

Chapter 9

Transgendered Male Androphilia in the Human Ancestral Environment

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Beyond Gay: Male Sexual Orientation in Cross-Cultural Perspective

Gay men represent an increasingly visible aspect of Western culture. Previous polls have shown that the number of individuals who state that they personally know someone who openly identifies as “gay” grows with every passing year (e.g., Rubin 2000). Consequently, regardless of their sexual orientation, it might come as a surprise to most individuals living in the West that “gay men” do not necessarily exist in other cultures. Indeed, it is not at all uncommon for individuals living in non-Western cultures to claim that “gay men” or “homosexuals” are unknown in their societies. Many of the individuals who are most vehement in making such assertions are biological males who have sex with other biological males.

What are we to make of such claims? Research has demonstrated that the identity categories of “gay” and “homosexual” are culturally and historically “situated” and, as such, do not necessarily translate to other places and times (e.g., Asthana and Oostvogels 2001). Such categories, if they are known at all, might mean something to people in other cultures, but whatever that might be, they are not categories of personhood that individuals draw upon when constructing personal narratives about who they are. As such, the way in which many non-Western, same-sex attracted males think about themselves and pattern their lives (sexual or otherwise) differs radically in many respects from Western gay men. Thus, when individuals from non-Western cultures say that there are no “gays” or “homosexuals” in their societ-

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ies, they are not necessarily lying. Based on their understanding of what it means to be “gay” or “homosexual,” no one in their societies identifies or behaves as such, and neither do they identify other members of their culture in that way.

Given this, any attempt to undertake comparative cross-cultural research on sexual orientation must focus on the *deep structure* of sexual orientation that transcends differences related to how male same-sex sexual attraction is socially constructed within culturally specific contexts. The deep structure of male same-sex sexuality can be thought of as a set of traits that characterize same-sex attracted males regardless of the cultural context in which they are found. To this end, a focus on cross-culturally universal *sexual feelings* facilitates comparisons in a manner that culturally specific identity categories do not. As such, we employ the terms *androphilia* and *gynephilia* in our discussion of sexual orientation across cultures. Androphilia refers to sexual attraction and arousal to adult males, whereas gynephilia refers to sexual attraction and arousal to adult females. Although same-sex attracted “gay men” in Western societies differ in many dramatic ways from same-sex attracted males in a range of non-Western societies, in terms of the deep structure of sexual orientation, both can be accurately described as androphilic biological males.

An additional advantage of this terminology is that it avoids reference to sexual *behavior*, which may be constrained by cultural circumstances (e.g., taboos against same-sex sexual behavior), or enacted for reasons unrelated to sexual attraction and arousal (e.g., ritual, prostitution, coercion, etc.). As such, the terms “androphilia” and “gynephilia” make no assumptions about whether sexual behavior has been expressed. Consequently, an individual can be androphilic or gynephilic without ever having engaged in sexual behavior.

How Male Androphilia Is Publically Expressed Varies Cross-Culturally

As should be evident from the discussion above, the manner in which male androphilia is publically expressed varies across cultures (Murray 2000). This expression typically takes one of two forms, which are related to gender role enactment and gender identity. 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.” 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.

Transgendered androphilic males typically behave in an effeminate manner and often identify as neither “men” nor “women,” but 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 activi-

ties. Such transgendered male androphilia has been referred to as *role structured homosexuality* (Herdt 1997). 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). Similarly, in some cultures, such as the Mohave and the Yorok, all *berdache* (transgendered male androphiles) were shamans (e.g., Devereux 1937; Kroeber 1925).

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 tends to be much more common in many Western cultures; in contrast, the transgendered form appears to be more common in many non-Western cultures (Murray 2000). In places where these two forms coexist, albeit with one predominating, the two often consider each other to be members of the same community (Whitam 1983).

In addition to these two forms of male androphilia, a third form, transgenerational homosexuality, has also been reported in the ethnographic literature. Transgenerational homosexuality involves sexual interactions between a sexually immature or younger male and a sexually mature, older male (Murray 2000). It is not clear whether 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 ritualistic purposes (e.g., Herdt 1981). 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).

Some Correlates of Male Androphilia Reoccur Consistently Across Diverse Cultures

Attempts to draw comparisons between the sex-gender congruent and transgendered forms of male androphilia have been characterized as misguided because, critics argue, these forms are so culturally distinct in terms of what they mean within a particular cultural setting that any comparisons one might make would be largely facile (Johnson et al. 2000). As such, the overall impression one gleans from this social constructionist literature is that a panoply of male “androphilias” exist cross-culturally. Not surprisingly, researchers whose work is informed by evolutionary theory have questioned whether a common biological basis underlies the diverse cultural expressions characterizing this trait. If it were possible to establish that androphilic males from different cultural backgrounds shared traits that are indicators, at least in theory, of common etiology, then this would lend support to the possibility of a common biological basis. Indeed, quantitative research indicates

that the sex-gender congruent and transgendered forms of male androphilia share numerous developmental and biodemographic correlates that appear to be cross-culturally invariant.

In terms of biodemographic correlates of male androphilia that exist across cultures, both sex-gender congruent and transgendered male androphiles tend to 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,”¹ e.g., Bogaert and Skorska 2011; VanderLaan and Vasey 2011; Vasey and VanderLaan 2007), exhibit larger family sizes (e.g., Blanchard and Lippa 2007; Camperio-Ciani et al. 2004; Iemmola and Camperio Ciani 2009; King et al. 2005; 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 cultures (e.g., Smith et al. 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 et al. 2014). In addition, the odds ratios associated with the fraternal birth order 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 culturally diverse populations (e.g., Cantor et al. 2002; VanderLaan and 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 and Zucker 1995; Bartlett and 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 wish I was a girl”; Bailey and Zucker 1995; Vasey and 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 et al. 2011; Vasey et al. 2011; Zucker et al. 1996), which tends to be more common among girls compared to boys (e.g., Shear et al. 2006; VanderLaan et al. 2011). 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 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

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 and Skorska 2011).

a masculine manner (Bailey 2003; Berling 2001; Rieger and 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 adult transgendered male androphiles. 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 with the manner in which male androphilia is publically expressed.

Taken together, these numerous, cross-culturally uniform biodemographic and developmental correlates of male androphilia indicate that sex-gender congruent and transgendered male androphilia are cultural variants of what is essentially the same phenomenon with a common biological basis. In this regard, the cross-culturally invariant biodemographic and developmental correlates described above can be thought of as part of the deep structure of male androphilia.

Male Androphilia Is an Evolutionary Paradox

The existence of diverse forms of male androphilia across cultures, which nonetheless share a similar biological etiology, is an evolutionary paradox. There appears to be a genetic influence on male androphilia (e.g., Bailey et al. 2000; Kendler et al. 2000; Långström et al. 2010), yet androphilic males reproduce at significantly lower rates than gynephilic males, if at all (e.g., King et al. 2005; Schwartz et al. 2010; Vasey et al. 2014). Consequently, 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.

Nevertheless, prehistoric rock art and pottery suggests that male-male sexual activity has existed for millennia (e.g., Larco Hoyle 1998; Nash 2001). Further, graves containing male skeletal remains and female-typical artifacts are indicative of transgendered males in the distant past (e.g., Hollimon 1997). Prine (2000) argued that certain architecturally unusual dwellings inhabited by the Hidasta² 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 individuals are suggestive of the presence of male androphilia in human antiquity.

Furthermore, male androphilia occurs in the vast majority of cultures for which information is available (Murray 2000) and it appears to occur at similar frequencies (e.g., Smith et al. 2003; VanderLaan et al. 2013a; Whitam 1983). Some reports exist of cultures where male-male sexual behavior is unknown (e.g., Hewlett and

² The Hidasta are a native North American people that lived in palisaded villages along the modern-day Missouri River in North Dakota.

Hewlett 2010), but it is not clear whether some males in these populations have unexpressed androphilic feelings. Although male–male sexuality may be absent in a minority of cultures, these exceptions do not invalidate the conclusion that male androphilia is a predictably and reliably reoccurring phenomenon in most human cultures. The cross-culturally widespread nature of male androphilia suggests that it is a phylogenetically primitive aspect of the human sexual condition.

In sum, male androphilia has a genetic component, occurs at similar frequencies across many different cultures, and appears to have existed for millennia. Nevertheless, 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.

What Was the Human Ancestral Form of Male Androphilia

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? If it were possible to establish that one form of male androphilia was associated, more often than not, with sociocultural conditions thought to characterize ancestral humans, then this would bolster the conclusion that that particular form of male androphilia was ancestral. Implementation of this approach requires establishing at least some of the sociocultural features that characterized ancestral humans. There is widespread consensus that ancestral humans followed a hunter-gatherer pattern of subsistence until the beginning of the Holocene, and archaeological evidence supports this contention (McBrearty and Brooks 2000; Smith 1999). As such, ethnographic data derived from the study of hunter-gatherers has been widely used to model ancestral human sociocultural conditions.

For example, research on hunter-gatherers indicates that the residential groups³ in which human ancestors lived were likely to have been relatively small (Klein 1999; Ehrlich 2000). Binford (2001) examined group size during the most aggregated phase⁴ of subsistence settlement for 219 nonequestrian,⁵ hunter-gatherer eth-

³ “Residential group” refers to the same camp or settlement within which people regularly reside.

⁴ Hunter-gatherers exhibit a high degree of residential mobility, which is expressed in terms of a fission-fusion type of group organization whereby the group breaks apart into smaller foraging parties, which then reassemble each day into larger aggregates (Marlowe 2005).

⁵ Beginning in the 1700s, after the Spanish introduction of the horse, various North American Plains Indian ethnolinguistic groups subsequently became specialists in hunting bison from horseback (Shimkin 1983). This specialization in foraging pattern influenced the group sizes, home

nolinguistic groups who varied according to primary food source exploited (i.e., terrestrial plants, terrestrial animals, aquatic resources) and mobility (i.e., mobile settlements, semi-sedentary settlements). His analyses indicated that group size for these hunter-gatherers was, on average, 69 individuals. Marlowe's (2005) analysis of warm-climate,⁶ non-equestrian hunter-gatherer ethnolinguistic groups ($n=130$) indicates that residential groups contain a mean (\pm SD) of 37.46 (\pm 38.28) individuals. Hill et al. (2011) analyzed data from 32 hunter-gatherer societies and found that mean band size was 28.2 individuals. If these results for mean hunter-gatherer residential group size can be taken as representative of the conditions that characterized ancestral humans, then these analyses point to the conclusion that, on average, ancestral humans formed relatively small residential groups of approximately 28–69 individuals.

Research on hunter-gatherers also indicates that ancestral humans were likely egalitarian in terms of their political structure. Contemporary hunting and gathering societies that have economies based on immediate, rather than delayed, return of food resources tend to be egalitarian with respect to power, wealth, prestige, and religious beliefs/practices (Woodburn 1982). In immediate-return systems, all individuals have direct access to food resources, which are owned by no single individual. Food is neither elaborately processed, nor stored. Social groupings are flexible and constantly changing in composition and, as such, there are no fixed dwellings, base camps, storage areas, hunting or fishing apparatuses (i.e., weirs), or ritual sites. Individuals have a choice of whom they associate with in terms of residence, food acquisition, trade, and ritual contexts. Movement between groups does not result in economic penalties. Although sharing and mutuality are stressed, individuals are not dependent on food sharing, nor are they involved in long-term binding commitments and dependencies of the sort that characterize delayed return systems. Moreover, the accumulation of personal possessions is sanctioned. In these societies, there are either no leaders at all, or leaders who are constrained in terms of their ability to exercise authority or influence to acquire wealth and prestige.

With respect to the ancestral form of religion, some scholars have argued that shamanistic⁷ activity is depicted in Paleolithic rock art (Clottes and Lewis-Williams 1998; Deacon 1999). Furthermore, shamanism appears to be common in contemporary small-scale hunter-gatherers (Sanderson and Roberts 2008; Winkelman 2010).

ranges, hunting success rates, and travel costs of these groups. Because we are interested in reconstructing the sociocultural environment of ancestral humans prior to the domestication of the horse, we do not consider data from equestrian hunter-gatherers here.

⁶ It is only during the last 30,000 years that the arctic has been occupied by modern *Homo sapiens* (Vaughan 1994). Occupation of this biome had concomitant influences on residential group size. Consequently, Marlowe (2005) argues that if we are interested in the period prior to 30,000 years ago, it is reasonable to exclude arctic foragers from analysis pertaining to residential group size.

⁷ A religion is Shamanic when a shaman is the center of most religious practice, a strong belief in animism is present, there are no calendrical rites, and laypersons rely on a shaman as the sole intermediary between themselves and the supernatural (Sanderson and Roberts 2008).

Taken together, this evidence suggests that shamanism, which is closely associated with animism,⁸ represents the form of religion practiced by ancestral humans.

With these insights in mind, VanderLaan et al. (2013c) compared 46 “transgendered societies” (i.e., societies in which transgendered male androphilia predominated) with 146 “non-transgendered societies” using the standard cross-cultural sample (SCCS).⁹ Their goal was to ascertain whether human ancestral socio-cultural conditions (i.e., hunting and gathering, smaller group size, egalitarian political structure, and animistic/shamanistic religious beliefs) were more likely to be associated with one of these two types of societies. Their analysis indicated that transgendered societies were characterized by a significantly greater presence of ancestral sociocultural conditions, compared to non-transgendered societies. 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.

The existence of two forms of transgendered male androphilia (i.e., *institutionalized role structured* and *non-role structured*) raises the question as to which one preceded the other in evolutionary time. It seems likely that role structure transgendered male androphilia is derived from a more ancestral form of transgendered male androphilia that does not involve role specialization. Once transgendered male androphilia originated in humans, it could then be culturally elaborated upon to serve any number of distinct social roles. This represents the most parsimonious evolutionary sequence in the evolution of transgendered male androphilia because, phylogenetically, less specialized form of traits tend to precede more specialized ones (Dean et al. 2014).

The Fa’afafine of Samoa

To date, tests of evolutionary hypotheses pertaining to male androphilia have been conducted on a single population of transgendered androphilic males—the *fa’afafine* of Samoa. Our research group has conducted this work. Previous discussions pertaining to the evolution of male androphilia have centered almost exclusively sex-gender congruent male androphiles. Consequently, the remainder of this review showcases our Samoan *fa’afafine* research given its unique focus on transgendered male androphiles. For a review of the evolutionary literature that compares both sex-gender congruent and transgendered male androphiles, see Vasey and VanderLaan (2014).

In the Samoan language, *fa’afafine* means: “in the manner of a woman.” Within Samoan society, *fa’afafine* are not recognized as “men” or “women,” nor do they

⁸ Animism refers to the belief that spirits inhabit some or all natural objects and phenomena.

⁹ The SCCS provides data related to a subset of the world’s non-industrial societies and is employed to circumvent Galton’s problem (i.e., common cultural derivation and cultural diffusion) when conducting cross-cultural comparisons.

identify as such, and, consequently, they have been described as a type of “third” gender. Like men, *fa’afafine* are biological males. They differ from Samoa men, however, in that they are very feminine with respect to their gender role enactment. From a Western perspective, many *fa’afafine* would be considered transgendered. The majority are not transsexual, however, because they do not experience dysphoria with respect to their genitals (Vasey and Bartlett 2007). Unlike the *hijra* of India, *fa’afafine* have no institutionalized role in Samoa.

Fa’afafine are recognized in childhood by their families and the members of their community 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 boys into *fa’afafine*. Rather, in Samoan culture, boyhood femininity is interpreted to mean that individuals simply are *fa’afafine* and it is understood that such individuals will not grow up to be “men.” Some families react negatively to the presence of a *fa’afafine* child with corporal punishment, but many have a *laissez-faire* attitude, some even facilitate the child’s feminine behavior—sewing “him” dresses, 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. 2013). 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 other *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 gynephilic may have sex with *fa’afafine* if they are unable to access their preferred sexual partners (i.e., adult females). This may seem perplexing from a Western cultural perspective, however, it is important to note that in cultures where transgendered male androphilia predominates, many male gynephiles may experience relatively little sexual aversion to the idea of engaging in certain types of same-sex sexual interactions because, to a certain extent, transgendered male androphiles represent facsimiles of their preferred sex partners (i.e., adult females). The other men who have sex with *fa’afafine* appear to be a combination of *gynandromorphophilic* (i.e., peak sexual attraction and arousal to she-males), bisexual, or androphilic. In short, the Samoan category of “straight man” is a very heterogeneous one with respect to sexual orientation (Vasey and Petterson, unpublished data).

In Samoa, *fa’afafine* enjoy a high level of social acceptance that, while not absolute, stands in stark contrast to the situation experienced by Western transgendered male androphiles (Namaste 2000; Seil 1996). Indeed, *fa’afafine* are highly visible and active members of Samoa society. They occupy all manner of positions from stay-at-home caregivers to Assistant Chief Executive Officers in the government.

The Prime Minister of Samoa, the Honorabe Tuilaepa Sailele Malielegaoi, is Patron of the National *Fa'afafine* Association and has spoken publically on many occasions about the value of *fa'afafine* for Samoan society.

In the following sections, we describe our research on the Samoan *fa'afafine* that aimed at testing three hypotheses for the evolution of male androphilia, namely, the *Sexually Antagonistic Gene Hypothesis*, the *Over-Dominance Hypothesis* and the *Kin Selection Hypothesis*.

Tests of the Sexually Antagonistic Gene Hypothesis in Samoan *Fa'afafine*

Balancing selection hypotheses for male androphilia hold that the relatives of male androphiles exhibit increased reproductive success thereby offsetting any reproductive costs associated with male androphilia, itself. For example, 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 (e.g., Camperio-Ciani et al. 2004). 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 persist 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.

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), who also showed that elevated offspring production among the mothers of *fa'afafine* was not an artifact of the fraternal birth order effect. More recently, VanderLaan et al. (2012) extended these findings by demonstrating that *fa'afafine*'s maternal and paternal grandmothers exhibit elevated offspring production, compared to those of gynephilic men. However, elevated reproductive output by the maternal and paternal aunts of *fa'afafine* was not observed (VanderLaan et al. 2012).

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. Nevertheless, the cumulative weight of this evidence suggests that the Sexual Antagonistic Gene Hypothesis is still a tenable explanation for the evolution of male androphilia. Future research is needed, however, to ascertain whether group differences remain nonexistent for maternal and paternal aunts when using a larger sample. In addition, future research will be needed to assess whether VanderLaan et al.'s (2012) finding of group differences for maternal and paternal grandmothers can be replicated.

Apart from the fact that these studies were conducted in a population in which transgendered male androphilia predominates, another major strength of this Samoan-based research is that it examined female reproductive output in a population with a high fertility rate (Central Intelligence Agency 2012). Consequently, anomalous reproductive patterns should be less likely to occur in the Samoan population, compared to lower-fertility Western populations where similar research has been conducted. 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 associated with elevated reproductive output in both the maternal and the paternal lines. This is not the case for some of the research that has been presented from certain Western populations (e.g., Camperio-Ciani et al. 2004; Iemmola and Camperio Ciani 2009; Camperio Ciani and Pellizzari 2012; Rahman et al. 2008). On the basis of our Samoan research, it seems reasonable to 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 of sexually antagonistic selection for the evolution of male androphilia (Gavrilets and Rice 2006).

Tests of the Over-Dominance Hypothesis in Samoan Fa'afafine

Another balancing selection hypotheses for male androphilia—the Over-Dominance 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 (Miller 2000).¹⁰ Ample empirical evidence exists to support this assumption (Bailey and Zucker 1995; Bartlett and Vasey 2006; Cardoso 2005, 2009; Lippa 2005; VanderLaan et al. 2011; Vasey and 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

¹⁰ This hypothesis is also referred to as the “Balanced Polymorphism Hypothesis” for male androphilia.

this critical threshold, males who inherit some of these genes are gynephilic, but are feminized in terms of certain personality traits, which render them 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 and Shackelford 2008; Phillips et al. 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 gynephilic 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 Over-Dominance 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 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.

To date, only one study has been conducted by our research group that provides a test of the Over-Dominance Hypothesis in Samoa. VanderLaan et al. (2012) found that both the maternal and paternal uncles of Samoan *fa'afafine* did not differ from those of Samoan gynephilic males in terms of offspring production. As such, the research conducted in Samoa provides no support, at present, for the Over-Dominance Hypothesis.

Tests of the Kin Selection in Samoan *Fa'afafine*

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 could increase their indirect fitness by directing altruistic behavior toward kin, which, in principle, would allow those 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.

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) com-

mented that “...the effect is that in being homosexual, offspring become altruistic towards 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.

Research conducted on transgendered 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 significantly elevated compared to those of Samoan gynephilic males (VanderLaan and Vasey 2012; Vasey et al. 2007; Vasey and VanderLaan 2010a). *Fa'afafine* also exhibited significantly 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 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 should 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 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 be similar, but this was not the case. This same research also demonstrates that *fa'afafine*'s self-reports of elevated avuncular tendencies cannot be explained away as a desire by members of this group to appear more socially virtuous than women or gynephilic men. If this were the case, then one would expect *fa'afafine* to also report that they had elevated altruistic interest in non-kin children, but this was not the case. In fact, the three groups did not differ from each other in this regard.

Additional research indicates that *fa'afafine* exhibit similar levels of sexual/romantic relationships involvement compared to Samoan women and gynephilic men (VanderLaan and 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 relationships 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 *fa'afafine* 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 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 the *fa'afafine* are more dissociated from (i.e., co-vary 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/nephews in a more optimal manner (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 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 gynephilic men and androphilic women, *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 non-frivolous 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, 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.

Although quantitative data is lacking, anecdotal evidence suggests that elevated kin-directed altruism characterizes other populations of transgendered male androphiles. For example, Williams (1992, p. 54) quotes a Hupa *berdache* (i.e., a transgendered, androphilic male from the Hupa Valley in Northern California) as saying: "You live your life around your family. My aunt says 'I'm counting on you.' What she means is that someone like me has a special responsibility to help care for the elders." These sorts of statements concerning the focal importance of family for transgendered androphilic males are echoed over and over again in the cross-cultural literature and suggest that elevated attachment and commitment to family is a wide-spread cross-cultural pattern found among such males.

Kin Directed Altruism in an Adaptively Relevant Environment

Adaptively relevant environments (ARE) consist of those features of the environment that must be present in order for an adaptation to be functionally expressed (Irons 1998). Analyses by VanderLaan et al. (2013c) revealed that key aspects of the ARE of transgendered androphilic males likely facilitate elevated kin-directed altruism. For example, relative to non-transgendered societies, transgendered societies are more likely to exhibit bilateral¹¹ and double descent¹² systems than patrilineal, matrilineal, and ambilineal¹³ ones. 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 and Greaves 2011). Correlational analysis by VanderLaan et al. (2013c) showed that as the presence of ancestral sociocultural conditions increased, so too did the presence of bilateral (and double) descent systems. Consequently, it is reasonable to deduce that, ancestrally, these patterns of descent and post-marital residence would have allowed for more altruistic interactions by transgendered androphilic males with a full range of genetically related kin.

¹¹ 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.

¹² 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.

¹³ 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.

The evolution of maximally inclusive kinship systems of descent and residence (i.e., bilateral descent, bilocal residence) would have been contingent on the existence of tribal-level organization (Chapais 2008). Consequently, if kin selection played some role in the evolution of male androphilia within the context of maximally inclusive kinship systems of descent and residence, then tribal-level organization would have been a necessary condition of the sociocultural environment. As Chapais (2008) cogently argued, pair-bonding was a necessary prerequisite for the evolution of tribal-level organization. Some authors have argued that pair-bonding (and presumably tribal-level organization) characterized *Homo erectus* (Wrangham et al. 1999), but others have argued that pair-bonding had not evolved at this stage in the evolution of the genus *Homo* (Hawkes et al. 2003). Given that this debate remains unresolved at present, our conclusions should be taken as representative of *Homo sapiens*, which appear in the fossil record about 195 kya (McDougall et al. 2005), and then only those *Homo sapiens* who exhibited tribal-level organization.

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, it is likely that transgendered male androphilia is the ancestral form of this trait, key aspects of the transgendered androphilic male ARE (i.e., bilateral and double descent descent system, social tolerance of same-sex sexuality) would have facilitate elevated kin-directed altruism, and data from contemporary transgendered androphilic males (*fa'afafine*) 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 androphilia. As such, the elevated 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 (e.g., Abild et al., 2014; Bobrow and Bailey, 2001; Rahman and Hull, 2005; Forrester et al. 2011; Vasey and VanderLaan 2012).

Concluding Remarks

In recent years, progress has been made toward understanding how a trait like male androphilia persists over evolutionary time. One of the most important strides in this regard has been the finding that that the ancestral form of male androphilia in humans is likely the transgendered form. In contrast, the sex-gender congruent form of male androphilia is likely to be more derived and may reflect more historically

recent, cultural influences. The outcome of evolutionary processes may be obscured when using more derived forms of male androphilia as models. As such, 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.

To date, theories pertaining to the evolution of male androphilia have been tested in one population of transgendered male androphiles: the *fa’afafine* of Samoa. In keeping with the predictions of the Sexually Antagonistic Gene Hypothesis, it has been shown that the mothers, maternal grandmothers and paternal grandmothers of *fa’afafine* have more offspring than those of gynephilic males. However, definitive support for this hypothesis, in the form of elevated offspring production among the aunts of *fa’afafine* is lacking at present. In keeping with the predictions of the Kin Selection Hypothesis, it has been repeatedly shown that *fa’afafine* exhibit elevated avuncular tendencies compared to women and gynephilic men. Several studies also suggest that the avuncular cognition of *fa’afafine* exhibits hallmarks of adaptive design.

In light of these results, one potential way that male androphilia could be conceptualized is as a by-product of an adaptation (*sensu* Buss et al. 1998; Gould and 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 the 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 *fa’afafine* exhibits special design features (VanderLaan and Vasey 2012, 2013, 2014; Vasey and VanderLaan 2010b). It is likely that certain features of the ancestral sociocultural environment of transgendered androphilic males, including maximally inclusive descent systems (e.g. double or bilateral descent) and social tolerance of male-male sexuality, would have facilitated this process.

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References

- Abild, M., VanderLaan, D.P., & Vasey, P.L. (2014). Does proximity influence the expression of avuncular tendencies in Canadian androphilic males? *Journal of Cognition and Culture*, *14*, 40–62.
- Alvard, M.S. (2002). Carcass ownership and meat distributions by big game hunters. *Research in Economic Anthropology*, *21*, 99–131.
- Asthana, S., & Oostvogels, R. (2001). The social construction of male 'homosexuality' in India: Implications for HIV transmission and prevention. *Social Science and Medicine*, *52*, 707–721.
- Bailey, J.M. (2003). *The man who would be queen: The science of gender-bending and transsexualism*. Washington: Joseph Henry Press.
- Bailey, J.M., & Zucker, K.J. (1995). Childhood sex-typed behavior and sexual orientation: A conceptual analysis and quantitative review. *Developmental Psychology*, *31*, 43–55.
- Bailey, J.M., Dunne, M.P., & Martin, N.G. (2000). Genetic and environmental influences on sexual orientation and its correlates in an Australian twin sample. *Journal of Personality and Social Psychology*, *78*, 524–536.
- Barclay, P. (2010). Altruism as a courtship display: Some effects of third-party generosity on audience perceptions. *British Journal of Psychology*, *101*, 123–135.
- Bartlett, N.H., & Vasey, P.L. (2006). A retrospective study of childhood gender-atypical behavior in Samoan fa'afafine. *Archives of Sexual Behavior*, *35*, 559–566.
- Berling, T. (2001). *Sissyphobia: Gay men and effeminate behavior*. Philadelphia: Harrington Park Press.
- Binford, L.R. (2001). *Constructing frames of references: An analytical method for archaeological theory building using hunter-gatherer and environmental data sets*. Berkeley: University of California.
- Blanchard, R. (2004). Quantitative and theoretical analyses of the relation between older brothers and homosexuality in men. *Journal of Theoretical Biology*, *230*, 173–187.
- Blanchard, R., & Lippa, R.A. (2007). Birth order, sibling sex ratio, handedness, and sexual orientation of male and female participants in a BBC Internet research project. *Archives of Sexual Behavior*, *36*, 163–176.
- Bobrow, D., & Bailey, J.M. (2001). Is male homosexuality maintained via kin selection? *Evolution and Human Behavior*, *22*, 361–368.

- Bogaert, A.F., & Skorska, M. (2011). Sexual orientation, fraternal birth order, and the maternal immune hypothesis: A review. *Frontiers in Neuroendocrinology*, *32*, 247–254.
- Buss, D.M., & Shakelford, T.K. (2008). Attractive women want it all: Good genes, economic investment, parenting proclivities, and emotional commitment. *Evolutionary Psychology*, *6*, 134–146.
- Buss, D.M., Abbott, M., Angleitner, A., Asherian, A., Biaggio, A., & Blanco-Villasenor, A. (1990). International preferences in selecting mates: A study of 37 cultures. *Journal of Cross-Cultural Psychology*, *21*, 5–47.
- Buss, D.M., Haselton, M.G., Shackelford, T.K., Bleske, A.L., & Wakefield, J.C. (1998). Adaptations, exaptations, and spandrels. *American Psychologist*, *53*, 533–548.
- Camperio Ciani, A., & Pellizzari, E. (2012). Fecundity of paternal and maternal non-parental female relatives of homosexual and heterosexual men. *PLoS ONE*, *7*(12), e51088.
- Camperio-Ciani, A., Corna, F., & Capiluppi, C. (2004). Evidence for maternally inherited factors favoring male homosexuality and promoting female fecundity. *Proceedings of the Royal Society of London B*, *271*, 2217–2221.
- Cantor, J.M., Blanchard, R., Paterson, A.D., & Bogaert, A.F. (2002). How many gay men owe their sexual orientation to fraternal birth order? *Archives of Sexual Behavior*, *31*, 63–71.
- Cardoso, F.L. (2005). Cultural universals and differences in male homosexuality: The case of a Brazilian fishing village. *Archives of Sexual Behavior*, *34*, 103–109.
- Cardoso, F.L. (2009). Recalled sex-typed behavior in childhood and sports preferences in adulthood of heterosexual, bisexual, and homosexual men from Brazil, Turkey, and Thailand. *Archives of Sexual Behavior*, *38*, 726–736.
- Central Intelligence Agency. (2012). The World Factbook. <https://www.cia.gov/library/publications/the-worldfactbook/rankorder/2127rank.html>. Accessed Nov 31, 2012.
- Chapais, B. (2008). *Primeval kinship: How pair-bonding gave birth to human society*. Cambridge: Harvard University Press.
- Clottes, J., & Lewis-Williams, D. (1998). *The shamans of prehistory: Trance and magic in the painted caves*. New York: Harry N. Abrams.
- Crapo, R.H. (1995). Factors in the cross-cultural patterning of male homosexuality: A reappraisal of the literature. *Cross-Cultural Research*, *29*, 178–202.
- Daly, M., Salmon, C., & Wilson, M. (1997). Kinship: The conceptual hole in psychological studies of social cognition and close relationships. In J. A. Simpson & D. Kenrick (Eds.), *Evolutionary social psychology* (pp. 265–296). Mahwah: Erlbaum.
- Deacon, H.J. (1999). *Human beginnings in South Africa: Uncovering the secrets of the stone age*. CA: Altamira Press.
- Dean, L.G., Vale, G.L., Laland, K.N., Flynn, E., & Kendal, R.L. (2014). Human cumulative culture: A comparative perspective. *Biology Review*, *89*, 284–301.
- Devereux, G. (1937). Institutionalized homosexuality of the Mohave Indians. *Human Biology*, *9*, 498–527.
- Ehrlich, P.R. (2000). *Human natures: Genes, cultures, and the human prospect*. Washington: Island Press.
- Ember, C.R. (1975). Residential variation in hunter-gatherers. *Cross-Cultural Research*, *10*, 199–227.
- Forrester, D.L., VanderLaan, D.P., Parker, J., & Vasey, P.L. (2011). Male sexual orientation and avuncularity in Canada: Implications for the kin selection hypothesis. *Journal of Culture and Cognition*, *11*, 339–352.
- Gavrilets S., & Rice W.R. (2006) Genetic models of homosexuality: Generating testable predictions. *Proceedings of the Royal Society of London*, *273*, 3031–3038.
- Gorer, G. (1966). *The danger of equality*. London: Cresset.
- Gould, S.J., & Vrba, E.S. (1982). Exaptation—a missing term in the science of form. *Paleobiology*, *8*, 4–15.
- Hamilton, W.D. (1963). The evolution of altruistic behavior. *American Naturalist*, *97*, 354–356.
- Harrington, J.P. (1942). Culture element distributions 19: Central California coast. *Anthropological Records*, *7*(1), 1–46.

- Hawkes, K., O'Connell, J.E., & Blurton Jones, N.G. (2003). Grandmothers and the evolution of human longevity. *American Journal of Human Biology*, *15*, 380–400.
- Herd, G. (1981). *Guardians of the flutes*. New York: McGraw-Hill.
- Herd, G. (1997). *Same sex, different cultures*. Colorado: Westview Press.
- Hewlett, B. & Hewlett, B.L. (2010). Sex and searching for children among Aka foragers and Ngandu farmers of Central Africa. *African Studies Monographs*, *31*, 107–125.
- Hill, K.R., Walker, R.S., Bozicevic, M., Eder, J., Headland, T., Hewlett, B., Hurtado, A.M., Marlow, F., Wiessner, P., & Wood, B. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science*, *331*, 1286–1289.
- Hollimon, S.E. (1997). The third gender in California: Two-spirit undertakers among the Chumash, their neighbors. In C. Claassen & R. A. Joyce (Eds.), *Women in prehistory: North America and Mesoamerica*, (pp. 173–188). Philadelphia: University of Pennsylvania Press.
- Iemmola, F., & Camperio Ciani, A. (2009). New evidence of genetic factors influencing sexual orientation in men: Female fecundity increase in the maternal line. *Archives of Sexual Behavior*, *38*, 393–399.
- Irons, W. (1998). Adaptively relevant environments versus the environment of evolutionary adaptiveness. *Evolutionary Anthropology*, *6*, 194–204.
- Johnson, M., Jackson, P., & Herdt, G. (2000). Critical regionalities and the study of gender and sexual diversity in South East and East Asia. *Culture, Health, and Sexuality*, *2*, 361–375.
- Kendler, K.S., Thornton, L.M., Gilman, S.E., & Kessler, R.C. (2000). Sexual orientation in a U.S. national sample of twin and nontwin sibling pairs. *American Journal of Psychiatry*, *157*, 1843–1846.
- King, M.D., Green, J., Osborn, D.P.J., Arkell, J., Hetherington, J., & Pereira, E. (2005). Family size in white gay and heterosexual men. *Archives of Sexual Behavior*, *34*, 117–122.
- Klein, R. G. (1999). *The human career: Human biological and cultural origins*. Chicago: University of Chicago Press.
- Kramer, K.L., & Greaves, R.D. (2011). Postmarital residence and bilateral kin associations among hunter-gatherers: Pumé foragers living in the best of both worlds. *Human Nature*, *22*, 41–63.
- Kroeber, A.L. (1925). *Handbook of the Indians of California*. Bureau of American Ethnology Bulletin 78.
- Långström, N., Rahman, Q., Carlström, E., & Lichtenstein, P. (2010). Genetic and environmental effects on same-sex sexual behavior: A population study of twins in Sweden. *Archives of Sexual Behavior*, *39*, 75–80.
- Larco Hoyle, R. (1998). *Arte erotico en el antigua Peru*. Lima: Museo Arqueologico Rafael Larco Herrera.
- Lippa, R.A. (2005). *Gender, nature, nurture* (2nd ed.). Mahwah: Erlbaum.
- Marlowe, F.W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology*, *14*, 54–67.
- McBrearty, S. & Brooks, A.S. (2000). The revolution that wasn't: A new interpretation of the origins of modern human behavior. *Journal of Human Evolution*, *39*, 453–563.
- McDougall, I., Brown, F. H., & Fleagle, J. G. (2005). Stratigraphic placement and age of modern humans from Kibish, Ethiopia. *Nature*, *433*, 733–736.
- Miller, E.M. (2000). Homosexuality, birth order, and evolution: Toward and equilibrium reproductive economics of homosexuality. *Archives of Sexual Behavior*, *29*, 1–34.
- Murray, S.O. (2000). *Homosexualities*. Chicago: The University of Chicago Press.
- Nanda, S. (1999). *Gender diversity: Cross-cultural variations*. Long Grove: Waveland Press.
- Namaste, V. (2000). *Invisible lives: The erasure of transsexual and transgendered people*. Chicago: University of Chicago Press.
- Nash, G. (2001). The subversive male: homosexual and bestial images on European mesolithic rock art. In L. Bevan (Ed.), *Indecent exposure: Sexuality, society and the archaeological record*. (pp. 43–55). Glasgow: Cruithne Press.
- Phillips, T., Barnard, C., Ferguson, E., & Reader, T. (2008). Do humans prefer altruistic mates? Testing a link between sexual selection and altruism toward nonrelatives. *British Journal of Psychology*, *99*, 555–572.

- Prine, E. (2000). Searching for third genders: Toward a prehistory of domestic space in Middle Missouri villages. In R. A. Schmidt, & B. L. Voss (Eds.), *Archaeologies of sexuality* (pp. 197–219). London: Routledge.
- Rahman, Q., Collins, A., Morrison, M., Orrells, J.C., Cadinouche, K., Greenfield, S., et al. (2008). Maternal inheritance and familial fecundity factors in male homosexuality. *Archives of Sexual Behavior*, *37*, 962–969.
- Rahman, Q., & Hull, M.S. (2005). An empirical test of the kin selection hypothesis for male homosexuality. *Archives of Sexual Behavior*, *34*, 461–467.
- Rieger, G., & Savin-Williams, R.C. (2012). Gender nonconformity, sexual orientation, and psychological well-being. *Archives of Sexual Behavior*, *41*, 611–621.
- Rubin, A.J. (2000). Public more accepting of gays, poll finds. *Los Angeles Times*, June 19.
- Ruse, M. (1982). Are there gay genes? Sociobiology and homosexuality. *Journal of Homosexuality*, *6*, 5–34.
- Sanderson, S.K., & Roberts, W.W. (2008). The evolutionary forms of the religious life: A cross-cultural, quantitative analysis. *American Anthropologist*, *110*, 454–466.
- Schwartz, G., Kim, R.M., Kolundziji, A.B., Rieger, G., & Sanders, A.R. (2010). Biodemographic and physical correlates of sexual orientation in men. *Archives of Sexual Behavior*, *39*, 93–109.
- Seil, D. (1996). Transsexuals: The boundaries of sexual identity and gender. In R.P. Cabaj & T.S. Stein (Eds.), *Textbook of homosexuality and mental health* (pp. 743–62). Washington: American Psychiatric Press.
- Shear, K., Jin, R., Ruscio, A.M., Walters, E.E., & Kessler, R.C. (2006). Prevalence and correlates of estimated DSM-IV child and adult separation anxiety disorder in the national comorbidity survey replication. *American Journal of Psychiatry*, *163*, 1074–1083.
- Shimkin, D.D. (1983). Introduction of the horse. In D’Azevedo W.L. (Ed.), *Great Basin: Vol. 11. Handbook of North American Indians* (pp. 517–524). Washington: Smithsonian Institution Press.
- Smith, A.B. (1999). Archaeology and the evolution of hunter-gatherers. In R.B. Lee & R. Daly (Eds.), *The Cambridge encyclopedia of hunters and gatherers* (pp. 384–390). Cambridge: Cambridge University Press.
- Smith, A.M., Rissel, C.E., Richters, J., Grulich, A.E., & de Visser, R.O. (2003). Sex in Australia: Sexual identity, sexual attraction, and sexual experience among a representative sample of adults. *Australian and New Zealand Journal of Public Health*, *27*, 138–145.
- Tessman, I. (1995). Human altruism as a courtship display. *Oikos*, *74*, 157–158.
- Whitam, F.L. (1983). Culturally invariant properties of male homosexuality: Tentative conclusions from cross-cultural research. *Archives of Sexual Behavior*, *12*, 207–226.
- Wilson, E.O. (1975). *Sociobiology: The new synthesis*. Cambridge: Belknap Press.
- VanderLaan, D.P., & Vasey, P.L. (2011). Male sexual orientation in Independent Samoa: Evidence for fraternal birth order and maternal fecundity effects. *Archives of Sexual Behavior*, *40*, 495–503.
- VanderLaan, D.P., & Vasey, P.L. (2012). Relationship status and elevated avuncularity in Samoan fa’afafine. *Personal Relationships*, *19*, 326–339.
- VanderLaan, D.P., & Vasey, P.L. (2013). Birth order and avuncular tendencies in Samoan men and fa’afafine. *Archives of Sexual Behavior*, *42*, 371–379.
- VanderLaan, D.P. & Vasey, P.L. (2014). Evidence of enhanced cognitive biases for maximizing indirect fitness in Samoan fa’afafine. *Archives of Sexual Behavior*, *43*, 1009–1022.
- VanderLaan, D.P., Gothreau, L., Bartlett, N.H., & Vasey, P.L. (2011). Recalled separation anxiety and gender atypicality in childhood: A study of Canadian heterosexual and homosexual men and women. *Archives of Sexual Behavior*, *40*, 1233–1240.
- VanderLaan, D.P., Forrester, D.L., Petterson, L.J., & Vasey, P.L. (2012). Offspring production among the extended relatives of Samoan men and fa’afafine. *PLoS ONE*, *7*(4), e36088.
- VanderLaan, D.P., Forrester, D.L., Petterson, L.J., & Vasey, P. L. (2013a). The prevalence of fa’afafine relatives among Samoan men and fa’afafine. *Archives of Sexual Behavior*, *42*, 353–359.

- VanderLaan, D.P., Vokey, J.R., & Vasey, P.L. (2013b). Is male androphilia familial in non-Western cultures? The case of a Samoan village. *Archives of Sexual Behavior*, *42*, 361–370.
- VanderLaan, D.P., Ren, Z., & Vasey, P.L. (2013c). Male androphilia in the ancestral environment: An ethnological analysis. *Human Nature*, *24*, 375–401.
- Vasey, P.L., & Bartlett, N.H. (2007). What can the Samoan *fa'afafine* teach us about the Western concept of “Gender Identity Disorder in Childhood”? *Perspectives in Biology and Medicine*, *50*, 481–490.
- Vasey, P.L., & VanderLaan D.P. (2007) Birth order and male androphilia in Samoan *fa'afafine*. *Proceedings of the Royal Society of London B*, *274*, 1437–1442.
- Vasey, P.L., & VanderLaan, D.P. (2009). Materteral and avuncular tendencies in Samoa: A comparative study of women, men and *fa'afafine*. *Human Nature*, *20*, 269–281.
- Vasey, P.L., & VanderLaan, D.P. (2010a). Avuncular tendencies in Samoan *fa'afafine* and the evolution of male androphilia. *Archives of Sexual Behavior*, *39*, 821–830.
- Vasey, P.L., & VanderLaan, D.P. (2010b). An adaptive cognitive dissociation between willingness to help kin and non-kin in Samoan *fa'afafine*. *Psychological Science*, *21*, 292–297.
- Vasey, P.L., & VanderLaan, D.P. (2010c). Monetary exchanges with nieces and nephews: A comparison of Samoan men, women, and *fa'afafine*. *Evolution and Human Behavior*, *31*, 373–380.
- Vasey, P.L., & VanderLaan, D.P. (2012). Male sexual orientation and avuncularity in Japan: Implications for the Kin Selection Hypothesis. *Archives of Sexual Behavior*, *41*, 209–215.
- Vasey, P.L., & VanderLaan, D.P. (2014). Evolutionary perspectives on male androphilia in humans. In V. Weekes-Shackelford & T. Shackelford (Eds.), *Evolutionary perspectives on human sexual psychology and behavior* (pp. 369–392). New York: Springer.
- Vasey, P.L., Pocock, D.S., & VanderLaan, D.P. (2007). Kin selection and male androphilia in Samoan *fa'afafine*. *Evolution and Human Behavior*, *28*, 159–167.
- Vasey, P.L., VanderLaan, D.P., Gothreau, L., & Bartlett, N.H. (2011). Traits of separation anxiety in childhood: A comparison of Samoan men, women and *fa'afafine*. *Archives of Sexual Behavior*, *40*, 511–517.
- Vasey, P.L., Parker, J.L., & VanderLaan, D.P. (2014). Comparative reproductive output of Samoan men and *fa'afafine*. *Archives of Sexual Behavior*, *43*, 363–367.
- Vaughan, R. (1994). *The Arctic: A history*. Dover: Sutton.
- Wilson, E.O. (1975). *Sociobiology: The new synthesis*. Cambridge: Belknap Press.
- Williams, G.C. (1966). *Adaptation and natural selection*. Princeton: Princeton University Press.
- Williams, W.L. (1992). *The spirit and the flesh: Sexual diversity in American Indian culture*. Boston: Beacon Press.
- Winkelman, M. (2010). *Shamanism: A biopsychosocial paradigm of consciousness and healing*. Santa Barbara: Praeger.
- Woodburn, J. (1982). Egalitarian societies. *Man*, *17*, 431–451.
- Wrangham, R. W., Jones, J. H., Laden, G., Pilbeam, D., & Conklin-Brittain, N. (1999). The raw and the stolen: Cooking and the ecology of human origins. *Current Anthropology*, *40*, 567–594.
- Zucker, K.J., Bradley, S.J., & Sullivan, C.B.L (1996). Traits of separation anxiety in boys with gender identity disorder. *Journal of the American Academy of Child and Adolescent Psychiatry*, *35*, 791–798.