruent and transgendered male androphilic males have been characterized as misguided because, critics argue, these unique patterns cannot be understood outside of the specific cultural contexts in which they exist (Johnson, Jackson, & Herdt, 2000). As such, the overall impression one gleans from this literature is that a panoply of male "androphilias" exists. Not surprisingly, there has been debate in the literature concerning whether distinct or common underlying causal processes characterize male androphilia in different cultures. If it were possible to establish that androphilic males from different cultural backgrounds shared associated features that are indicators, at least in theory, of underlying causal processes, then this would give support to the possibility of common biological bases. Indeed, quantitative research indicates that the sex-gender congruent and transgendered forms of male androphilia share numerous developmental and biodemographic correlates that are cross-culturally invariant.

In terms of biodemographic correlates that exist across cultures, sex-gender congruent and transgendered male androphiles tend to be later born among their siblings (e.g., Blanchard, 2004; VanderLaan & Vasey, 2011; Vasey & VanderLaan, 2007), have greater numbers of older biological brothers ("fraternal birth order effect,"[1] e.g., Bogaert & Skorska, 2011; VanderLaan & Vasey, 2011; Vasey & VanderLaan, 2007), exhibit larger family sizes (Blanchard & Lippa, 2007; Camperio-Ciani et al., 2004; Iemmola & Camperio Ciani, 2009; King, Green, Osborn, Arkell, Heatherton, & Pereira, 2005; Rahman, Collins, Morrison, Orrells, Cadinouche, Greenfield et al., 2008; Schwartz, Kim, Kolundziji, Rieger, & Sanders, 2010; VanderLaan, Forrester, Petterson, & Vasey, 2012; VanderLaan & Vasey, 2011; Vasey & VanderLaan, 2007), cluster within families (e.g., Schwartz et al., 2010; VanderLaan, Forrester, Petterson, & Vasey, 2013a; VanderLaan, Vokey, & Vasey, 2013b), occur at similar prevalence rates across different populations (e.g., Smith, Rissel, Richters, Grulich, & de Visser, 2003; VanderLaan et al., 2013a; Whitam, 1983), and exhibit little or no reproductive success (e.g., King et al., 2005; Schwartz et al., 2010; Vasey, Parker, & VanderLaan, 2014). In addition, the odds ratios associated with the fraternal brother effect in various populations of sex-gender congruent and transgendered male androphiles are remarkably consistent, suggesting that the manner in which older brothers influence the development of male androphilia is constant across diverse populations (e.g., Cantor, Blanchard, Paterson, & Bogaert, 2002; VanderLaan & Vasey, 2011).

Prospective and retrospective cross-cultural research on early psychosocial development among transgendered and sex-gender congruent male androphiles has shown that the childhood behavior of such males is characterized by greater levels of female-typical behavior (e.g., nurturing play with dolls) and lower levels of male-typical behavior (e.g., rough-and-tumble play; Bailey & Zucker, 1995; Bartlett & Vasey, 2006; Cardoso, 2005, 2009; Whitam, 1983). In addition, both types of male androphiles express elevated cross-sex beliefs and wishes in childhood (e.g., "I think I really am a girl") (Bailey & Zucker, 1995; Vasey &

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[1] The *fraternal birth order effect* refers to the well-established finding that the number of older biological brothers increases the odds of androphilia in later born males (Blanchard, 2004; Bogaert & Skorska, 2011).

Bartlett, 2007; Whitam, 1983). Furthermore, both sex-gender congruent and transgendered male androphiles also experience elevated traits of childhood separation anxiety (i.e., anxiety related to separation from major attachment figures such as parents; VanderLaan, Gothreau, Bartlett, & Vasey, 2011a; Vasey, VanderLaan, Gothreau, & Bartlett, 2011; Zucker, Bradley, & Sullivan, 1996), which tend to be more common among girls compared to boys (e.g., Shear, Jin, Ruscio, Walters, & Kessler, 2006; VanderLaan et al., 2011a). In adulthood, male androphiles from a range of cultures exhibit preferences for a variety of female-typical occupations and hobbies (e.g., interior design) (Lippa, 2005; Whitam, 1983).

Even though sex-gender congruent androphilic males are relatively feminine as boys compared to their gynephilic counterparts (Bailey & Zucker, 1995), they behaviorally defeminize to varying degrees as they develop. It has been suggested that this behavioral defeminization probably occurs in response to culturally specific gender role expectations, which hold that male-bodied individuals should behave in a masculine manner (Bailey, 2003; Berling, 2001; Rieger & Savin-Williams, 2012). In contrast, in cultures where transgendered male androphilia is the norm, feminine boys develop into feminine adult males. Consequently, adult sex-gender congruent male androphiles are relatively masculine when compared to transgendered adult male androphiles (Murray, 2000). Conversely, they are, on average, relatively feminine when compared to adult male gynephiles (Bailey, 2003; Lippa, 2005). Thus, regardless of how it is manifested, male androphilia is associated with gender atypicality in childhood and adulthood. However, the strength of this association varies depending on the manner in which male androphilia is publically expressed.

Taken together, these numerous, cross-culturally invariant biodemograpphic and developmental correlates of male androphilia indicate that sex-gender congruent and transgendered male androphilia share a common etiological basis despite being superficially different in appearance.

Male Androphilia Is an Evolutionary Paradox

The biodemographic and developmental evidence outlined above suggests that sex-gender congruent and transgendered male androphilia are cultural variants of what is essentially the same phenomenon with a common biological basis. The existence of diverse forms of male androphilia across cultures, which nonetheless appear to share similar a etiology, is an evolutionary paradox. There appears to be some genetic influence on male androphilia (e.g., Bailey, Dunne, & Martin, 2000; Kendler, Thornton, Gilman, & Kessler, 2000; Långström, Rahman, Carlström, & Lichtenstein, 2010), yet androphilic men reproduce at significantly lower rates than gynephilic men (e.g., King et al., 2005; Schwartz et al., 2010; Vasey et al., 2014). Consequently, one would have expected genes for male androphilia to become extinct given the relative reproductive costs associated with this trait and the reproductive benefits associated with male gynephilia.

Nevertheless, prehistoric rock art and pottery suggest that male–male sexual activity has existed for millennia (e.g., Larco Hoyle, 1998; Nash, 2001; Yates, 1993). Further, graves containing male skeletal remains and female-typical artifacts are indicative of transgendered males in the distant past (e.g., Hollimon, 1997; Knüsel & Ripley, 2000). Prine (2000) argued that certain architecturally unusual dwellings, inhabited by the Hidatsa[2] people between 1400 and 1800 AD, were the homes of transgendered males known locally as *miati*. Given what we know about the exclusive androphilic orientation of most transgendered males from comparable populations (e.g., Harrington, 1942; Murray, 2000; Nanda, 1999), archaeological indicators of such individual are suggestive of the presence of male androphilia in human antiquity.

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[2] The Hidatsa are a native North American people that lived in palisaded villages along the Missouri River in North Dakota from 1400 to 1800 AD.

In sum, male androphilia has a genetic component and appears to have existed for millennia; yet male androphiles reproduce at a fraction of the rate that gynephilic males do, if they reproduce at all. For these reasons, male androphilia is widely considered one of the outstanding paradoxes of evolutionary psychology. A trait that lowers direct reproduction and persists over evolutionary time requires explanation when viewed within the context of natural selection, a process that favors the evolution of reproductively viable traits.

Male Androphilia in the Ancestral Environment

Given that the manner in which male androphilia is publically expressed varies cross-culturally, the question arises as to which form, sex-gender congruent or transgendered, was the ancestral form. Identifying the ancestral form of male androphilia is critical if we seek to test hypotheses pertaining to the evolution of this trait in an accurate manner. More derived forms of this trait might reflect historically recent, cultural influences.

With this concern in mind, VanderLaan, Ren, and Vasey (2013) attempted to identify the ancestral form of male androphilia. They did so by examining whether societies in which transgendered male androphilia predominates exhibit more of the sociocultural features that are believed to have characterized the human ancestral past relative to a comparison group of societies in which transgendered male androphilia did not predominate. Numerous researchers have presented evidence indicating that the ancestral human sociocultural environment was likely characterized by hunter-gatherers living in small groups with relatively egalitarian sociopolitical structures and animistic religious belief systems (e.g., Binford, 2001; Hill, Walker, Bozicevic, Eder, Headland, Hewlett et al., 2011; Marlowe, 2005; McBrearty & Brooks, 2000; Sanderson & Roberts, 2008; Smith, 1999; Winkelman, 2010; Woodburn, 1982). If these conditions are more often associated with societies in which transgendered male androphilia predominates, then this would bolster the argument that male androphilia was predominantly expressed in the transgendered form under ancestral conditions.

Using information derived from the Standard Cross-Cultural Sample (SCCS), VanderLaan Ren et al. (2013c) compared 46 transgendered societies with 146 non-transgendered societies. Their goal was to ascertain whether the former were more likely to be characterized by human ancestral sociocultural conditions (i.e., smaller group size, hunting and gathering, egalitarian political structure, and animistic religious beliefs) compared to the latter. The SCCS provides data related to a subset of the world's nonindustrial societies and circumvents Galton's problem (i.e., common cultural derivation and cultural diffusion) when conducting cross-cultural comparisons. Compared to non-transgendered societies, transgendered societies were characterized by a significantly greater presence of ancestral sociocultural conditions. Given the association between transgendered male androphilia and ancestral human sociocultural conditions, it seems parsimonious to conclude that the ancestral form of male androphilia was the transgendered form. Consistent with this conclusion is the fact that sex-gender congruent male androphilia appears to be a historically recent phenomenon with little precedent outside of a Western cultural context until very recently (Murray, 2000). Accordingly, caution needs to be exercised in utilizing sex-gender congruent male androphiles such as "gay" men as models to test hypotheses pertaining to the evolution of male androphilia.

Kin Selection and the Evolution of Male Androphilia

The Kin Selection Hypothesis holds that genes for male androphilia could be maintained in a population if enhancing one's indirect fitness offset the cost of not reproducing directly (Wilson, 1975). Indirect fitness is a measure of an individual's impact on the fitness of kin (who share some identical genes by virtue of descent), weighted by the degree of relatedness (Hamilton, 1963). Theoretically speaking, androphilic males can increase their indirect fitness by directing altruistic behavior toward kin, which, in principle, allows kin to increase their reproductive success. In particular, androphilic men should allocate altruistic behavior toward close kin because they share more genes in common with such individuals.

In formulating this theory, Wilson (1975) stated that "Freed from the special obligations of parental duties, they [androphilic males] could have operated with special efficiency in assisting close relatives" (p. 555). Similarly, Ruse (1982) commented that "…the effect is that in being homosexual, offspring become altruistic toward close relatives in order thereby to increase their own overall inclusive fitness" (p. 20). Given that what is at issue here is a theory that can account for the origin of same-sex sexual attraction, it seems reasonable to interpret these statements as indicating that same-sex sexual attraction, itself, is a prerequisite for the expression of elevated kin-directed altruism, *not* childlessness. If so, then male androphiles should exhibit elevated kin-directed altruism, whereas male gynephiles (childless or otherwise) should not. Such a pattern would be consistent with the notion that male androphilia is a specially designed adaptation for promoting kin-directed altruism. To date, the most detailed tests of the Kin Selection Hypothesis for male androphilia have been conducted by our own research group. Our cross-cultural tests of this hypothesis have been conducted in Samoa, Canada, and Japan on both transgendered and sex-gender congruent male androphiles.

Test of the Kin Selection Hypothesis in Samoan Transgendered Male Androphiles

Research conducted on transgendered male androphiles in Samoa has repeated furnished support for the Kin Selection Hypothesis. In Samoa, transgendered androphilic males are known locally as *fa'afafine*. Translated literally, *fa'afafine* means "in the manner of a woman." Within Samoan society, *fa'afafine* are not recognized as "men" or "women" and, as such, have been described as a type of "third" gender. From a Western cultural perspective, most *fa'afafine* would be considered transgendered or, at the very least, highly effeminate. Most *fa'afafine* do not experience dysphoria with respect to their genitals and, as such, could not be accurately characterized as transsexual (Vasey & Bartlett, 2007). With respect to sexual orientation, *fa'afafine* are, almost without exception, exclusively androphilic. Not surprisingly, then, they do not have children of their own (Vasey et al., 2014). *Fa'afafine* enjoy a high level of social acceptance that, while not absolute, is in striking contrast to the situation experienced by Western transgendered male androphiles (Namaste, 2000; Seil, 1996).

Research demonstrates that the avuncular (uncle-like) tendencies of *fa'afafine* are significantly elevated compared to those of Samoan gynephilic males (VanderLaan & Vasey, 2012; Vasey, Pocock, & VanderLaan, 2007; Vasey & VanderLaan, 2010a). *Fa'afafine* also exhibited significantly elevated avuncular tendencies compared to the materteral (aunt-like) tendencies of Samoan women (Vasey & VanderLaan, 2009). Elevated avuncular tendencies among *fa'afafine* were also documented when comparing them to control groups of childless women and gynephilic men (Vasey & VanderLaan, 2009, 2010a). These latter comparisons indicated that the *fa'afafine's* elevated avuncular tendencies cannot be characterized as a simple by-product that is due to a lack of parental care responsibilities, and thus, greater availability of resources for avuncular investment. If this were true, then the avuncular tendencies of *fa'afafine* would be similar to those of childless men and women, but this was not the case. Moreover, these same findings indicate that the elevated avuncular tendencies of *fa'afafine* could not be characterized as a simple by-product that is due to the male members of this "third" gender group adopting feminine gender roles, which included expectations for elevated childcare. If this were true, then the materteral tendencies of Samoan mothers and childless women would be similar to the avuncular tendencies of *fa'afafine*, but again this was not the case.

We have also demonstrated that *fa'afafine's* avuncular tendencies are significantly higher than their altruistic interest in non-kin children (Vasey & VanderLaan, 2010b). As such, *fa'afafine's* elevated avuncular tendencies are not a by-product of general altruistic interested in all children. If this were true, the *fa'afafine's* avuncular tendencies toward nieces and nephews and their altruistic tendencies toward non-kin children would be similar, but this was not the case.

Additional research indicates that *fa'afafine* exhibit similar levels of sexual/romantic relationship involvement compared to Samoan women and gynephilic men (VanderLaan & Vasey, 2012). As such, the *fa'afafine's* relatively elevated avuncular tendencies cannot be characterized as a simple by-product of their failure to form, and invest in, intimate sexual/romantic relationships, which, in turn, leaves them with more time and resources. If that were true, *fa'afafine* should exhibit reduced levels of sexual/romantic relationship involvement compared to men and women, but once again this was not the case.

It should be clear from the research described above that much of our work has focused on falsifying the Kin Selection Hypothesis for male androphilia by examining alternative explanations that might account for the *fa'afafine's* elevated avuncularity. It should be equally clear that none of the alternative explanations we have tested, to date, have been supported. Taken together, this body of work is consistent with the conclusion that elevated avuncularity by androphilic males is an adaptation that evolved via kin selection. That being said, establishing that a given trait is an adaptation involves repeatedly satisfying adaptive design criteria empirically while simultaneously ruling out alternatives (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998). Adaptive design implies complexity, economy, efficiency, reliability, precision, and functionality (Williams, 1966).

We have conducted several studies that indicate that compared to Samoan women and gynephilic men, the avuncular cognition of *fa'afafine* appears to be more adaptively designed. First, the avuncular tendencies of the *fa'afafine* are more dissociated from (i.e., covary less with) their altruistic interest in non-kin children, compared to Samoan women and gynephilic men (Vasey & VanderLaan, 2010b). Such a dissociation would allow *fa'afafine* to channel resources toward nieces and nephews in a more optimal manner, while minimizing (i.e., economical, efficient, reliable, and precise), while minimizing resources directed toward non-kin children. Second, whereas Samoan men and women show a tendency to decrease their willingness to invest in nieces and nephews when they have sexual/romantic relationship partners, the cognition of *fa'afafine* appears to protect against this tendency by maintaining a high level of willingness to invest in nieces and nephews regardless of relationship status (VanderLaan & Vasey, 2012). Third, due to the mechanics of human reproduction, individuals can always be certain that their sisters' offspring are their genetic relatives. Yet, due to the possibility of cuckoldry, individuals are necessarily less certain in the case of brothers' offspring. The elevated avuncular tendencies of *fa'afafine* are contingent on the presence of sisters, not brothers, which suggests that the avuncular cognition of *fa'afafine* is sensitive to the relative fitness benefits of investing in sisters' versus brothers' offspring (VanderLaan & Vasey, 2013).

Elevated avuncular tendencies must translate into real-world avuncular behavior if they are to have any impact on the fitness of nieces and nephews and the uncles themselves. Vasey and VanderLaan (2010c) used money given to, and received from, oldest and youngest siblings' sons and daughters as a behavioral assay of expressed kin-directed altruism. In line with the predictions of the Kin Selection Hypothesis, compared to women and gynephilic men, *fa'afafine* gave significantly more money to their youngest siblings' daughters. No other group differences were observed for money given to, or received from, nieces and/or nephews. Moreover, among women and gyephilic men, there were no correlations between the number of children parented and monetary exchanges with the niece and nephew categories examined, suggesting that childlessness cannot account for why *fa'afafine* give more money to their youngest siblings' daughters.

Test of the Kin Selection Hypothesis in Western Populations of Sex-Gender Congruent Male Androphiles

Almost no evidence in support of the Kin Selection Hypothesis has been garnered from studies conducted on sex-gender congruent ("gay") males from Western cultures. For example, Bobrow and Bailey (2001) found that sex-gender congruent androphilic males in the USA did not differ significantly from gynephilic males in terms of general familial affinity, generosity, neediness, avuncular tendencies, money received from kin, or money given to parents. Moreover, contrary to the predictions of the Kin Selection Hypothesis, they found that androphilic males gave significantly less money to their siblings, compared to gynephilic males. Likewise, using a UK sample, Rahman and Hull (2005) found no significant differences between gynephilic and sex-gender congruent androphilic men in terms of family affinity, generosity, avuncular tendencies, money received from the family, or money and gifts given to the family.

It has been suggested that the social environments that characterize Western cultures may not be representative of the context in which male androphilia evolved (Bobrow & Bailey, 2001; Vasey et al., 2007), and the relevant ethnological research indicates that this concern is valid (VanderLaan et al., 2013c). Consequently, if an altruistic androphilic male phenotype exists, such social environments may not be conducive to its development. In the absence of a social context that approximates the adaptively relevant environment (ARE) for genetic factors underlying male androphilia, the theorized functional behavioral expression of such genetic factors is simply not manifested (for a more general discussion of this point, see Irons, 1998; see also Tooby & Cosmides, 2005).

The question thus becomes what features of Western environments might constrain the expression of elevated avuncularity in androphilic males? It has been suggested that sex-gender congruent androphilic males living in Western cultures experience greater than average familial estrangement due to homophobia (D'Augelli, Hershberger, & Pilkington, 1998) and this constrains their ability to exhibit elevated kin-directed altruism (Bobrow & Bailey, 2001). Forrester, VanderLaan, Parker, and Vasey (2011) investigated whether androphilic men would exhibit relatively higher avuncular tendencies in Canada—a relatively non-homophobic culture. Despite Canada's cultural similarity to the USA and the UK, previous authors have cautioned against characterizing all Western populations on the basis of only a few and have encouraged systematic research on differences and similarities among Western nations (Henrich, Heine, & Norenzayan, 2010). In contrast to the USA and the UK, Canadian social and political attitudes are markedly more tolerant and accepting toward homosexuality (Anderson & Fetner, 2008; Widmer, Treas, & Newcombe, 1998). Since 1981, Canada has experienced a dramatic decrease in the stigmatization of homosexuality (Anderson & Fetner, 2008), and conversely, there has been a dramatic increase in support for gay men and lesbians. For example, a 1994 poll found that 46 % of Canadians felt that homosexuality was "not wrong at all," compared to 19 % of the US citizens and 26 % of the UK citizens (Widmer et al., 1998). In 2005, Canada became the fourth nation in the world to legalize same-sex marriage. Part of this process involved the amendment of 68 federal statutes to recognize same-sex couples (e.g., old age pension, income tax, bankruptcy protection). Taken together, this information suggests that gays and lesbians in Canada enjoy more legal rights and social acceptance than almost any other nation. Hence, if the development of elevated avuncular tendencies in androphilic males is contingent on a cultural environment that is less homophobic, then Canadian androphilic men should be more likely to exhibit such tendencies. Consistent with previous studies, however, Forrester et al. (2011) found that gynephilic men and sex-gender congruent androphilic men in Canada did not differ from each other in terms of their willingness to help nieces and nephews.

Interestingly, however, Forrester et al. (2011) did find that the avuncular tendencies of Canadian androphilic men were significantly more dissociated (i.e., covaried less) from their altruistic interest in non-kin children, compared to gynephilic men and androphilic women. As discussed above, similar findings have been reported for Samoan androphilic males, and it was argued that such a cognitive dissociation would allow for allocation of resources to nieces and nephews in a more economical, efficient, reliable, and precise (i.e., adaptive) manner (Vasey & VanderLaan, 2010b). As such, although Canadian androphilic males do not express elevated avuncular tendencies (possibly because their social environment is not conducive to the development of this trait), Forrester et al.'s (2011) results are consistent with the conclusion that the avuncular cognition of Canadian androphilic males has undergone selection for enhancing indirect fitness, as posited by the Kin Selection Hypothesis.

It has also been suggested that sex-gender congruent androphilic males living in Western cultures may be less geographically connected to their kin compared to their non-Western counterparts, thus mitigating their ability to exhibit elevated kin-directed altruism (Bobrow & Bailey, 2001). Indeed, research indicates that sex-gender congruent androphilic men routinely move away from their families to live in urban environments where they can more easily achieve personal goals (Bagley & Tremblay, 1998; Knopp, 1990). If geographic disconnect from kin constrains the expression of avuncularity by sex-gender congruent androphilic males, then releasing this constrain should, in theory, potentiate the expression of elevated avuncularity. To examine this possibility, Abild, VanderLaan, and Vasey (2014) examined whether Canadian androphilic males expressed elevated willingness to engage in altruistic activities toward nieces and nephews, compared to gynephilic men and androphilic women, when the activities in question could be executed from a distance (e.g., willingness to answer questions about dating, willingness to keep in touch via the Internet). Contrary to their prediction, when comparing groups for willingness to engage in avuncular/materteral activities that could be performed from a distance, they did not find that Canadian androphilic men exhibited significantly higher avuncular tendencies. Thus, even when Canadian androphilic males are able to execute avuncular activities from a distance, they do not express increased willingness to do so. This suggests that geographic disconnect from kin cannot, in and of itself, account for the absence of elevated avuncularity in sex-gender congruent males from Western cultures.

At the same time, however, Abild et al.'s (2014) Canadian participants expressed significantly greater willingness to engage in avuncular/materteral activities that required proximity to kin as opposed to those that could be performed from a distance. Thus, it appears that proximity to kin *is* an important facilitator of kin-directed altruism in Canada. In contrast to Canada, Samoan extended family members often live together or in closely situated dwellings (Mageo, 1998). Furthermore, given Samoa's small landmass (2,934 km^2; Lal & Fortune, 2000), kin members are likely to be less geographically dispersed from each other than in much larger Western nations such as Canada (Bagley & Tremblay, 1998; Knopp, 1990). Thus, differences in spatial proximity among kin members may be one factor contributing, at least in part, to the documented cross-cultural differences in avuncularity by Samoan and Canadian androphilic males.

Given that, in Western cultures, sex-gender congruent androphilic males often move away from their kin to live in urban environments (Bagley & Tremblay, 1998; Knopp, 1990), VanderLaan, Gothreau, Bartlett, and Vasey (2011b) suggested that the avuncular tendencies of these individuals might be expressed in a nonfunctional manner, namely, by directing altruism toward more accessible recipients like the children of close friends. In other words, androphilic males may interact with "social kin" (i.e., friends) as the closest possible facsimile of family who are then the recipients of avuncular-like acts rather than genetically related, but geographically distant, kin. Indeed, a number of studies have demonstrated that friends are treated like kin in some more industrialized societies (Silk, 2003; Stewart-Williams, 2007). Korchmaros and Kenny (2006) noted that proximate factors such as one's sense of emotional closeness and obligation toward another individual, rather than genetic relatedness per se, likely influence the expression of altruism. With this logic in mind, Abild, VanderLaan, and Vasey (2013) examined whether sex-gender congruent androphilic males in a Canadian sample exhibited elevated altruistic tendencies toward their friends' children compared to gynephilic men and androphilic women. Contrary to their predictions, they found that sex-gender congruent androphilic males did not exhibit elevated altruistic tendencies toward friends' children when compared to the other two groups. They did, however, find that Canadian women were more likely to treat friends' children like kin, in keeping with previous findings reported in the literature (Ackerman, Kenrick, & Schaller, 2007).

Test of the Kin Selection Hypothesis in Japanese Sex-Gender Congruent Male Androphiles

Vasey et al. (2007) suggested differences in *individualism* versus *collectivism* might account for why androphilic males in Samoa exhibit elevated avuncularity, but those in Western countries such as the USA, the UK, and Canada do not. Individualistic cultures emphasize that people are independent of their groups and contain relatively more *idiocentric* individuals whose psychology and behavior are influenced primarily by their own beliefs and emotions rather than by input from other people. Consequently, the members of individualistic cultures tend to exhibit greater hedonism and, relatively speaking, they are more emotionally distant from the groups to which they belong. In contrast, collectivistic cultures emphasize interdependence and a merging of the self into the group. They contain more *allocentric* individuals who value input from other members of the groups to which they belong. Consequently, the members of collectivistic cultures tend to follow social norms and sacrifice personal goals for the good of the group. In addition, they exhibit high family integrity and close emotional ties with the groups to which they belong. Research demonstrates that patterns of resource distribution are influenced by whether individuals live in collectivistic or individualistic cultures (Leung, 1997; Mills & Clark, 1982). For example, in collectivistic societies, some individuals show a generosity rule with in-group members even when their contributions are clearly higher than the contribution of other members (Triandis, 2001).

The important influences that the individualistic or collectivistic dimensions of culture can have on individual psychology have been well documented (Triandis, 2001). For example, Samoans, who come from a relatively collectivistic culture, are more willing to deceive others if it involves protecting group or family concerns. In contrast, Americans, who come from a relatively individualistic culture, are more willing to deceive others if it involves protecting their personal privacy (Aune & Waters, 1994). Similarly, the more collectivistic Samoans are more likely to favor food products when they are advertised as being for consumption "when the family is at home," whereas the more individualistic New Zealanders favor those that are advertised as being for when "you are on the move" (Jaeger, 2000).

Vasey et al. (2007) hypothesized that the development of elevated avuncularity in androphilic males may be contingent on a relatively collectivistic cultural context. To test this possibility, Vasey and VanderLaan (2012) conducted research in Japan—a relatively collectivistic culture whose members tend to be allocentric (e.g., Kitayama, Markus, Matsumoto, & Norasakkunkit, 1997; Yamaguchi, 1994). Sex-gender congruent male androphilia predominates in Japan, but the idea of a "gay identity" is a relatively new concept compared to the West (McLelland, 2000). Vasey and VanderLaan (2012) found that gynephilic and sex-gender congruent androphilic Japanese men did not differ from each other in terms of their avuncular tendencies. In this regard, research on the avuncular tendencies of sex-gender congruent androphilic males in Japan who do not necessarily identify as "gay" is consistent with similar research on Western sex-gender congruent androphilic males who do identify as "gay."

Triandis (1995) proposed that collectivism could be characterized as *vertical* or *horizontal*. Vertical collectivistic cultures emphasize hierarchical organization of members, whereas horizontal collectivistic cultures emphasize equality of members. Samoa, with its *matai* (chief) system, can be characterized in terms of vertical collectivism (Duranti, 1994; Ochs, 1988; Ritchie & Ritchie, 1989; Shore, 1981). Similarly, Triandis (1995) argued that vertical collectivism is very prevalent in Japan, where citizens have a strong sense of hierarchy, which is reflected in required language forms for each type of status relationship. As such, differences in the expression of avuncularity by androphilic and gynephilic males across these two cultures appear to be unrelated to this aspect of collectivism.

Given Vasey and VanderLaan's (2012) findings from Japan, it appears that if the Kin Selection Hypothesis for male androphilia is correct, and the development of an adaptively designed avuncular male androphilic phenotype is contingent on a particular social environment, then a collectivistic cultural context is insufficient, in and of itself, for the development and expression of such a phenotype. That being said, a collectivistic cultural context might be one important facet of a suite of social factors that promote elevated avuncularity in androphilic males. The simultaneous absence of key social factors (e.g., geographic proximity) or the presence of others (e.g., trans-/homophobia) could theoretically mitigate the trait's expression even when factors thought to promote its development (i.e., collectivism) are present.

In contrast to findings from Samoa (Vasey & VanderLaan, 2010b) and Canada (Forrester et al., 2011). Vasey and VanderLaan (2012) found no evidence that Japanese androphilic males' avuncular tendencies were significantly dissociated (i.e., covaried less) from their altruistic interest in nonkin children, compared to Japanese women and gynephilic men. It is unclear why the findings from Japan differ from those obtained in Samoa and Canada. Null findings, like those observed in Japan, can be difficult to interpret and raise the question of whether these differences in findings are owing to differences in some aspects of the methodologies employed (e.g., sampling method, cultural differences in questionnaire response patterns). Alternatively, these conflicting findings might be reflective of true cultural differences. If this latter scenario is the case, then potentially relevant factors include those that systematically differ between Samoa and Canada versus Japan and also bear relevance to the development of kin-directed altruism (e.g., societal acceptance of androphilic males; Halman, Inglehart, Díez-Medrano, Luijkx, Moreno and Basáñez, 2008; Inglehart, 1990; Widmer et al., 1998).

Kin Selection and the Evolution of Male Androphilia: Concluding Remarks

Tests of the Kin Selection Hypothesis for male androphilia clearly indicate that the avuncular tendencies and behavior of androphilic males vary cross-culturally. Research has demonstrated repeatedly that transgendered male androphiles from Samoa exhibit elevated avuncular tendencies compared to women and gynephilic males (VanderLaan & Vasey, 2012; Vasey et al., 2007;

Vasey & VanderLaan, 2009, 2010a, 2010b, 2010c). In contrast, sex-gender congruent androphilic males from the USA, the UK, Canada, and Japan do not exhibit elevated avuncular tendencies (Abild et al., 2014; Bobrow & Bailey, 2001; Forrester et al., 2011; Rahman & Hull, 2005; Vasey & VanderLaan, 2012). As such, one possible factor influencing the observed cross-cultural differences relates to the manner in which male androphilia is publically expressed. Namely, elevated avuncularity by androphilic males may be contingent on whether they exhibit the transgendered form of male androphilia. To examine whether this is indeed the case, future tests of the Kin Selection Hypothesis for male androphilia will be need in other populations where transgendered male androphiles predominate.

As mentioned previously, research by VanderLaan et al. (2013c) indicates that the ancestral form of male androphilia is likely the transgendered form. Additional analyses by these authors revealed key aspects of the adaptively relevant environment (ARE) of transgendered androphilic males that likely facilitated elevated kin-directed altruism. AREs consist of those features of the environment that must be present in order for an adaptation to be functionally expressed (Irons, 1998). VanderLaan et al. (2013c) found that societies in which transgendered male androphilia predominates were more likely to show social characteristics that facilitate investment in kin, compared to non-transgendered societies. For example, relative to non-transgendered societies, transgendered societies were more likely to exhibit bilateral[3] and double descent[4] systems than patrilineal, matrilineal, and ambilineal[5] descent systems. In addition, correlational analysis showed that as the presence of ancestral sociocultural conditions increased, so too did the presence of bilateral (and double) descent systems. Ethnologists have argued that bilateral decent systems and bilocal patterns of residence following marriage are maximally inclusive of kin because they do not bias individuals to interact with only one subset of relatives (Alvard, 2002; Ember, 1975; Kramer & Greaves, 2011). Humans have evolved, via kin selection, to preferentially allocate altruism toward close relatives (Daly, Salmon, & Wilson, 1997). Consequently, it is reasonable to deduce that these patterns of bilateral and double descent and bilocal postmarital residence would allow for more altruistic interactions with a full range of genetically related kin. Taken together, these analyses are consistent with the conclusion that bilateral descent characterized ancestral humans and that such patterns were features of ancestral societies in which male androphilia was expressed in the transgendered form.

VanderLaan et al. (2013c) also examined the acceptance of homosexuality in 27 transgendered societies for which information could be obtained. The significant majority of these societies expressed no negative reactions to same-sex sexual behavior. Overall then, the same-sex sexual orientation of transgendered males in transgendered societies appears to be socially tolerated. Such tolerance, particularly on the part of the kin of transgendered androphilic males, might be considered essential for kin selection to be deemed as a plausible contributing factor toward the persistence of male androphilia over evolutionary time. Unless transgendered androphilic males are accepted by their families, their opportunity to invest in kin is likely mitigated.

In sum, transgendered male androphilia is likely the ancestral form of male androphilia, key aspects of the transgendered androphilic male ARE (i.e., bilateral and double descent system, social tolerance of same-sex sexuality) would have facilitate elevated kin-directed altruism, and data from contemporary transgendered males indicates that they exhibit elevated avuncularity. Given all this, it seems reasonable to suggest that kin selection played some role in the evolution of male

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[3] In bilateral descent systems, ego's mother's and father's lineages are equally important for emotional, social, spiritual, and political support, as well as for transfer of property or wealth.

[4] In double descent systems of descent, individuals receive some rights and obligations from the father's side of the family and others from the mother's side.

[5] Some sources treat ambilineal and bilateral descent systems as synonymous, but ambilineal descent systems are defined as existing when individuals have the option of choosing one of their lineages for membership.

androphilia. As such, the increased kin-directed altruism documented in Samoan *fa'afafine* is more likely to be characteristic of ancestral androphilic males, compared to the lack thereof documented in sex-gender congruent androphilic men from industrialized cultures.

The Sexually Antagonistic Gene Hypothesis and the Evolution of Male Androphilia

Sexually antagonistic selection is a form of balancing selection that occurs when genetic factors that produce fitness costs in one sex result in fitness benefits in the other sex. The Sexually Antagonistic Gene Hypothesis for male androphilia posits that genes associated with the development of androphilia result in decreased reproductive output in male carriers, but the same genes result in increased reproductive output in female carriers. For this reason, this hypothesis is routinely referred to as the Female Fecundity Hypothesis for male androphilia. Given that kin share a disproportionate number of genes in common, the female kin of male androphiles should experience, on average, greater increased reproductive output than females with no androphilic male relatives. In theory, the fitness benefits that accrue to the female relatives of male androphiles balance out the fitness costs associated with male androphilia. Consequently, sexually antagonistic selection occurs for the genes in question owing to their fitness-enhancing properties in female carriers. A by-product of this sexually antagonistic selection is that male androphilia persists in populations over evolutionary time, despite its fitness-reducing consequences. Given all this, the basic prediction that flows from the Sexual Antagonistic Gene Hypothesis is that the female relatives of androphilic males should tend to produce more offspring than those of gynephilic males.

Tests of the Sexually Antagonistic Gene Hypothesis in Western Populations of Sex-Gender Congruent Male Androphiles

To date, several studies carried out in Western populations have compared the reproductive output of the female relatives of male androphiles versus those of male gynephiles. A series of such studies has been conducted by Andrea Camperio Ciani's research group at the University of Padova in Padua, Italy. In three Western European samples (i.e., Italian, Spanish, and French), elevated reproduction was reported in the matrilineal, but not the patrilineal, aunts of male androphiles (Camperio-Ciani et al., 2004; Camperio Ciani & Pellizzari, 2012; Iemmola & Camperio Ciani, 2009). In addition, two of these studies tested for, and found, increased reproduction in the mothers of male androphiles (Camperio-Ciani et al., 2004; Iemmola & Camperio Ciani, 2009). None of the studies by Camperio Ciani's research group has documented significantly elevated offspring production in the grandmothers of androphilic men compared to those of gynephilic men.

Increases in the reproductive output of an androphilic male's mother could, theoretically, occur as a result of the fraternal birth order effect (Blanchard, 2012; Iemmola & Camperio Ciani, 2009) and not because of some true female fecundity effect that influences the production of other sibling categories (i.e., younger brothers, older and younger sisters). As such, it is important to discern whether the observed patterns of offspring production in the mothers of androphilic males reflect fraternal birth order effects, fecundity effects, or both. By comparing the offspring production of mothers with firstborn androphilic sons, to mother's with firstborn gynephilic sons, Iemmola and Camperio Ciani (2009) found that a maternal fecundity effect exists in the absence of any fraternal birth order effect for their Western European sample. However, in a large Western sample of 40,197 firstborn heterosexual men and 4,784 firstborn homosexual men, a contradictory pattern was found. The mothers of firstborn heterosexual men had significantly more offspring than those of firstborn homosexual men (Blanchard, 2012).

In a British sample of Caucasian men, elevated reproduction was also documented among the maternal, but not the patrilineal, aunts of androphilic men (Rahman et al., 2008). Other categories of female kin were examined (i.e., mothers, grandparents), but no significant group differences were observed. In diametric opposition to the predictions of the Sexually Antagonistic Gene Hypothesis, the mothers, paternal aunts, and possibly the maternal and paternal grandmothers of non-Caucasian gynephilic men exhibited significantly higher offspring production than those of non-Caucasian androphilic men. Data pertaining to grandmothers and grandfathers was lumped together in this study as the category "grandparents" and, as such, it is not possible to speak definitively about the unique reproductive output of grandmothers versus grandfathers. Offspring production by maternal aunts did not differ between the groups. In an attempt to account for these unusual results, LeVay (2010) has suggested that Rahman et al.'s (2008) non-Caucasian sample might have been primarily composed of British immigrants who belong to larger families, whose definition of "family" is more inclusive, and who are less accepting and open about homosexuality. All of these factors would have contributed to a less than ideal sample, thereby biasing Rahman et al.'s (2008) results and contributing to the observed racial differences.

Given that this particular group of studies has documented elevated reproduction in maternal-line female relatives, but not in paternal-line ones, Camperio Ciani and his colleagues have argued that the genetic factors influencing the development of male androphilia are located on the X chromosome (Camperio-Ciani et al., 2004; Camperio Ciani & Pellizzari, 2012; Iemmola & Camperio Ciani, 2009). However, similar matrilineal effects have not been found with other samples drawn from Western populations. For example, in one British study of male sexual orientation and family size, androphilic males were shown to have significantly more aunts, uncles, and cousins in the paternal, but not maternal, line (King et al., 2005). This suggests that elevated offspring production characterizes the paternal grandmothers and possibly the paternal aunts of androphilic males, but not their maternal counterparts. Unfortunately, data pertaining to offspring of paternal aunts and paternal uncles ("paternal cousins") was lumped together in this study and, as such, the results cannot be used to speak definitively about the unique reproductive output of aunts versus uncles.

In a study conducted in the USA, elevated reproduction was documented among mothers and paternal grandmothers of androphilic males, compared to those of gynephilic males (Schwartz et al., 2010). The same study documented no group differences in the reproductive output of maternal grandmothers. Further, androphilic and gynephilic males did not differ for number of maternal or paternal cousins, which suggests no group differences in the reproductive output of maternal and paternal aunts. Unfortunately, once again, data pertaining to aunts and uncles was lumped together in this study and, as such, it is not possible to speak definitively about the unique reproductive output of aunts versus uncles on their own.

One important limitation of this literature is its focus on samples drawn from Western European and North American populations. Such populations exhibit relatively low fertility (Central Intelligence Agency, 2012), which is often due to "stopping rules" associated with reproduction. Stopping rules refer to the cessation of reproduction once a certain number of children are produced or once at least one child of each sex is produced. Sampling from low fertility populations that employ stopping rules can obscure natural (i.e., evolved) reproductive output (Blanchard & Lippa, 2007; Zucker, Blanchard, Kim, Pae, & Lee, 2007). The susceptibility of low fertility populations to producing anomalous reproductive patterns raises the possibility that some subset, or possibly all, of the aforementioned tests of the Sexually Antagonistic Gene Hypothesis in Western populations do not provide clear indications of the precise categories of female kin that exhibit elevated reproductive output. Hence, examining the reproductive output of androphilic and gynephilic males' kin in a high fertility population in which women are more likely to be reproducing closer to their maximum capacities could provide valuable insight.

Tests of the Sexually Antagonistic Gene Hypothesis in Samoan Transgendered Male Androphiles

To date, tests of the Sexually Antagonistic Gene Hypothesis have been conducted in one nonindustrialized, non-Western nation: Samoa. Samoa represents a more optimal location in which to test the Sexually Antagonistic Gene Hypothesis because the population is characterized by higher fertility compared to Western European and North American populations (Central Intelligence Agency, 2012). In addition, as outlined above, the purported ancestral form of male androphilia—the transgendered form—predominates in Samoa (VanderLaan et al., 2013c).

Three studies have been conducted in Samoa by our research group that furnish data pertaining to the Sexually Antagonistic Gene Hypothesis. Vasey and VanderLaan (2007) demonstrated that the mothers of *fa'afafine* produce more offspring than those of gynephilic men. This finding was replicated by VanderLaan and Vasey (2011). More recently, VanderLaan et al. (2012) demonstrated that *fa'afafine's* maternal and paternal grandmothers exhibit elevated offspring production, but their maternal or paternal aunts do not.

The main strength of these Samoan studies is that they examine reproductive output among the female relatives of androphilic and gynephilic males in a population that has higher fertility compared to the Western samples that have been examined to date. Consequently, anomalous reproductive patterns should be less likely to occur in the Samoan population. If the Samoan population is relatively free of susceptibility to anomalous reproductive patterns compared to Western populations, then the study by VanderLaan et al. (2012) indicates that male androphilia is actually associated with elevated reproductive output by female kin in both the maternal and paternal lines. Moreover, the study by VanderLaan and Vasey (2011) demonstrated that a true maternal fecundity effect exists independent of any coexisting fraternal birth order effect.

The Sexually Antagonistic Gene Hypothesis and the Evolution of Male Androphilia: Concluding Remarks

The studies reviewed above are largely consistent with the basic prediction of the Sexually Antagonistic Gene Hypothesis. Namely, the female kin of male androphiles exhibited elevated offspring production compared to the female kin of male gynephiles. However, the exact categories of female kin that demonstrate elevated offspring production remain unclear. Identifying the precise categories of female kin that exhibit elevated offspring production is necessary for proper tests of the Sexually Antagonistic Gene Hypothesis. Elevated reproduction by the mothers and the maternal and paternal grandmothers of androphilic males does not provide definitive support for the Sexually Antagonistic Gene Hypothesis because reproduction by these categories of female kin is naturally confounded with that of fathers and grandfathers, all of whom share genes with androphilic and gynephilic male probands.

Elevated reproductive output by androphilic males' maternal aunts, paternal aunts, or both would provide the clearest support for the Sexually Antagonistic Gene Hypothesis because androphilic and gynephilic male probands do not share genes with their aunts' male reproductive partners. All this being said, the existing research reviewed above indicates that the only categories of androphilic male relatives to show elevated reproduction were those comprised partially (i.e., reproduction of aunts and uncles combined) or entirely of female kin. The cumulative weight of this evidence suggests that the Sexual Antagonistic Gene Hypothesis is still a tenable explanation for the evolution of male androphilia.

Identifying whether elevated female reproduction is most likely inherent to both the maternal and paternal lines of androphilic males has important implications regarding the proximate mechanism(s) underlying this pattern. As outlined above, Camperio Ciani's research group have argued on the basis of data derived from various Western European samples that elevated reproductive output is unique to maternal-line female relatives and that such a pattern is indicative of sexually antagonistic genes located on the X-chromosome (Camperio-Ciani et al., 2004; Camperio Ciani & Pellizzari, 2012; Iemmola & Camperio Ciani, 2009; Rahman et al., 2008). However, as our Samoan research and other studies have shown, elevated reproduction has been documented among the patrilineal female kin of androphilic males as well (King et al., 2005; Schwartz et al., 2010; VanderLaan et al., 2012).

Based on these findings, it seems reasonable to argue that X-linked sexual antagonism might not be the form of selection responsible for the evolution of male androphilia. One might instead argue that sexually antagonistic genetic factors are present on the autosomal chromosomes because androphilic males share genetic factors on these chromosomes with both paternal and maternal relatives. Indeed, autosomal linkage of sexually antagonistic genetic factors favoring the evolution of male androphilia is plausible given previously reported mathematical models (Gavrilets & Rice, 2006).

The Balanced Polymorphism Hypothesis and the Evolution of Male Androphilia

The Balanced Polymorphism Hypothesis for male androphilia has been most fully articulated by Miller (2000).[6] This hypothesis takes as its starting point the assumption that male androphilia is not an isolated trait, but rather is part of a larger package of gender-atypical traits. Ample empirical evidence exists to support this assumption (Bailey & Zucker, 1995; Bartlett & Vasey, 2006; Cardoso, 2005, 2009; Lippa, 2005; VanderLaan et al., 2011a; Vasey & Bartlett, 2007; Whitam, 1983; Zucker et al., 1996). Miller (2000) proposed that multiple genes influence the development of male androphilia and these genes shift male brain development in a female-typical direction. Males who inherit a critical number of these genes become androphilic. Below this critical threshold, males who inherit some of these genes are gynephilic, but are feminized in terms of certain personality traits, which render then more sensitive, empathetic, tender, and kind. These personality traits, in turn, are thought to render gynephilic males more attractive as mates. Indeed, ample empirical evidence exists to support this assumption (e.g., Barclay, 2010; Buss et al., 1990; Buss & Shakelford, 2008; Phillips, Barnard, Ferguson, & Reader, 2008; Tessman, 1995). Owing to their increased attractiveness, Miller (2000) argues that these males obtain more female sexual partners and father more children compared to gynephilic males who have no androphilic male relatives. These males are also hypothesized to be better fathers compared to fathers with no androphilic male relatives. The increased reproductive success experienced by the heterosexual male relatives of androphilic males favors selection for the feminizing genes in question. As such, positive selection for these genes occurs despite the reproductive costs associated with male androphilia itself.

A number of predictions flow from the Balanced Polymorphism Hypothesis. First, androphilic men are more likely to be feminine than masculine. Second, gynephilic males should be more feminine if they have androphilic male relatives, compared to those who do not. Third, gynephilic males should be more attractive if they have androphilic male relatives, compared to those who do not. Fourth, gynephilic males should obtain more female sexual partners if they have androphilic male relatives, compared to those who do not. Fifth, gynephilic males should father more children

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[6] This hypothesis is sometimes referred to as the "Overdominance Hypothesis" for male androphilia.

if they have androphilic male relatives, compared to those who do not. Sixth, gynephilic males should be better fathers if they have androphilic male relatives, compared to those that do not.

Tests of the Balanced Polymorphism Hypothesis

To date, two studies have been conducted with the explicit goal of testing the Balanced Polymorphism Hypothesis and these have utilized samples of sex-gender congruent males from Western populations. Using a community-based sample of Australian twins, Zietsch et al. (2008) examined whether gynephilic males with an androphilic male co-twin had more opposite sex sexual partners, compared to gynephilic males with no androphilic male co-twin. Contrary to the fourth prediction of the Balanced Polymorphism Hypothesis as stated above, no significant group differences were found.

Using a Finnish sample, Santilla, Högbacka, Jern, Johansson, Varjonen, Witting et al. (2009) compared three groups: (1) gynephilic males with gynephilic brothers, (2) gynephilic males with androphilic monozygotic co-twins ($r_g = 1.00$), and (3) gynephilic males with androphilic brothers ($r_g = 0.50$; e.g., dizygotic twins, sibling-sibling pairs). Based on the second prediction of the Balanced Polymorphism Hypothesis as stated above, one would predict that gynephilic males with androphilic brothers would score lower on measures of psychopathic traits (i.e., sensation seeking, tendency toward ignoring social norms and laws) and sexual aggression/coercion, compared to gynephilic males with no androphilic brothers. However, Santilla et al. (2009) found no such group differences. Likewise, contrary to the fourth prediction of the Balanced Polymorphism Hypothesis as stated above, no relevant group differences were found with respect to estimated number of sexual partners over the last year, lifetime number of one-night stands, or experience with vaginal intercourse. In addition to these sociosexual variables, Santilla et al. (2009) found that there were no group differences in age of first intercourse. Finally, contrary to the fifth prediction of the Balanced Polymorphism Hypothesis as stated above, there were no group differences in the number of children produced.

A number of studies exist that have not been conducted with the explicit goal of testing the Balanced Polymorphism Hypothesis but which nonetheless furnish relevant data because they examined offspring production in the uncles of androphilic and gynephilic males. Using an Italian sample, Camperio-Ciani et al. (2004) found that the maternal and paternal uncles of androphilic males did not differ from those of gynephilic males in terms of their offspring production. Iemmola and Camperio Ciani (2009) replicated these results for maternal uncles, but found, in contrast to theoretical predictions, that the paternal uncles of gynephilic males had significantly more children than those of male androphiles. Using a British sample composed of Caucasians, Rahman et al. (2008) found no differences in offspring production between the maternal or paternal uncles of gynephilic versus androphilic males. Likewise, the authors found no significant group differences in offspring production for maternal uncles when a British sample of non-Caucasian gynephilic and androphilic males was employed. They did, however, find that paternal uncles of non-Caucasian gynephilic males had significantly more children than those of androphilic males in contrast to theoretical predictions (Rahman et al., 2008).

To date, one study relevant to testing the Balanced Polymorphism Hypothesis has been conducted in a population where transgendered male androphilia predominates. VanderLaan et al. (2012) found that the maternal and paternal uncles of Samoan *fa'afafine* did not differ from those of Samoan gynephilic males in terms of their offspring production. Taken together, none of the studies that have looked at the offspring production of the uncles of androphilic males have furnished support for the Balanced Polymorphism Hypothesis.

General Concluding Remarks

Male androphilia has a genetic component, yet most male androphiles reproduce little, if at all. A heritable trait that lowers reproductive output should be selected against, but archaeological evidence suggests that male-male sexual behavior has persisted for millennia. For these reasons, male androphilia represents one of the outstanding paradoxes of evolutionary psychology.

In recent years, progress has finally been made toward understanding how male androphilia persists over evolutionary time. Research indicates that the ancestral form of male androphilia was likely to be the transgendered form. No support for the Kin Selection Hypothesis has been garnered from research conducted in Western and non-Western populations on sex-gender congruent male androphiles. However, research has repeatedly furnished support for the Kin Selection Hypothesis in Samoa where transgendered male androphiles (*fa'afafine*) exhibit elevated avuncular tendencies and behavior compared to women and gynephilic men. Research on Samoan *fa'afafine* has also furnished evidence that their avuncular cognition exhibits hallmarks of adaptive design.

Tests of the Sexually Antagonistic Gene Hypothesis have been conducted in diverse populations of transgendered and sex-gender congruent male androphiles. Overall, this research indicates that the female kin of male androphiles produce more offspring than those of male gynephiles. However, the precise categories of female kin that exhibit elevated offspring production remain unclear. Further, tests to determine whether a true maternal fecundity effect exists independent of any coexisting fraternal birth order effect have been inconsistent. No support has been garnered for the Balanced Polymorphism Hypothesis.

In light of these results, it is possible that male androphilia could be conceptualized as a by-product of an adaptation (sensu Buss et al., 1998; Gould & Vrba, 1982) for increased female fecundity that results from sexually antagonistic selection. By-products of adaptations are characteristics that evolve in association with particular adaptations because they happen to be coupled with those adaptations (Buss et al., 1998). Although they may have some beneficial effect on fitness, they did not originally evolve to solve adaptive problems, and thus, at their point of origin they did not have an evolved fitness-enhancing function, nor were they products of natural selection. In such a situation, increased avuncularity among male androphiles could potentially facilitate reproduction by female kin and thereby have positive "effects" on the genetic factors for both increased fecundity in females and, by extension, its conjectured by-product, male androphilia. Williams (1966) invoked the term "effect" to designate the fortuitous operation of a useful characteristic not built by selection for its current role.

Humans have evolved, via kin selection, to preferentially allocate altruism toward close relatives (e.g., Daly et al., 1997). Consequently, kin nepotism should characterize all individuals, regardless of their sex, sexual orientation, or gender identity. However, markedly elevated avuncularity, such as that observed among *fa'afafine*, might result in distinct fitness advantages that could form a unique basis on which kin selection might act. If so, then cognitive underpinnings mediating avuncularity in male androphiles may have subsequently undergone *secondary* adaptive modification. Such a conclusion is consistent with our findings that the avuncular cognition of androphilic males in some populations exhibits special design features (Forrester et al., 2011; VanderLaan & Vasey, 2012; Vasey & VanderLaan, 2010b).

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