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## Male Androphilia is an Evolutionary Paradox

*Androphilia* refers to sexual attraction to adult males, whereas *gynephilia* refers to sexual attraction to adult females. Research indicates that male androphilia is influenced by genetic factors (e.g., Alanko et al. 2010; Hamer et al. 1993; Långström et al. 2010). Nevertheless, androphilic males reproduce at significantly lower rates than gynephilic males, and often they do not reproduce at all (e.g., King et al. 2005; Schwartz et al. 2010; Vasey et al. 2014).

Since male androphilia appears to have a genetic component, but male androphiles reproduce little, if at all, one would have expected genes for male androphilia to have become extinct given the relative reproductive costs associated with this trait and the reproductive benefits associated with male gynephilia. Any species-typical trait that has a genetic component, but 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. For this reason, the existence of male androphilia represents one of the outstanding paradoxes of evolutionary biology.

If it could be definitively demonstrated that male androphilia was a historically recent phenomenon that did not extend back into the evolutionary past, then one might reasonably dismiss the characterization of male androphilia as an *evolutionary paradox*. However, archaeological and cross-cultural evidence suggest that this conclusion lacks credibility. *Sexual orientations* such as gynephilia or androphilia are not part of the archaeological record, nor could they ever be, because sexual orientations cannot be preserved in the form of archaeological artifacts. However, depictions of *sexual behaviors* involving same-sex individuals do exist as part of the archaeological record, albeit rarely (e.g., Gebhard 1970; Nash 2001) and, on the basis of these depictions, it seems reasonable to suggest, at a very minimum, that some prehistoric peoples understood that such activity was within the realm of possibility. A somewhat stronger supposition would be that such depictions are, in fact, evidence that same-sex sexual behavior existed in prehistoric times.

Certain constellations of funerary remains may also be indicative of male androphilia in the ancestral past. For example, graves containing male skeletal remains and female-typical artifacts are indicative of transgender males in the

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distant past (e.g., Hollimon 1997). Given what we know about the exclusive androphilic orientation of most transgender males from comparable populations (e.g., Harrington 1942), archaeological indicators of such individuals are once again suggestive of the presence of male androphilia in human antiquity.

All told, the archaeological evidence for male androphilia in the prehistoric past is suggestive, but limited. Perhaps more compelling is the research that suggests that male androphilia occurs in the majority of cultures for which data are available (e.g., Murray 2000) and its population prevalence rate appears to be similar (~1.5–5%) across a variety of different cultures (e.g., Smith et al. 2003; VanderLaan et al. 2013a; Whitam 1983). Although male–male sexuality may truly be absent in a minority of cultures (e.g., Hewlett and Hewlett 2010), these exceptions do not invalidate the conclusion that male androphilia appears to be a predictably and reliably reoccurring phenomenon in the vast majority of human cultures. The cross-culturally widespread and consistent nature with which male androphilia is expressed suggests that it is not an evolutionarily recent aspect of the human sexual condition.

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### The Expression of Male Androphilia Varies Cross-Culturally

The manner in which male androphilia is publicly expressed varies across cultures (Murray 2000). This expression typically takes one of two forms, that are related to gender role enactment. These two forms are *sex-gender congruent* and *transgender* 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, transgender androphilic males typically behave in an effeminate manner and often identify as neither “men” nor “women,” but rather, as a member of some “third” gender category. In some cultures, transgender male androphilia is linked to particular institutionalized labor practices, which often involve specialized religious activities. Such transgender male andro-

philia has been referred to as “institutionalized role structured homosexuality” (Herdt 1997). For example, on the Indian subcontinent, transgender male androphiles known as *hijra* bestow blessings from Hindu gods and goddesses for luck and fertility at weddings and at the birth of baby boys (Nanda 1998). Similarly, in some cultures such as the Mohave and the Yorok, all *berdache* (transgender male androphiles) were recognized as shamans (e.g., Devereux 1937; Kroeber 1925). In Sulawesi, Indonesia, transgender androphilic males known as *bissu* are shamans who bless people for good health and successful journeys and who play important ritual roles in weddings. Historically, *bissu* were also guardians of sacred royal regalia and the protectors of nobility (Peletz 2009)<sup>1</sup>.

Both sex-gender congruent and transgender 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. In contrast, in many non-Western cultures, the transgender form appears to be more common (Murray 2000).

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### Cross-Culturally Invariant Correlates of Male Androphilia

Quantitative research indicates that the sex-gender congruent and transgender 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 transgender male androphiles tend to both be later born among their siblings (e.g., Blanchard 2004; VanderLaan and Vasey 2011; Vasey and VanderLaan 2007), have greater numbers of older biological brothers (“fraternal birth order effect<sup>2</sup>,” e.g., Bogaert and Skorska

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<sup>1</sup> These institutionalized religious roles sometimes carry with them the expectation of asceticism, but often this ideal is not realized (e.g., Nanda 1998; Peletz 2009).

<sup>2</sup> The *fraternal birth order effect* refers to the well-established finding that the number of older biological broth-

2011; VanderLaan and Vasey 2011; Vasey and VanderLaan 2007), exhibit larger family sizes (Blanchard and Lippa 2007; Camperio-Ciani et al. 2004; Iemmola and Camperio Ciani 2009; King et al. 2005; Rahman et al. 2008; Schwartz et al. 2010; VanderLaan et al. 2012; VanderLaan and Vasey 2011; Vasey and VanderLaan 2007), cluster within families (e.g., Schwartz et al. 2010; VanderLaan et al. 2013a, b), occur at similar prevalence rates across different populations (e.g., Smith et al. 2003; VanderLaan et al. 2013a; Whitam 1983) and produce few—if any—offspring (e.g., King et al. 2005; Schwartz et al. 2010; Vasey et al. 2013). In addition, the odds ratios associated with the fraternal brother effect in various populations of sex-gender congruent and transgender 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 et al. 2002; VanderLaan and Vasey 2011).

Prospective and retrospective cross-cultural research on early psychosocial development among transgender 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) compared to gynephilic males (Bailey and Zucker 1995; Bartlett and Vasey 2006; Cardoso 2005, 2009; Whitam 1983). In addition, both types of male androphiles express elevated cross-gender wishes in childhood (e.g., “I wish I was a girl”; Bailey and Zucker 1995; Vasey and Bartlett 2007; Whitam 1983). Furthermore, both sex-gender congruent and transgender male androphiles also experience elevated traits of childhood separation anxiety (i.e., anxiety related to separation from major attachment figures such as parents; VanderLaan et al. 2011a; Vasey et al. 2011; Zucker et al. 1996), which tend to be more common among girls compared to boys (e.g., Shear et al. 2006; VanderLaan et al. 2011a). In adulthood,

male androphiles from a range of cultures exhibit preferences for a variety of female-typical occupations (e.g., florist) 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 and 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 and Savin-Williams 2012). In contrast, in cultures where transgender 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 adult transgender 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 publicly expressed. Taken together, these numerous, cross-culturally invariant biodemographic and developmental correlates of male androphilia indicate that sex-gender congruent and transgender male androphilia share a common etiological basis despite being different in appearance.

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### Male Androphilia in the Ancestral Environment

Given that the manner in which male androphilia is publicly expressed varies cross-culturally, the question arises as to which form, sex-gender congruent or transgender 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.

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ers increases the odds of androphilia in later-born males (Blanchard 2004; Bogaert and Skorska 2011).

With this concern in mind, VanderLaan et al. (2013c) attempted to identify the ancestral form of male androphilia. They did so by examining whether societies in which transgender male androphilia predominates exhibit more of the socio-cultural features that are believed to have characterized the human ancestral past relative to a comparison group of societies in which transgender 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 et al. 2011; Marlowe 2005; McBreaarty and Brooks 2000; Sanderson and Roberts 2008; Smith 1999; Winkelman 2010; Woodburn 1982). If these conditions are more often associated with societies in which transgender male androphilia predominates, then this would bolster the argument that male androphilia was predominantly expressed in the transgender form under ancestral conditions.

Using information derived from the Standard Cross-Cultural Sample (SCCS)<sup>3</sup>, VanderLaan et al. (2013c) compared 46 societies in which transgender male androphiles were coded as predominating with 146 societies in which they were not. 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. Compared to non-transgender societies, transgender societies were characterized by a significantly greater presence of ancestral sociocultural conditions. Given the association between transgender male androphilia and ancestral human sociocultural conditions, it seems parsimonious to conclude that the ancestral form of male androphilia was the transgender 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. This is particularly true if the hypotheses under consideration propound a role for the social behavior of male androphiles in the evolutionary maintenance of genes associated with same-sex sexual orientation.

The existence of two forms of transgender male androphilia (i.e., *institutionalized role structured* and *non-role structured*) raises the question as to which one preceded the other in evolutionary time. Given that less specialized forms of traits tend to precede more specialized ones in evolutionary time (Dean et al. 2014), it seems parsimonious to propose that institutionalized role structure transgender male androphilia is derived from a more ancestral form of transgender male androphilia that did not involve role specialization and was not institutionalized. Once transgender male androphilia originated in humans, it could then be culturally elaborated to serve any number of distinct social roles, which, in turn, could become institutionalized.

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## The Fa’afafine of Samoa

Translated literally, *fa’afafine* means “in the manner of a woman.” Although they are biological males, within Samoan society, *fa’afafine* are not recognized as “men” nor are they recognized as “women” and, as such, they have been described as a type of “third” gender. From a Western cultural perspective, the vast majority of *fa’afafine* would be considered transgender individuals or, at the very least, highly effeminate males. Most *fa’afafine* do not experience dysphoria with respect to their genitals and, as such, could not be accurately characterized as transsexual (Vasey and Bartlett 2007).

Inclusion in the category *fa’afafine* is contingent on feminine gender role presentation,

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<sup>3</sup> 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.

not on same-sex sexual activity. Consequently, long before they engage in any sexual activity, prepubescent boys are identified as *fa'afafine* based on their tendencies to engage in female-typical activities (e.g., playing with girls) and their aversion toward male-typical activities (e.g., rough-and-tumble play). This process of recognition does not mean that Samoans make male children into *fa'afafine*. Rather, in Samoan culture, boyhood femininity is interpreted to mean that such individuals simply are *fa'afafine* and it is understood that they will not grow up to be “men.” Some families react negatively to the presence of a *fa'afafine* child with corporal punishment, but the majority have a *laissez-faire* attitude; some even facilitate the child's feminine behavior by sewing dresses for the child, for example (Bartlett and Vasey 2006; Vasey and Bartlett 2007).

In adulthood, the vast majority of *fa'afafine* are exclusively androphilic and, consequently, they do not have children of their own (Vasey et al. 2014). All *fa'afafine* recognize the term “gay” although the precise meaning of this term varies depending on the individual asked. That being said, none of the *fa'afafine* use the term “gay” to describe themselves. “Gays” as one *fa'afafine* told the first author “sleep with each other, but *fa'afafine* don't do that.” Indeed, *fa'afafine* express disgust at the thought of engaging in sexual activity with another *fa'afafine* and stress that they do not do so. Instead, they point out, in contrast to “gays,” they have sex with “straight men.”

In a Samoan cultural context, regardless of sexual orientation, “straight man” means a male who is masculine and who self-identifies as a “man.” Some “straight men” in Samoa are gynephilic and only have sex with women. However, other men who are bisexual will have sex with *fa'afafine* when they are unable to access their preferred sexual partners (i.e., adult females). The majority of men who sleep with *fa'afafine* likely fall into this group (Pettersen et al. 2015). The remaining minority of men who have sex with *fa'afafine* appear to be a combination of individuals who are androphilic or *gynandromorphophilic* (i.e., peak sexual attrac-

tion to individuals with penises and breasts). In short, the Samoan category of “straight man” is a very heterogeneous one with respect to sexual orientation.

In Samoa, *fa'afafine* enjoy a high level of social acceptance that, while by no means absolute, stands in stark contrast to the situation experienced by Western transgender male androphiles (e.g., Meyer 2003; Namaste 2000; Seil 1996). Indeed, the prime minister of Samoa, the Honorable Tuilaepa Sailele Malielegaoi, is patron of the National *Fa'afafine* Association and has spoken publically on several occasions about the value of *fa'afafine* for Samoan society. *Fa'afafine* are highly visible and active members of Samoan society. Although it is not unusual for *fa'afafine* to occupy certain occupations (e.g., florist) more than others (e.g., mechanic), they are not associated with any institutionalized social role. *Fa'afafine* occupy all manner of positions from stay-at-home caregivers to assistant chief executive officers in the government.

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## Kin Selection and the Evolution of Male Androphilia

To date, tests of evolutionary hypotheses pertaining to male androphilia that utilize transgender androphilic males as models have been conducted on a single population—the *fa'afafine* of Samoa. Our own group has conducted this research. The most prominent hypothesis that posits a role for the social behavior of male androphiles in the evolutionary maintenance of genes associated with same-sex sexual orientation is the kin selection hypothesis. This 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 could increase their indirect fitness by directing altruistic behavior toward kin, which, in principle, would allow such kin to increase their

reproductive success. In particular, androphilic males should allocate altruistic behavior toward close kin because they share more genes in common with such individuals.

Research conducted on transgender male androphiles in Samoa has repeatedly furnished support for the kin selection hypothesis. Research demonstrates that the avuncular (uncle-like) tendencies of *fa'afafine* are elevated compared to those of Samoan gynephilic males (VanderLaan and Vasey 2012; Vasey et al. 2007; Vasey and VanderLaan 2010a). *Fa'afafine* also demonstrate elevated avuncular tendencies compared to the materteral (aunt-like) tendencies of Samoan women (Vasey and VanderLaan 2009). Elevated avuncular tendencies among *fa'afafine* were also documented when comparing them to control groups of childless women and gynephilic men (Vasey and 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* should have been 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 should have been 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 much higher than their altruistic interest in non-kin children (Vasey and VanderLaan 2010b). As such, *fa'afafine*'s elevated avuncular tendencies are not a by-product of general altruistic interest 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 have been 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 and Vasey 2012). As such, *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 have exhibited reduced levels of sexual/romantic relationship involvement compared to men and women, but once again, this was not the case.

Finally, there is no evidence that Samoans hold unique (trans)gender role expectations that *fa'afafine* will engage in elevated levels of avuncular activity compared to women and gynephilic men (VanderLaan et al. 2014a). Equally, there is no evidence that *fa'afafine* hold such expectations for themselves (VanderLaan et al. 2014a). Because Samoans in general, and *fa'afafine* themselves, did not believe that *fa'afafine* are primarily responsible for the care of nieces and nephews, elevated avuncular tendencies among *fa'afafine* cannot be explained in terms of such (trans)gender role expectations.

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 not inconsistent 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 not only ruling out alternative explanations but also repeatedly satisfying adaptive design criteria empirically (Buss et al. 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 *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 and VanderLaan 2010b). Such a dissociation would allow *fa'afafine* to channel resources toward nieces and nephews in a more optimal manner 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 and 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 the avuncular cognition of *fa'afafine* is sensitive to the relative fitness benefits of investing in sisters' versus brothers' offspring (VanderLaan and Vasey 2013). Fourth, compared to women and gynephilic men, *fa'afafine* are generally better at allocating investment toward indirect fitness-maximizing categories of kin (i.e., sisters' younger daughters) and they do so in a manner that reflects greater sensitivity to nonfrivolous versus frivolous investment contexts (VanderLaan and Vasey 2014).

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 gynephilic men, there were no correlations between the number of children parented and monetary exchanges with the niece and nephew categories examined, suggesting, once again, that childlessness cannot account for why *fa'afafine* give more money to their youngest siblings' daughters.

Analyses by VanderLaan et al. (2013c) revealed that key aspects of the adaptively relevant environment (ARE) of transgender androphilic males likely facilitated the expression of 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 transgender male androphilia predominates were more likely to show social characteristics that facilitate investment in kin, compared to non-transgender societies. For example, relative to non-transgender societies, transgender societies were more likely to exhibit bilateral<sup>4</sup> and double descent<sup>5</sup> systems than patrilineal, matrilineal, and ambilineal<sup>6</sup> descent systems. In addition, correlational analysis showed that as the presence of ancestral socio-cultural conditions increased, so too did the presence of bilateral (and double) descent systems. Ethnologists have argued that bilateral descent 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 and Greaves 2011). Consequently, it is reasonable to deduce that these patterns of descent would have allowed for more altruistic interactions with a full range of genetically related kin. Taken together, these analyses

<sup>4</sup> 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.

<sup>5</sup> In double descent systems, individuals receive some rights and obligations from the father's side of the family and others from the mother's side.

<sup>6</sup> Ambilineal descent systems are defined as existing when individuals have the option of choosing one of their lineages for membership.

are consistent with the conclusion that bilateral descent characterized the ancestral societies in which male androphilia was expressed in the transgender form.

VanderLaan et al. (2013c) also examined the acceptance of same-sex sexuality in 27 transgender societies for which information could be obtained. The vast majority of these societies expressed no negative reactions to same-sex sexual behavior. Overall then, the same-sex sexual orientation of transgender males appears to be socially tolerated in societies where this form of male androphilia predominates. Such tolerance, particularly on the part of the kin of transgender 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 transgender androphilic males are accepted by their families, their opportunity to invest in kin is likely mitigated.

In sum, transgender male androphilia is likely the ancestral form of male androphilia, key aspects of the transgender androphilic male ARE (i.e., bilateral and double descent systems, social tolerance of same-sex sexuality) would have facilitated elevated kin-directed altruism, and data from contemporary transgender male androphiles (*fa'afafine*) indicates that they exhibit elevated avuncularity. Given all of this, it seems reasonable to suggest that kin selection played some role in the evolution of male androphilia. As such, the elevated kin-directed altruism documented in Samoan *fa'afafine* is more likely to have characterized ancestral androphilic males compared to the lack thereof documented in sex-gender congruent androphilic men from industrialized cultures (Abild et al. 2014; Bobrow and Bailey 2001; Forrester et al. 2011; Rahman and Hull 2005; Vasey and VanderLaan 2012).

Our research has identified a number of features of the ARE that would have facilitated the expression of kin-directed altruism by androphilic males. What needs more careful consideration is the process by which this putative evolved trait develops over the life span. Research on childhood separation anxiety among gender nonconforming boys who grow up to be androphilic may provide insight in this regard.

## Childhood Separation Anxiety: A Developmental Precursor of Elevated Kin-Directed Altruism?

Childhood separation anxiety occurs in response to separation from major attachment figures such as parents and it tends to be more commonly manifest by girls compared to boys (e.g., Shear et al. 2006; VanderLaan et al. 2011a). As such, it can be described as a female-typical characteristic. Interestingly, in clinical samples drawn from Western populations, it is not uncommon for extremely feminine boys who are diagnosed with gender dysphoria in children (GDC)<sup>7</sup> to exhibit elevated traits of childhood separation anxiety (Coates and Person 1985; Zucker et al. 1996). The majority of boys diagnosed with GDC grow up to be androphilic in adulthood (Green 1987; Wallien and Cohen-Kettenis 2008; Singh 2012; Steensma 2013).

Recall that androphilic males are relatively feminine compared to gynephilic males, although often not necessarily to the extreme that characterizes GDC boys (Bailey and Zucker 1995; Bartlett and Vasey 2006; Cardoso 2005, 2009; Lippa 2005; Vasey and Bartlett 2007; Whitam 1983). Consequently, it is perhaps not surprising that *nonclinical* samples of adult androphilic males recall more traits of childhood separation anxiety compared to their gynephilic counterparts. This pattern of recall holds for both nonclinical samples of sex-gender congruent androphilic males in Canada (VanderLaan et al. 2011a) and nonclinical samples of transgender androphilic males in Samoa (Vasey et al. 2011).

<sup>7</sup> According to the American Psychiatric Association's *Diagnostic and Statistical Manual of Mental Disorders* (DSM-V; American Psychiatric Association 2013), gender dysphoria in children (GDC) is a mental disorder that characterizes individuals who experience dysphoria with respect to their sexed bodies or assigned genders or both. In Western parlance, such individuals are commonly referred to as transsexual or transgender. The full diagnostic criteria for GDC can be found in the DSM-V (American Psychiatric Association 2013). For an entree into the substantial controversy surrounding this diagnosis, see, for example, Bartlett et al. (2000) and Vasey and Bartlett (2007).



When considering these clinical and nonclinical studies from an evolutionary perspective, the question arises as to what the functional (i.e., adaptive) basis of elevated childhood separation anxiety might be in feminine, (pre)androphilic boys in general, as opposed to GDC boys more specifically. For some readers it may seem incongruous to entertain the idea that a “negative” emotion like separation anxiety might be adaptive. However, if one considers that emotions evolved to guide behavior toward adaptive courses of action, then there is no necessary reason why emotional states should be associated with positive affect in order to be considered adaptive (Keller and Miller 2006; Nesse 2005). Because separation anxiety occurs in response to separation from major attachment figures (Coates and Person 1985; Zucker et al. 1996), it seems reasonable to suggest that elevated traits of childhood separation anxiety in relatively feminine, (pre)androphilic boys are indicative of marked attachment to parents and other close family members.

In light of this literature, VanderLaan et al. (2011b) suggest that traits of elevated childhood separation anxiety in (pre)androphilic boys may be a developmental precursor of an evolved predisposition in adulthood for prosocial tendencies, particularly kin-directed altruism such as elevated avuncularity. According to this model, in childhood, concern for one’s kin manifests as elevated separation anxiety in (pre)androphilic boys and is part of an overall pattern of feminine behavior. Later, in adulthood, concern for one’s kin is expressed as elevated kin-directed altruism by adult male androphiles. The model stipulates that this adult pattern of elevated kin-directed altruism is contingent on the continued expression of femininity in adulthood. As such, elevated traits of childhood separation anxiety are predicted to occur in all (pre)androphilic boys, regardless of their cultural milieu. In contrast, elevated kin-directed altruism in adulthood is predicted to occur in transgender male androphiles such as *fa’afafine* who are feminine, but not in sex-gender congruent male androphiles such as gay men, who present publicly in a relatively masculine manner.

In support of this evolutionary developmental model, retrospective research has shown that Samoan *fa’afafine* recall more gender-atypical behavior and more traits of separation anxiety in childhood than gynephilic men (Bartlett and Vasey 2006; Vasey and Bartlett 2007; Vasey et al. 2011). *Fa’afafine* scored highest for items used to measure childhood separation anxiety involving worrying about parents (e.g., “I worried that something terrible might happen to my parents”). These findings are reinforced by qualitative data collected during interviews with adult *fa’afafine*. The anxiety that some *fa’afafine* recalled experiencing with respect to something terrible happening to their parents seemed to generalize into a pattern of extreme worry about all aspects of the parents’ (especially the mothers’) lives. For example, one *fa’afafine* participant recounted the following story:

When my mom brought my lunch to school and she was wearing a *puletasi* [a traditional Samoan two-piece dress], I knew she wasn’t too rushed and had time to make herself look pretty. But when she came wearing a *lavalava* [a colourful Samoan garment similar to a sarong] and a t-shirt, I knew she was too busy to make herself beautiful. I would ask her if I could go home with her to help but she would tell me to stay at school. I would be worried all afternoon and wouldn’t be able to focus on my work. I just waited for that final bell to ring. I would have rather helped my mom at home but I had to stay behind.

Research conducted in Canada also furnishes support for VanderLaan et al.’s (2011b) evolutionary development model. For example, retrospective research in Canada indicates that sex-gender congruent androphilic men are also more gender-atypical in childhood compared to gynephilic men (Bailey and Zucker 1995; VanderLaan et al. 2011a). Moreover, they recalled significantly more traits of childhood separation anxiety compared to gynephilic men, but did not differ in this regard from women (VanderLaan et al. 2011a). Those who recalled higher levels of boyhood gender atypicality were more likely to also recall higher levels of childhood separation anxiety (VanderLaan et al. 2011a). Like *fa’afafine*, Canadian sex-gender congruent androphilic males also scored highest for items used to measure

childhood separation anxiety involving worrying about parents, as opposed to items used to measure concern for one's own well-being (VanderLaan et al. 2011a).

In another Canadian study, VanderLaan et al. (2014b) demonstrated that elevated concern for parental well-being was a source of childhood separation anxiety that characterized androphilic males and females significantly more than gynephilic males. The heterosexual sex and male sexual orientation differences in concern about parental well-being were accounted for by childhood feminine behavior. These findings suggest that female-typical behavior in childhood is an important proximate factor in the expression of elevated concern for the well-being of kin among (pre)homosexual boys.

Also consistent with VanderLaan et al.'s (2011b) evolutionary developmental model is the finding that, unlike *fa'afafine* who are feminine in adulthood, sex-gender congruent androphilic men in Canada and other industrialized nations (i.e., USA, UK, Japan) do not exhibit elevated avuncular tendencies in adulthood (Abild et al. 2014; Bobrow and Bailey 2001; Forrester et al. 2011; Rahman and Hull 2005; Vasey and VanderLaan 2012). In these cultures, gender role expectations hold that male-bodied individuals should behave in a masculine manner and, as such, boys are socialized to behave accordingly (Bailey 2003; Berling 2001; McLelland 2000; Rieger and Savin-Williams 2012). VanderLaan et al. (2011b) have speculated that the behavioral masculinization and defeminization that characterizes the development of sex-gender congruent males in such cultures may lower the expression of elevated kin-directed altruism in adulthood.

## Concluding Remarks

In recent years, progress has finally been made toward gaining an empirically based understanding of how male androphilia persists over evolutionary time. Although male androphilia varies dramatically with respect to the manner in which it is publicly expressed, there are multiple lines of developmental and biodemographic evidence indicating that different cultural forms of male

androphilia (i.e., transgender sex-gender congruent) share the same etiological basis. Quantitative research indicates that the transgender form of male androphilia was likely ancestral to the sex-gender congruent form.

The most prominent hypothesis that posits a role for the social behavior of male androphiles in the evolutionary maintenance of genes associated with same-sex sexual orientation is the kin selection hypothesis. Research in Samoa has repeatedly furnished support for the kin selection hypothesis where transgender male androphiles known locally as *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.

VanderLaan et al. (2011b) proposed that elevated traits of childhood separation anxiety are part of a general constellation of feminine characteristics exhibited by androphilic males. Moreover, they argued that elevated traits of childhood separation anxiety in androphilic males primarily reflect concern for close kin. The research that exists is consistent with these predictions. On the basis of these ideas, VanderLaan et al. (2011b) argued, further, that childhood concern for kin, as manifested in terms of elevated traits of childhood separation anxiety, is a developmental precursor of elevated kin-directed altruism in adulthood. The expression of elevated adult kin-directed altruism by androphilic males is, however, contingent on the continued expression of femininity in adulthood. As such, elevated kin-directed altruism is expected to occur in transgender male androphiles, but not sex-gender congruent male androphiles. Again, existing research, while limited, is consistent with these predictions.

To provide more detailed tests of VanderLaan et al.'s (2011b) evolutionary developmental model, additional research is needed on other populations of sex-gender congruent and transgender male androphiles to ascertain whether the expression of elevated traits of childhood separation anxiety is indeed a cross-culturally invariant pattern of psychosexual development in such individuals. Future research is also needed to provide further tests of the hypothesis that child-

hood separation anxiety in androphilic males is primarily related to concern for kin, as opposed to concern for oneself. Similarly, more research is needed to explore the purported link between separation anxiety in childhood and kin-directed altruism in adulthood in androphilic males. Lastly, it will be important to test the kin selection hypothesis in additional populations of transgender male androphiles to ascertain whether other such populations exhibit elevated avuncular tendencies.

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