THE CROSS-CULTURAL CORRELATES AND EVOLUTION OF MALE ANDROPHILIA

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GENERAL ABSTRACT

The present thesis attempts to address two outstanding questions regarding male androphilia (i.e., sexual attraction to adult males): 1) *Do transgender and cisgender androphilic males share similar sex-atypical behavioral and psychological traits across cultures?* and 2) *How do genes associated with male androphilia persist throughout evolutionary time despite this trait reducing reproduction?* I addressed these questions with research among the Istmo Zapotec of southern Mexico. Cognitive abilities were also examined in Samoa. Results demonstrated that both cisgender and transgender androphilic males among the Istmo Zapotec exhibit elevated sex-atypical behavior and psychology in childhood and adulthood. Sex-atypical cognitive abilities were also observed among transgender androphilic males in Samoa, but not among the Istmo Zapotec. Finally, Istmo Zapotec androphilic males were found to have elevated kin-directed altruism and female kin with elevated reproduction. These findings can help explain how genes associated with male androphilia can persist throughout evolutionary time.

PREFACE

The present dissertation consists of six empirical chapters. All the research methods described in these empirical chapters received approval from the Human Subject Research Committee at the University of Lethbridge.

Chapters 2, 3, 5, 6, and 7 have been published in peer-reviewed journals, and Chapter 4 has not been submitted for publication. The introduction for all empirical chapters were slightly modified from their published version to avoid repetition of the literature review presented in the thesis introduction. The references for all citations are provided at the end of the dissertation. For all the empirical chapters, the dissertation author (Francisco R. Gómez Jiménez) designed the studies, sought ethics approval, collected the data in the Istmo region of Oaxaca, Mexico, conducted the statistical analyses, and wrote the full manuscript. Paul Vasey contributed to the design of all studies and the editing and revision of all chapters. All co-authors have given permission to include modified versions of the published manuscripts in the present thesis and reviewed and approved the original manuscript before submission for publication. Their specific contributions are listed below.

A version of Chapter 2 was published in Gómez Jiménez, F. R., Court, L., & Vasey, P. L. (2020). A retrospective study of childhood sex-typed behavior in Istmo Zapotec men, women, and *muxes*. *Archives of Sexual Behavior*, *49*(2), 467–477. https://doi.org/10.1007/s10508-019-01544-6. Lucas Court collected a portion of the data in the Istmo region. Paul L. Vasey aided in study design and the editing of the manuscript.

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09417-5 (reproduced with permission from Springer Nature). Lucas Court collected a portion of the data in the Istmo region. Paul L. Vasey aided in study design and the editing of the manuscript.

Chapter 4 has not been submitted to a peer-reviewed journal. Paul Vasey collected the data in Samoa and assisted in study design and the editing of the manuscript.

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LIST OF ABBREVIATIONS

ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
BP	Before present
BMI	Body mass index
CFTB	Childhood female-typical behavior
CMTB	Childhood male-typical behavior
CSAB	Childhood sex-atypical behavior
CSTB	Childhood sex-typed behavior
CAIS	Complete androgen insensitivity syndrome
CI	Confidence interval
PhD	Doctor of Philosophy
EFA	Exploratory factor analysis
FTOP	Female-typical occupational preferences
FBOE	Fraternal birth order effect
IQR	Interquartile range
KSH	Kin selection hypothesis
LSD	Least significant differences
MTOP	Male-typical occupational preferences
MF-Occ	Male-versus-female-typical occupational preferences
MIH	Maternal immune hypothesis
M	Mean
Mdn	Median
OH	Overdominance hypothesis
PCB	Polychlorinated biphenyls
RMSEA	Root mean square error of approximation
SAGH	Sexually antagonistic genes hypothesis
SNP	Single-nucleotide polymorphisms
SD	Standard deviation
SE	Standard error
WEIRD	Western, educated, industrialized, rich, and democratic

Chapter 1: Introduction

Male Androphilia Across Cultures

Androphilia refers to sexual attraction towards adult males, whereas *gynephilia* refers to sexual attraction towards adult females. The gender presentation of androphilic males exists on a spectrum that ranges from highly masculine to highly feminine. For heuristic purposes, male androphiles tend to be divided into two groups—*transgender* and *cisgender*—although, as with any spectrum, demarcations between the two are not absolute (Whitam & Mathy, 1986).

The gender role enactment of cisgender androphilic males is relatively typical for their sex and largely corresponds to the gender that was assigned to them at birth. Consequently, they behave in a masculine manner when compared to cisgender androphilic women, but, in some domains (e.g., childhood behavior, occupational preferences), they are relatively feminine when compared to cisgender gynephilic men (Bailey, 2003; Bailey & Zucker, 1995; Lippa, 2005a, 2008a, 2020; Petterson et al., 2017; VanderLaan et al., 2011a). In contrast, the gender role enactment of transgender male androphiles is atypical for their sex and does not correspond to the gender role that was assigned to them at birth. Consequently, they behave in a markedly feminine manner when compared to both cisgender gynephilic and androphilic males, and, in some domains (e.g., childhood behavior, occupational preferences), they report being as feminine, if not more so, than cisgender androphilic women (e.g., Bartlett & Vasey, 2006; Gómez et al., 2017; Semenyna & Vasey, 2016; Vasey et al., 2011). Above and beyond behavioral feminization, some transgender male androphiles undergo hormonal or surgical treatments to feminize their bodies to varying degrees (e.g., breast augmentation), although genital reconstructive surgery remains relatively rare (Kailas et al., 2017; Puckett et al., 2018).

The identities that male androphiles adopt vary enormously between cultures and across historical time periods. In Euro-American cultures, the cisgender form commonly identifies in a manner that is typical for their sex and that corresponds to the gender they were assigned at birth. Consequently, they identify as “men.” This primary identity is routinely modified with qualifiers the most common of which is currently “gay.” These sexual orientation qualifiers mark androphilic men as distinct from most men (who are gynephilic). The precise qualifiers that are employed vary depending on the historical and sub-cultural context (e.g., “queer”; Aldrich, 2006). In non-Western cultures, some cisgender androphilic males also identify as gay men, especially those living in large urban centers (e.g., McLelland, 2000; Shahani, 2008). Often, however, cisgender androphilic males living outside the West simply identify as men without any additional qualifiers, because, in many non-Western cultures, identities are not formulated on the basis of sexual orientation (e.g., Petterson et al., 2018). In cultures that recognize more than two genders, some cisgender androphilic males may identify, and be identified by others, as a non-binary gender (e.g., Gómez Jiménez & Vasey, 2021b).

In Euro-American cultures, transgender male androphiles routinely identify as trans women or simply as women without any additional qualifier. In many non-Euro-American cultures, transgender androphilic males tend to identify, and are identified by others, as a non-binary gender (i.e., neither men, nor women). These gender categories tend to be culturally specific. Examples include, but are by no means limited to, the *fa’afafine* of Samoa (Vasey & VanderLaan, 2014), and the Istmo Zapotec *muxes* of Mexico (Mirandé, 2017).

Androphilic males tend to commonly express sexual interest in *masculine* adult males (regardless of the masculine adult males’ sexual orientation) and sexual aversion toward *feminine* adult males (Bailey et al., 1994; Petterson et al., 2018). Although this pattern of sexual psychology is shared by both cisgender and transgender male androphiles, it motivates them to form different types of relationships. Cisgender androphilic males routinely engage in sexual activity, and form romantic relationships, with other cisgender androphilic males because such partners are relatively masculine and, unlike cisgender gynephilic males, they are sexually and romantically interested in other cisgender males. These relationships have been described as *homogendered* and *egalitarian* because they involve two individuals who occupy the same gender category (typically, both individuals identify as *men*), do not differ appreciably with respect to age, and they treat each other as social equals (Adams, 1986; Murray, 2000).

Transgender androphilic males also seek out sexual relationships with cisgender males, however, the majority of these are mostly gynephilic, while an appreciable minority are ambiphilic (i.e., sexually attracted and aroused to both adult males and females) (e.g., Petterson et al., 2020; Rosenthal et al., 2017; Stief, 2017; Whitam, 1992). This is because transgender androphilic males' sexual partners are likely to be sexually attracted to femininity (Bailey et al., 1994; Petterson et al., 2018). These relationships have been described as *heterogendered or gender-stratified,* because the cisgender males in question typically identify as *men*, while their transgender partners identify otherwise. Given their gender-differentiated characteristics, the partners often adopt special social roles relative to each other and, consequently, they do not treat each other as social equals (Adams, 1986; Murray, 2000).

Cross-cultural and historical evidence indicate that both forms of male androphilia are often present within the same culture (Gómez Jiménez & Vasey, 2021b; Kennedy, 2005; Petterson et al., 2018; Vatsyayana, 1929; Whitam & Mathy, 1986), but typically one form predominates (Hames et al., 2017). In Euro-American cultures, cisgender androphilic males outnumber their transgender counterparts (Bailey, 2003). In contrast, in many non-Euro-

American cultures, transgender androphilic males are more common than their cisgender counterparts (Hames et al., 2017; Whitam & Mathy, 1986). When the two forms co-occur, they sometimes consider each other to be members of the same community, although this sentiment varies depending on the cultural context (Whitam & Mathy, 1986).

Cross-Cultural Universal Correlates of Male Androphilia

Despite significant differences in outward appearance and gender role enactment, cross-cultural research suggests that both forms of male androphilia share numerous biodemographic and psychodevelopmental correlates. With respect to biodemographic correlates, it has been consistently found that compared to gynephilic males, both forms tend to have more older brothers (e.g., Ablaza et al., 2022; Apostolou, 2020; Blanchard, 2018a; Bozkurt et al., 2015; Gómez Jiménez et al., 2020b; Gomez-Gil et al., 2011; Khorashad et al., 2020; King et al., 2005; Li & Wong, 2018; Nila et al., 2019; Rahman et al., 2009; Schagen et al., 2012; VanderLaan, Blanchard, et al., 2017; Xu et al., 2019), come from larger families (e.g., Camperio Ciani & Pellizzari, 2012; Iemmola & Camperio Ciani, 2009; King et al., 2005; Rahman et al., 2008; Schwartz et al., 2010; Semenyna, Petterson et al., 2017; VanderLaan et al., 2012), have more androphilic male relatives (e.g., Gómez et al., 2018; Gómez-Gil et al., 2010; Schwartz et al., 2010; Semenyna, VanderLaan, et al., 2017; VanderLaan, Forrester, et al., 2013), occur at similar prevalence rates across cultures (~2-6%) (e.g., Gates, 2011; Gómez et al., 2018; Leser, 1961; Rahman et al., 2020; Semenyna VanderLaan, et al., 2017; Whitam & Mathy, 1986), and exhibit reduced reproductive output (e.g., Bell & Weinberg, 1978; Coome et al., 2020; Ganna et al., 2019; Iemmola & Ciani, 2009; King et al., 2005; Nila et al., 2018; Schwartz et al., 2010; Vasey et al., 2014).

With respect to psychodevelopmental correlates, research demonstrates that cisgender and transgender androphilic males recall elevated separation anxiety in childhood when compared to gynephilic males (e.g., Gómez et al., 2017; VanderLaan, et al., 2011a; Vasey et al., 2011). Furthermore, both types of male androphiles express elevated cross-sex beliefs and wishes in childhood (e.g., "I wish I was a girl") (Bailey & Zucker, 1995; Vasey & Bartlett, 2007; Whitam, 1983). Moreover, prospective and retrospective research has found that when compared to gynephilic males, both transgender and cisgender androphilic males are characterized in childhood by greater levels of female-typical behavior (e.g., play with dolls) and lower levels of male-typical behaviors (e.g., rough and tumble play) (Bailey & Zucker, 1995; Bartlett & Vasey, 2006; Besharat et al., 2016; Cardoso, 2005, 2009; Green, 1987; Li et al., 2017; Petterson et al., 2017; Rieger et al., 2008; Semenyna & Vasey, 2016, 2017; Whitam, 1983). Such feminine predispositions are often retained through adulthood given that when compared to gynephilic males, both forms of male androphilia exhibit a higher preference for people-orientated occupations (e.g., counseling, teaching, and nursing), which are more female-typical across culture in contrast to more thing-orientated occupations (e.g., carpentry, mechanics, and engineering) that are more male-typical (e.g., Ellis et al., 2012; Hart, 1968; Lippa, 2002, 2005a, 2008a, 2020; Semenyna & Vasey, 2016; Stief, 2017; Whitam & Mathy, 1986; Zheng et al., 2011).

Although both forms of male androphilia demonstrate higher feminine behavior and psychology when compared to gynephilic males, there is considerable variability among groups. For example, in Samoa, transgender androphilic males—locally known as *fa'afafine*—tend to exhibit patterns of female typical behavior and psychology (e.g., female-typical occupational preferences and childhood sex-atypical behavior) that is similar to women (Semenyna & Vasey, 2016, 2017; Vasey et al., 2011; VanderLaan, Petterson, & Vasey, 2017), whereas Euro-American "gay" men demonstrate ones that are in between gynephilic men and androphilic women and, thus, *shifted* in a female-typical direction (e.g., Bailey, 2003; Bailey & Zucker, 1995; Lippa, 2005a, 2008a; VanderLaan et al., 2011a, 2015, 2016). Although some studies have directly compared the two types of male androphiles and found that transgender ones have higher female-typical behavior and interests during childhood than cisgender ones (e.g., Singh et al., 2021; Wallien & Cohen-Kettenis, 2008), such studies have been mostly conducted within clinical settings in Euro-American cultures. Thus, further research comparing non-clinical populations of cisgender and transgender androphilic males within the same non-Euro-American culture is needed to assess the extent to which their childhood and adulthood femininity differs.

Cognitive Correlates of Male Androphilia

A variety of cognitive correlates are associated with androphilia in both males and females (reviewed in Xu et al., 2017). First, like androphilic females, androphilic males tend to score lower on tests of mental rotation and the judgment of line orientation than gynephilic males (e.g., Rahman & Wilson, 2003). In contrast, androphilic males and females tend to outperform gynephilic males in tests of object location memory (e.g., Rahman et al., 2011; Rahman, Wilson, & Abrahams, 2003). Similarly, both androphilic males and females tend to display greater verbal fluency than gynephilic males (e.g., Rahman, Abrahams, Wilson, 2003). Taken together, this research suggest that androphilic males are shifted in a female-typical manner with respect to various cognitive domains. Nonetheless, this research has been mostly conducted using cisgender androphilic males within Euro-American cultures. As such, further research is needed to determine whether both cisgender and transgender androphilic males in non-Euro-American cultures share similar cognitive profiles with androphilic males from Euro-American cultures.

The Evolutionary Paradox of Male Androphilia

The multiple correlates shared between cisgender and transgender male androphiles cross-culturally suggest that androphilic males, regardless of their gender role expression or culture, share a similar biological etiology. Indeed, findings derived from familial clustering studies (e.g., Gómez et al., 2018; Gómez-Gil et al., 2010; Schwartz et al., 2010; Semenyna, VanderLaan, et al., 2017; VanderLaan, Forrester, et al., 2013), twin studies (e.g., Alanko et al., 2010; Bailey et al., 2000; Kendler et al., 2000; Långström et al., 2010), and molecular genetic studies (e.g., Ganna et al., 2019; Hamer, 2002; Mustanski et al., 2005; Sanders et al., 2015; Wang et al., 2012), indicate that male androphilia has a genetic component and is, thus, partly heritable. Nevertheless, androphilic males tend to reproduce at far lower rates, if at all, when compared to gynephilic males (e.g., Bell & Weinberg, 1978; Coome et al., 2020; Ganna et al., 2019; Iemmola & Ciani, 2009; King et al., 2005; Nila et al., 2018; Schwartz et al., 2010; Vasey et al., 2014). Given the reproductive costs associated with this trait and the reproductive benefits associated with male gynephilia, one would predict that any gene associated with male androphilia should have become extinct due to the forces of sexual selection (Darwin, 1871).

Despite this evolutionary logic, textual evidence indicates that male androphilia has existed for well over a millennium (e.g., Crompton, 2003; Peled, 2016; Sweet & Zwilling, 1993) and prehistoric rock art, which some researchers suggest depicts male same-sex sexual activity, dates to the Mesolithic era (15,000–5,000 BP) (e.g., Taylor, 1996).[1] Furthermore, cross-cultural and historical research demonstrates that male androphilia is present in most cultural regions of the world (Hames et al., 2017; Murray, 2000) and at similar (albeit low) frequencies (e.g., Gates, 2011; Gómez et al., 2018; Leser, 1961; Rahman et al., 2020; Semenyna, VanderLaan, et al., 2017; Whitam & Mathy, 1986). On the basis of this evidence, it appears that male androphilia is a *context independent universal* (Brown, 1991) that occurs regardless of socio-cultural context so

[1] For a particularly compelling prehistoric example of male-male sexual activity, see the Pre-Columbian cave art at Naj Tunich, Guatemala (Stone, 2011, Plate 12), which Bruhns & Kelker (2010) have described as "homosexual love that is undoubtedly genuine" (p. 126).

long as the population in question is large enough for this low frequency trait to be expressed. No matter how rigorously a society attempts to eliminate it, male androphilia emerges (see, for example, "G", 1980; Schuvaloff, 1976). Accordingly, claims that male androphilia is entirely absent in a population should be viewed with skepticism, especially when small sample sizes are employed (e.g., Hewlett & Hewlett, 2010) or when male androphilia is viewed with opprobrium (e.g., Nimmo, 1978). Because of this, male androphilia is considered to be an evolutionary paradox that requires an explanation when viewed from a Darwinian perspective. Some of the most prominent explanations for this evolutionary conundrum include the kin selection hypothesis, the sexual antagonistic genes hypothesis, and the hypergyny hypothesis.

The Kin Selection Hypothesis

The Kin Selection Hypothesis (KSH) holds that genes for male androphilia persist over evolutionary time because androphilic males behave altruistically towards their close kin, with whom they share identical genes (Wilson, 1975). Elevated kin-directed altruism functions to increase the fitness of close kin, thereby offsetting the costs of not producing one's own offspring. In this manner, relatives of androphilic males could have more children if their androphilic male relatives assist them with childcare.

Research conducted in low-fertility, industrialized cultures (i.e., Canada, France, Italy, Japan, Spain, UK, and the USA) has provided little or no support for the KSH (Abild et al., 2014; Bobrow & Bailey, 2001; Camperio Ciani et al., 2016; Forrester et al., 2011; Rahman & Hull, 2005; Vasey & VanderLaan, 2012). In contrast, research conducted in Samoa has repeatedly found support for the KSH in the form of elevated altruistic tendencies on the part of androphilic males toward their nieces and nephews (VanderLaan, Petterson, & Vasey, 2017; VanderLaan & Vasey, 2012; Vasey & VanderLaan, 2009, 2010a, 2010b, 2010c; Vasey et al., 2007). Another study conducted in Indonesia also found elevated avuncularity (i.e., uncle-like behavior) among androphilic males (Nila et al., 2018). Nevertheless, these elevated altruistic tendencies have only been assessed from the androphilic males' perspective. No test of the KSH has sought to corroborate androphilic males' altruistic tendencies among their relatives. Thus, further research is required to assess whether androphilic males' siblings report receiving more childcare support compared to the siblings of gynephilic men, and whether androphilic males outside of Southeast Asia and Polynesia also exhibit elevated avuncular tendencies.

The Sexually Antagonistic Genes Hypothesis

The Sexually Antagonistic Genes Hypothesis (SAGH) states that genes associated with the development of androphilia in males will inhibit reproduction in male carriers but enhance reproduction when carried by their female relatives (Camperio Ciani et al., 2004). As such, the SAGH would predict that the female relatives of androphilic males should have more offspring than those of gynephilic males. It is possible that the elevated reproductive output exhibited by these females would offset the lack of (or reduced) reproduction exhibited by their androphilic male relatives and allow genes for male androphilia to persist across generations.

Research conducted in Euro-American cultures have tested the SAGH and provide some, albeit contradictory, support for the SAGH. For example, while some studies have found elevated reproduction among the female relatives of androphilic males (e.g., Camperio Ciani et al., 2004; Camperio Ciani & Pellizzari, 2012; Iemmola & Camperio Ciani, 2009) others have shown increased reproduction among only male relatives, or both male and female relatives (e.g., Blanchard & Lippa, 2007; King et al., 2005; Rahman et al., 2008; Rieger et al., 2012; Schwartz et al., 2010). One important limitation when testing the SAGH in Euro-American cultures is that such populations often exhibit relatively low fertility rates (Central Intelligence Agency, 2022a) which may prevent the female relatives of androphilic males from exhibiting the elevated reproductive potential hypothesized by the SAGH and may further account for the inconsistencies found across studies.

Circumventing these limitations, research conducted in Samoa—a non-Euro-American population where females have high fertility rates (Central Intelligence Agency, 2022a)—has repeatedly found that the parents and grandparents of androphilic males have more offspring than those of gynephilic males (Semenyna, Petterson, et al., 2017; VanderLaan & Vasey, 2011; Vasey & VanderLaan, 2007). While these findings are consistent with the SAGH, it is unclear whether this elevated fertility was attributable to male relatives (i.e., fathers and grandfathers) or the female relatives (i.e., mothers and grandmothers), as specifically suggested by the hypothesis, given that they both share their reproduction. Further test of the SAGH in additional high fertility populations would aid in understanding the possible role of this hypothesis in the evolution of male androphilia.

The Hypergyny Hypothesis

Similar to the SAGH, the hypergyny hypothesis states that genes associated with male androphilia reduces fitness when present in males but increase fitness when present in females. This hypothesis, however, takes a step further by suggesting that the female relatives of androphilic males have elevated fitness because they possess traits that signal high fertility—such as elevated attractiveness—that allows them to obtain male sexual partners of higher social-economic status and, by extension, more resources to produce and sustain multiple offspring (Barthes et al., 2013). Nevertheless, the only study that has tested the premises of the hypergyny hypothesis did not found evidence to suggest that the female relatives of androphilic males in Thailand are more attractive than women without androphilic male relatives (Skorska et al., 2020). Thus, evidence for Barthes' et al. (2013) hypergyny hypothesis remains equivocal. Conducting similar tests of the hypergyny hypothesis in distinct cultures will help determine whether elevated attractiveness is one of the mechanisms that facilitates the elevated reproduction observed among the female relatives of androphilic males.

Expanding on the Cross-Cultural Correlates and the Evolution of Male Androphilia

My Doctoral thesis is aimed at expanding the research on the cross-cultural universal correlates of androphilic males as well as testing evolutionary hypotheses for the existence of male androphilia. Specifically, the first objective of the thesis is to understand the following: ***Do transgender and cisgender androphilic males share similar female-typical traits and cognitive abilities across cultures?*** To address this question, my thesis goes beyond assessing differences between androphilic and gynephilic males by undertaking comparisons between cisgender and transgender androphilic within a culture where both forms of male androphilia are highly prevalent—the Istmo Zapotec of the Istmo region of Oaxaca, Mexico. In this culture, most androphilic males identify as a non-binary gender known as *muxes*, although a small minority identify as men or women (Mirandé, 2017; Miano Borruso, 2001). Among *muxes*, those who have female-typical gender presentations are known as *muxe gunaa*, which is Zapotec for *muxe* "woman," whereas those that have male-typical gender presentations are known as *muxe nguiiu*, which is Zapotec for *muxe* "man."

The second objective of the thesis is focused on answering the following question: ***How does male androphilia persist across cultures and evolutionary time despite its direct cost to reproduction?*** In addressing this question, my thesis provides meaningful contributions to the literature on the evolution of male androphilia by: 1) assessing the KSH from the perspective of the sisters of androphilic males; 2) testing the SAGH among both cisgender and transgender androphilic males within the same culture; and 3) assessing the KSH, the SAGH, and the hypergyny hypothesis in a novel, non-Euro-American culture—the Istmo Zapotec.

Each empirical chapter of my thesis consists of a unique and independent research study addressing one of the two main objectives highlighted above. The first objective is explored within Chapters 2, 3, and 4, and the second objective is explored within Chapters 5, 6, and 7. Chapters 2 and 3 look at the differences in recalled childhood sex-typed behavior and adulthood occupational preferences, respectively, between Istmo Zapotec gynephilic men, androphilic women, cisgender *muxe nguiiu*, and transgender *muxe gunaa*. Chapter 3 also incorporates some of the data from Chapter 2 to determine whether recalled sex-atypical behavior in childhood is correlated with occupational preferences in adulthood. Chapter 4 examines sex and male sexual orientation differences in cognitive abilities among Samoans and the Istmo Zapotec, as well as differences between cisgender and transgender androphilic males among the Istmo Zapotec. Chapter 5 tests the kin selection hypothesis among the Istmo Zapotec by comparing the kin-directed altruistic tendencies of gynephilic men, androphilic women, cisgender *muxe nguiiu*, and transgender *muxe gunaa*. Chapter 5 also looks at the kin-directed altruistic tendencies of gynephilic men and *muxes* as reported by their sisters to corroborate the *muxes'* self-report data. Chapter 6 tests the sexually antagonistic genes hypothesis by comparing the reproductive output of Istmo Zapotec gynephilic men, *muxe nguiiu*, *muxe gunaa*, and both *muxe* groups combined. Chapter 7 tests the second premise of the hypergyny hypothesis by comparing the facial attractiveness between the sisters of Istmo Zapotec gynephilic men and *muxes*. In doing so, Chapter 7 assesses whether facial attractiveness is one of the proximate factors responsible for the elevated reproduction of the female relatives of androphilic males predicted by the sexually antagonistic genes hypothesis. Finally, Chapter 8 provides a general discussion to the thesis by summarizing the main findings throughout Chapters 2-7, discussing their overarching significance, and providing directions for future research.

Chapter 2: A Retrospective Study of Childhood Sex-Typed Behavior in Istmo Zapotec Men, Women, and *Muxes*

Abstract

Previous research has consistently demonstrated that both transgender and cisgender androphilic males display and recall higher levels of childhood female-typical behavior (CFTB) and lower levels of childhood male-typical behavior (CMTB) compared to gynephilic males. In adulthood, the recalled CFTB and CMTB scores of cisgender androphilic males tend to be intermediate to those of opposite-sex-attracted men and women, whereas transgender androphilic males tend to score similar to women. These studies have been mostly conducted in Euro-American cultures. We examined recalled childhood sex-typed behavior (CSTB) among the Istmo Zapotec—a pre-Colombian culture in the Istmo region of Oaxaca, Mexico, where cisgender and transgender androphilic males are recognized as a third gender, known locally as *muxes*. The present study sought to determine whether Istmo Zapotec men ($n = 180$), cisgender *muxe nguiiu* ($n = 63$), transgender *muxe gunaa* ($n = 120$), and women ($n = 138$) differ with respect to recalled CFTB and CMTB. Our results indicate that men recalled significantly less CFTB and more CMTB than women. Cisgender *muxes* scored in between men and women. Transgender *muxes* scored similar to women. These findings provide further evidence that childhood sex-atypical behavior is a cross-culturally universal and normative developmental aspect of male androphilia, regardless of whether it manifests in the cisgender or transgender form. This is the first study to present quantitative data comparing the recalled CSTB of cisgender and transgender androphilic males from within the same non-Euro-American culture.

Keywords: gender identity; gender role; sexual orientation; *muxes*; cross-cultural universals; Istmo Zapotec

Introduction

Childhood sex-atypical behavior (CSAB) in males is characterized by higher levels of childhood female-typical behaviors (CFTB), which can include interest in: (1) girls' toys (e.g., dolls), (2) girls as playmates, (3) taking on female personas during imaginary play (e.g., Wonder Woman), and (4) girls' clothing (e.g., dresses, jewelry). This CFTB occurs in conjunction with lower levels of childhood male-typical behaviors (CMTB), which can include interest in: (1) boy's toys (e.g., trucks), (2) boys as playmates, (3) taking on male personas during imaginary play (e.g., Superman), and (4) rough-and-tumble play. The onset of CSAB usually occurs during the preschool years (at ~ 3–4 years of age) (Li et al., 2017; Rieger et al., 2008); however, it can emerge as early as 1 year of age (Zucker & Bradley, 1995).

Prospective studies conducted in Euro-American cultures demonstrate that the majority of boys (62–81%) who exhibit clinically significant levels of CSAB (i.e., strong and persistent cross-sex behavior and/or identification for at least 6 months resulting in clinically significant distress or impairment in important areas of functioning) eventually grow up to be androphilic in adulthood (Green, 1987; Singh et al., 2021; Wallien & Cohen-Kettenis, 2008; Zucker & Bradley, 1995). Prospective studies of children in the general population furnish similar results (Li et al., 2017; Steensma et al., 2013). As such, both types of prospective research demonstrate that a positive relationship exists between CSAB and male androphilia in adulthood. Bailey (2003) suggested that the estimates of male androphilia provided by these prospective studies should be considered minimum estimates because many of the participants were interviewed in adolescence or as young adults and may have been motivated to conceal their androphilic orientations.

Retrospective studies conducted in Euro-American cultures have also found that androphilic men recall significantly higher levels of CSAB when compared to gynephilic men (e.g., Bailey & Zucker, 1995; Bogaert, 2003; Cardoso, 2005, 2009; Dunne et al., 2000; VanderLaan et al., 2011a; VanderLaan et al., 2015, 2016; Whitam, 1980; Zucker et al., 2006). These retrospective findings are corroborated by a study in which home videos taken in childhood were evaluated by judges who were naïve to the targets' sexual orientations and recalled CSAB. This study found (pre)androphilic boys to be more sex-atypical in behavior than (pre)gynephilic ones (Rieger et al., 2008). A similar study employed childhood pictures and found that the non-gynephilic twins (i.e., Kinsey 4, 5, 6) were rated as more sex-atypical in appearance than their gynephilic counterparts (Watts et al., 2018).

Retrospective research conducted in a wide range of non-Euro-American cultures, including Iran, Japan, the Philippines, Thailand, and Turkey, is consistent with the conclusion that cisgender androphilic males recall higher levels of CSAB compared to cisgender gynephilic males (e.g., Besharat et al., 2016; Cardoso, 2009; Petterson et al., 2017; Whitam & Mathy, 1986). Overall, the retrospective research conducted on cisgender androphilic males indicates that their CMTB and CFTB are shifted in a female-typical direction and, thus, intermediate between that of cisgender gynephilic males and cisgender androphilic females.

With respect to transgender male androphiles, prospective research conducted in Canada and the Netherlands indicates that individuals whose sex-atypical behavior persists into adulthood exhibit more extreme levels of CSAB than those whose sex-atypical behavior dissipates over time (Singh et al., 2021; Wallien & Cohen-Kettenis, 2008). Retrospective studies demonstrate that British and Dutch androphilic male-to-female transsexuals recall higher levels of CFTB than CMTB (Green, 1974; Smith et al., 2005). Retrospective research conducted in

Samoa, a Polynesian island nation, shows that transgender androphilic males (known locally as *fa'afafine*) recall levels of CMTB and CFTB that are similar to, or sometimes even hyper-feminized, compared to those of Samoan women (Bartlett & Vasey, 2006; Semenyna & Vasey, 2016, 2017; VanderLaan, Petterson, & Vasey, 2017). Taken together, these results suggest that the CMTB and CFTB of transgender androphilic males are not merely shifted in a female-typical direction; rather, it generally mirrors a female-typical pattern. In a similar vein, Whitam (1997) argued that transgender male androphiles exhibit more CSAB than cisgender ones. This suggestion remains tentative, however, because, outside of Euro-American cultural context, quantitative studies of childhood sex-typed behavior (CSTB) that compare clearly delineated groups of transgender and cisgender androphilic males are, to the best of our knowledge, nonexistent.

In light of this body of research, we sought to determine whether androphilic males among the Istmo Zapotec recall high levels of CSAB compared to gynephilic men. The Zapotec are an indigenous group found primarily in the southern Mexican states of Oaxaca (Danver, 2013; Instituto Nacional de Estadística y Geografía, 2009). They have existed in this area for thousands of years prior to the arrival of Spanish explorers. A subgroup of Zapotec living in a circumscribed area of Oaxaca—the Istmo region—recognize three genders: men, women, and *muxes*. Istmo Zapotec consider *muxes* to be distinct from men and women, while possessing characteristics of both genders (Chiñas, 1992). The term *muxe* likely originates from a Zapotec adaptation of the word *mujer* (i.e., Spanish for "women") (Miano Borruso, 2002). However, it has also been suggested that the word *muxe* derives from the word *namuxe'*, which is Zapotec for "shy," "timid," or "cowardly" (Bennholdt-Thomsen, 1997; Mirandé, 2017). Currently, the Istmo

Zapotec use the term *muxe* as a third gender identity category when referring to any male who is androphilic and assumed to routinely adopt the receptive position during anal intercourse.

Unlike gay men from Euro-American cultures, *muxes* do not engage in sexual interaction with each other. Instead, they seek out masculine men who self-identify as "straight." These men are commonly known as *mayates* (i.e., Spanish for "dung beetle")[2] in the Istmo region of Oaxaca as well as in many other parts of Mexico (Bennholdt-Thomsen, 1997; Carrier, 1995; Miano Borruso, 2002; Mirandé, 2017; Prieur, 1998; Trono, 1999). *Mayates* are masculine men who play the insertive role during anal intercourse with androphilic males. Often, *mayates* engage in sexual activity with androphilic males for some form of economic profit such as money, food, alcohol, or clothes, and sometimes just for pleasure (Carrier, 1995; Mirandé, 2017; Prieur, 1998). Nonetheless, *mayates* also marry and have sex with women and, for the most part, consider themselves to be "straight" (Carrier, 1995; Mirandé, 2017; Prieur, 1998).

Qualitative accounts suggest that, like most androphilic males, *muxes* exhibit numerous sex-atypical behaviors from a relatively young age. As early as 3 years of age, male children who exhibit sex-atypical behavior can be identified as *muxes* by their families and other community members (Chiñas, 1995; Miano Borruso, 2002). Common displays of CSAB in *muxes* include preferences for playing with dolls and other girl toys, having girls as playmates, imitating their mothers more than their fathers, preferences for dressing up in girls' clothing, and doing house chores that are usually given to girls more often than boys (Chiñas, 1992; Miano Borruso, 2002; Mirandé, 2017; Trono, 1999). Additionally, Istmo Zapotec mothers sometimes take their

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[2] Prieur (1998) explains that "the word *mayate* originated as the name of the scarab beetle which makes a ball out of dung, lays its eggs in it, and then pushes the ball in front of itself using its snout. This reflects the expectation that *mayates* are supposed to be the active party during anal intercourse" (p. 27).

feminine sons out into the market and the streets in order to teach them how to conduct business, as they normally would with their daughters (Miano Borruso, 2002; Mirandé, 2017).

Muxes vary in terms of the degree to which they present publically in a feminine manner (Mirandé, 2016). Not surprisingly then, the Istmo Zapotec recognize two types of *muxes*: *muxe gunaa* and *muxe nguiiu* (i.e., Zapotec for *muxe* woman and *muxe* man, respectively). *Muxe gunaa* are transgender androphilic males, comparable to the Samoan *fa'afafine*. They routinely dress in women's clothing and present publicly in a relatively feminine manner. In contrast, *muxe nguiiu* are cisgender androphilic males, comparable to Euro-American "gay" men, who dress in men's clothes and present publicly in a relatively masculine manner. Both types of *muxes* are commonly found in the Istmo region of Oaxaca.

Despite differences in their gender role presentation, empirical research conducted on transgender and cisgender *muxes* demonstrates that, compared to Zapotec gynephilic men, both recall elevated indicators of childhood separation anxiety (Gómez et al., 2017)—a female-typical trait (Shear et al., 2006; VanderLaan et al., 2011a, 2016; VanderLaan, Petterson, & Vasey, 2017). This suggests that both transgender and cisgender *muxes* are shifted in a female-typical manner with respect to childhood separation anxiety.

The relatively high prevalence of both forms of male androphilia among the Istmo Zapotec afforded us the opportunity to conduct a within-culture comparison of recalled CFTB and CMTB in transgender (*muxe gunaa*) and cisgender (*muxe nguiiu*) androphilic males. To the best of our knowledge, this is the first study to do so outside of a Euro-American cultural context. The two types of *muxes* were, in turn, compared to Istmo Zapotec gynephilic men and androphilic women. In light of previous research, we predicted that women and both forms of *muxes* would recall engaging in higher levels of CFTB and lower levels of CMTB compared to gynephilic males. Furthermore, we predicted that *muxe nguiiu* would recall levels of CFTB and CMTB that were intermediate between those of Istmo Zapotec men and women. In contrast, we predicted that *muxe gunaa* would recall patterns of CFTB and CMTB behavior that were similar to those of women. Thus, we predicted that both cisgender *muxe nguiiu* and transgender *muxe gunaa* would recall more CSAB than Zapotec men and women, but the latter would recall higher levels of CSAB than the former.

Method

Participants

All participants were recruited using a network sampling procedure which consisted of contacting initial participants, who gave referrals for additional participants, who, in turn, provided further referrals, and so on. Data were collected in the city of Juchitán de Zaragoza, as well as 14 towns and villages within the Juchitán and Tehuantepec districts in the Istmo region of Oaxaca, Mexico. Three field trips took place between November and December 2015, February and March 2016, and November and December 2016. Participants were required to provide informed written consent prior to participating in the study.

A total of 180 gynephilic men, 138 androphilic women, 120 *muxe gunaa*, and 63 *muxe nguiiu* were interviewed for this study. Participants' sexual orientation was assessed using a Kinsey scale (Kinsey et al., 1948) for sexual feelings over the previous year. Istmo Zapotec recognize that *muxes* are biological males as evidenced by the fact that they possess male genitalia and secondary sexual characteristics. Nevertheless, participants were informed that the category "males" included men and/or *muxes*, whereas the category "females" only included women, in order to assess the sex that they are attracted to as opposed to the gender. All men identified as exclusively (Kinsey rating = 0, n = 175) or predominantly gynephilic (Kinsey rating = 1, *n* = 5). All women identified as exclusively (Kinsey rating = 6, *n* = 136) or predominantly androphilic (Kinsey rating = 5, *n* = 2). All *muxe gunaa* identified as exclusively androphilic (Kinsey rating = 6, *n* = 120). All *muxe nguiiu* identified as predominantly (Kinsey rating = 5, *n* = 7) or exclusively androphilic (Kinsey rating = 6, *n* = 56).

Procedure and Measures

Participants were interviewed using standardized questionnaires, which were available in Spanish after being translated and back-translated by fluent Spanish–English speakers. Two of the authors, as well as Spanish-speaking research assistants, were available to answer participants' questions. A Zapotec-speaking research assistant was also present for interviews, when participants were not fully fluent in Spanish. Questions were read out loud by research assistants in Spanish or Zapotec as necessary.

Biographic Information

Participants were asked to report information regarding their age (in years), level of education, and level of income. Level of education was reported by stating the highest level of education achieved (1 = "None," 2 = "Primary school," 3 = "Junior high school," 4 = "High school or college"). Level of income was based on an average weekly income scale that ranged from 1 (0–250 Mexican Pesos) to 9 (more than 2000 Mexican Pesos).

Childhood Gender Identity Scale

Recalled CMTB and CFTB were assessed using a version of the Childhood Gender Identity Scale. This scale has been previously validated to differentiate children who have been diagnosed with clinically significant levels of sex-atypical behavior from those that have not (Johnson et al., 2004). The Childhood Gender Identity Scale consists of a CFTB subscale containing five items and a CMTB subscale containing four items. Participants were asked to recall how often they exhibited female-typical (e.g., “put on girls’ makeup, clothes, or accessories”) and male-typical (e.g., “rough and tumble play”) behavior before the age of 12 years using a 5-point Likert-type scale that ranged from 1 = “Never” to 5 = “Always/All the time.”

Cronbach’s alpha coefficients for the recalled CFTB and CMTB subscales reliability were acceptable for gynephilic men (CFTB $\alpha = .64$; CMTB $\alpha = .62$), *muxe nguiiu* (CFTB $\alpha = .89$; CMTB $\alpha = .70$), *muxe gunaa* (CFTB $\alpha = .73$; CMTB $\alpha = .67$), women (CFTB $\alpha = .78$; CMTB $\alpha = .83$), and all groups combined (CFTB $\alpha = .95$; CMTB $\alpha = .88$). Mean scores were calculated from each of the two subscales to obtain recalled CFTB and CMTB subscale scores. Finally, a recalled childhood sex-typed behavior (CSTB) composite score was created for all groups. For *muxe gunaa*, *muxe nguiiu*, and gynephilic men, the recalled CSTB composite score was the average recalled CMTB score minus the average recalled CFTB score. For women, the recalled CSTB composite score was the average recalled CFTB score minus the average recalled CMTB scores. As such, more negative scores indicate greater recalled childhood sex-atypical behavior.

Results

Descriptive statistics for biographic information are presented in Table 2.1. One-way analysis of variance (ANOVA) revealed no significant group difference for age, $F(3, 497) = .061$, $p = .980$, and level of income, $F(3, 497) = 2.37$, $p = .069$. A Kruskal–Wallis H test showed that there was a significant difference in level of education between groups, $H(3) = 60.24$, $p < .001$. Post hoc pairwise comparisons using Dunn’s test with Bonferroni correction revealed that *muxe gunaa* had less education than all other groups (all $p < .001$), who did not differ from each other. Nonetheless, level of education was not used as a covariate in further analyses given that the direction and significance of our group comparisons for average recalled CFTB and CMTB subscale scores did not change when controlling for this biographic variable.

Table 2.1

Descriptive statistics for biographic information by group

	Men (n = 180)	*Muxe nguiiu* (n = 63)	*Muxe gunaa* (n = 120)	Women (n = 138)
Level of education				
None (%)	1.11	0.00	4.17	2.17
Primary school (%)	5.00	9.52	21.67	4.35
Junior high school (%)	25.00	19.05	40.00	18.84
High school or college (%)	68.89	71.43	34.17	74.64
Age (in years) M (SD)	30.58 (9.50)	31.11 (10.05)	30.73 (9.45)	30.51 (10.40)
Level of income M (SD)	4.96 (2.44)	5.11 (2.60)	4.79 (2.32)	4.30 (2.70)

Results for the comparisons between Istmo Zapotec gynephilic men, *muxe nguiiu*, *muxe gunaa*, and women, for average recalled CFTB and CMTB subscale scores, are shown in Table 2.2. Groups differed significantly for both recalled CFTB and CMTB subscales. With respect to the recalled CFTB subscale, post hoc pairwise comparison using the Games-Howell procedure revealed that women recalled significantly more CFTB than gynephilic men ($p < .001$, $d = 5.07$ [4.61, 5.51][3]) and *muxe nguiiu* ($p < .001$, $d = 1.62$ [1.27, 1.95]). *Muxe gunaa* recalled significantly more CFTB than gynephilic men ($p < .001$, $d = 5.05$ [4.57, 5.50]) and *muxe nguiiu* ($p < .001$, $d = 1.53$ [1.18, 1.87]). *Muxe nguiiu* recalled significantly more CFTB than gynephilic men ($p < .001$, $d = 1.91$ [1.57, 2.24]). No significant difference in recalled CFTB was observed

[3] Effect sizes are presented using Cohen's *d* statistics and their 95% confidence intervals.

Table 2.2

Comparison of men, muxe nguiiu, muxe gunaa, and women for female- and male-typical behaviors

	Men (*n* = 180)		*Muxe nguiiu* (*n* = 63)		*Muxe gunaa* (*n* = 120)		Women (*n* = 138)		One-way ANOVA[f]		
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*F*	*df*	*p*
Female-typical behavior subscale[a,b,c,d,e]	1.37	0.41	2.81	1.31	4.33	0.78	4.38	0.77	332	3, 157.48	<.001
Male-typical behavior subscale[a,b,c,d,e]	4.38	0.73	2.88	1.02	1.94	0.88	2.12	0.94	195.09	3, 312.38	<.001
Paired sample *t*-test	$t(179) = 46.84$ $p < .001$		$t(62) = 0.280$ $p = .780$		$t(119) = 19.42$ $p < .001$		$t(137) = 21.30$ $p < .001$				

Possible range for female-typical and male-typical behavior subscale scores [1, 5].
[a] Statistically significant difference ($p < .001$) between *muxe gunaa* and gynephilic men
[b] Statistically significant difference ($p < .001$) between *muxe gunaa* and *muxe nguiiu*
[c] Statistically significant difference ($p < .001$) between *muxe nguiiu* and women
[d] Statistically significant difference ($p < .001$) between gynephilic men and *muxe nguiiu*
[e] Statistically significant difference ($p < .001$) between gynephilic men and women
[f] The *F* statistics and degrees of freedom were reported using Brown-Forsythe because of significant Levene's tests for equality of variances, all $p < .05$.

between women and *muxe gunaa* (p = .960, d = .06 [-.18, .31]).

With respect to the recalled CMTB subscale, post hoc pairwise comparison using the Games-Howell procedure revealed that gynephilic men recalled significantly more CMTB than women (p < .001, d = 2.73 [2.42, 3.03]), *muxe gunaa* (p < .001, d = 3.08 [2.73, 3.40]), and *muxe nguiiu* (p < .001, d = 1.84 [1.51, 2.17]). *Muxe nguiiu* recalled significantly more CMTB than women (p < .001, d = .79 [.48, 1.09]) and *muxe gunaa* (p < .001, d = 1.01 [.68, 1.33]). No significant difference in recalled CMTB was observed between women and *muxe gunaa* (p = .376, d = .20 [-.44, .05]).

Within-group comparisons using a paired sampled t-test demonstrated that gynephilic men scored significantly higher on the recalled CMTB subscale than on the recalled CFTB subscale (p < .001, d = 5.08 [4.65, 5.50]). In contrast, women scored significantly higher on the recalled CFTB subscale than on the recalled CMTB subscale (p < .001, d = 2.62 [2.30, 2.94]), as did *muxe gunaa* (p < .001, d = 2.87 [2.50, 3.22]). *Muxe nguiiu* did not differ significantly on these two subscales (p = .780, d = .06 [-.29, .41]).

Finally, a one-way ANOVA demonstrated significant differences in recalled CSTB composite scores between gynephilic men (M = 3.00, SD = .86), *muxe nguiiu* (M = .07, SD = 2.00), *muxe gunaa* (M = -2.40, SD = 1.35), and women (M = 2.26, SD = 1.25), Brown–Forsythe F(3, 187.69) = 365.29, p < .001 (Fig. 1). Post hoc pairwise comparison using the Games-Howell procedure demonstrated that *muxe gunaa* recalled significantly more CSAB than gynephilic men (p < .001, d = 4.99 [4.51, 5.43]), women (p < .001, d = 3.59 [3.19, 3.97]), and *muxe nguiiu* (p < .001, d = 1.54 [1.19, 1.88]). *Muxe nguiiu* recalled significantly more CSAB than gynephilic men (p < .001, d = 2.33 [1.97, 2.68]) and women (p < .001, d = 1.44 [1.10, 1.76]). Women recalled significantly more CSAB than gynephilic men (p < .001, d = .71 [.48, .93]).

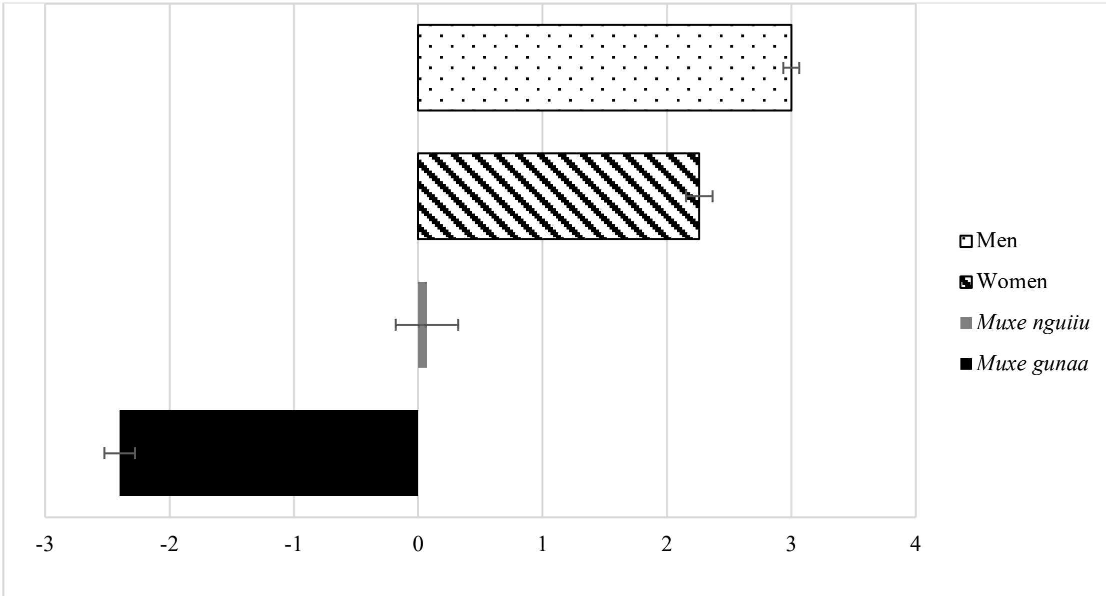

Figure 2.1: Childhood sex-typed behavior composite scores among men, women, *muxe nguiiu*, and *muxe gunaa*. In the x-axis, positive scores represent higher sex-typical behavior whereas negative scores represent higher sex-atypical behavior. The error bars represent the standard error for each group.

Discussion

The present study examined the differences in recalled CFTB and CMTB among Istmo Zapotec gynephilic men, androphilic women, transgender androphilic males (*muxe gunaa*), and cisgender androphilic males (*muxe nguiiu*). All androphilic groups (women, cisgender *muxes*, and transgender *muxes*) recalled engaging in higher levels of CFTB and lower levels of CMTB compared to gynephilic men. Cisgender *muxe nguiiu* recalled levels of CMTB and CFTB that were intermediate between those of Istmo Zapotec men and women. Transgender *muxe gunaa* recalled levels of CMTB and CFTB that were similar to those of Istmo Zapotec women. Thus, both cisgender and transgender *muxes* recalled more childhood sex-atypical behavior (CSAB) than Istmo Zapotec men and women. However, transgender *muxe gunaa* recalled even more CSAB than cisgender *muxe nguiiu*. As such, the results of this study were consistent with all of our stated predictions as well as with all of the existing retrospective and prospective research.

As with all psychological and behavioral phenomenon, sex differences and male sexual orientation differences were not absolute, but they were substantial, as evidenced by the large to very large effect sizes.

Many researchers contend that CMTB and CFTB are products of socialization, learned during childhood through interactions with parents, peers, and society (Bussey & Bandura, 1999). For example, it has been suggested that boys and girls develop gender identities by observing and learning from their same-sex parent, peers, and teachers, who then reinforce these behaviors by rewarding those that conform to culturally prescribed gender roles, and punishing those that do not (Fagot, 1977; Witt, 1997). Given such social learning theories, one would not expect to observe any within-sex sexual orientation differences in childhood sex-typed behavior (CSTB). Nonetheless, there now exist numerous studies demonstrating that same-sex-attracted individuals exhibit and recall more CSAB than their opposite-sex-attracted counterparts. These studies include prospective research utilizing clinical convenience and general population samples, studies of childhood home movies and photographs, as well as retrospective research conducted in a variety of disparate cultures worldwide (see Chapter 2 Introduction; reviewed in Bailey et al., 2016). Furthermore, CSTB (whether sex-typical or not) can emerge as early as the first year of life (Connellan et al., 2000; Hines, 2011; Zucker & Bradley, 1995), before most children realize the permanency of sex categories (Bem, 1989). In addition, nonhuman primates are not socialized in accordance with human gender role expectations, yet various monkeys and apes demonstrate behavioral sex differences during development that are comparable to those seen in boys and girls (*Cercopithecus aethiops*: Alexander & Hines, 2002; *Macaca mulatta*: Hassett et al., 2008; *Pan troglodytes*: Kahlenberg & Wrangham, 2010; reviewed in Lonsdorf, 2017). In light of this research, it seems unlikely that social factors alone can adequately explain the sex and sexual orientation differences in CSTB. Rather, it is more probable that cultural norms enforced by parents, peers, and society can act to suppress or reinforce pre-existing tendencies toward CMTB and CFTB.

Ample evidence now exists indicating that CSAB is a normative developmental aspect of male androphilia that consistently reoccurs across many different and diverse cultural settings (reviewed in Bailey et al., 2016). The uniformity of these findings in the face of enormous cultural variability suggests that androphilic males are biologically predisposed toward elevated CSAB. A number of biological mechanisms might influence these predispositions, including genes (Alanko et al., 2010; Bailey et al., 2000; Iervolino et al., 2005; Knafo et al., 2005; van Beijsterveldt et a l., 2006), hormones (Hines et al., 2015; Lamminmäki et al., 2012; Pasterski et al., 2015), and immunological factors (Blanchard, 2018a).

Despite the uniformity of these findings, there is considerable cross-cultural variability in degree to which CSAB is expressed by androphilic males. For example, in Samoa, *fa'afafine* recall patterns of CSTB and childhood separation anxiety that are similar to androphilic women (Bartlett & Vasey, 2006; Vasey et al., 2011; VanderLaan, Petterson, & Vasey, 2017), whereas Euro-American "gay" men demonstrate a pattern that is merely shifted in between gynephilic men and androphilic women (Bailey, 2003; Bailey & Zucker, 1995; VanderLaan et al., 2011a, 2015, 2016). Likewise, transgender *muxe gunaa* in this study consistently recalled a pattern of CSTB similar to women, whereas cisgender *muxe nguiiu* recalled one that is in between gynephilic men and androphilic women. Thus, although a substantial body of cross-cultural research indicates that both cisgender and transgender male androphiles recall elevated CSAB compared to male gynephiles, the two types of male androphiles differ, on average, in the degree to which this is the case.

The Istmo Zapotec are somewhat unique in that both the cisgender and transgender forms of male androphilia occur at appreciable levels in the culture. Why do some androphilic males follow a cisgender developmental pathway, while others, in the same culture, follow a transgender one? Semenyna, VanderLaan, & Vasey (2017) argued that cisgender male androphilia predominates in some cultures, whereas transgender male androphilia develops in others, because gender role expectations for male androphiles vary across these different cultural contexts. Among the Istmo Zapotec, we speculate that some (pre)androphilic males might experience intolerance toward their CFTB from family or peers and, as a consequence, repress their femininity inasmuch as possible, while attempting to adopt a more masculine gender role typical of *muxe nguiiu*. Conversely, familial and peer tolerance of CFTB may increase the likelihood that a (pre)androphilic Istmo Zapotec male will identify as a much more feminine *muxe gunaa*.

Familial and peer acceptance of male femininity may be influenced by socioeconomic status. Research across cultures, including among the Istmo Zapotec, suggests that androphilic males who exhibit greater femininity often come from lower socioeconomic classes compared to those who exhibit greater masculinity (e.g., Harry, 1985; MacFarlane, 1984; Miano Borruso, 2002; Mirandé, 2017; Prieur, 1998; Singh et al., 2021). Why this relationship between socioeconomic status and acceptance of male femininity exists remains unclear. One possibility among the Istmo Zapotec is that families from higher socioeconomic classes are less accepting of their androphilic male relatives' childhood femininity because the family stands to gain more economically if those male relatives engage in the wage labor market and obtaining such jobs appears to be contingent on cisgender presentation (see Céspedes Vargas, 2015). Conversely, families from lower socioeconomic classes may be more accepting of their androphilic male relatives' childhood femininity because wage labor jobs are largely unattainable and, in any case, feminine males can help their female kin in the local markets, as well as with household chores. Further, they can participate in the economy at large by engaging in female-typical labor at home, such as the embroidering of huipiles (i.e., a traditional garment worn by women and *muxe gunaa*), which can then be sold for profit. Assessing the differences between *muxe gunaa* and *muxe nguiiu's* socioeconomic status, acceptance of male femininity by their family and peers, as well as the interaction between the two, should be an additional focus of future research.

Finally, exposure to Euro-American cultures through mass media (e.g., the Internet, television, movies, magazines) or travel could also influence the gender role enactment of androphilic males. Exposure to Euro-American representations of cisgender androphilic males might prompt some *muxes* to adopt similar patterns of gender role presentation, especially since Euro-American representations of transgender androphilic males might be, relatively speaking, more negative in tone (Bailey, 2003; Bergling, 2001; Gates, 2011; Laumann et al., 1994; Murray, 2000; Rieger & Savin-Williams, 2012). The use of mobile dating/hookup apps such as *Grindr* could also influence the gender role enactment of androphilic males if successful participation in the mating market afforded by such apps is contingent on cisgender presentation. *Muxe nguiiu* may have more resources that afford them greater opportunities for exposure to Euro-American culture, whereas *muxe gunaa* may be more confined to traditional Istmo Zapotec culture, in which feminine males are commonplace and the transgender form of male androphilia is culturally embedded (Chiñas, 1992; Miano Borruso, 2002; Mirandé, 2017). The Istmo Zapotec represent a suitable culture in which to test whether these, or other, factors might be responsible for the developmental canalization toward cisgender or transgender male gender identity and gender role enactment.

Limitations

Retrospective reports of childhood behaviors have been characterized as flawed by critics who argue that such research is prone to selective recall bias and memory distortion (Fausto-Sterling, 2014; Gottschalk, 2003; Maughan & Rutter, 1997; Ross, 1980). As such, some critics might suggest that the *muxe gunaa* in our study recalled elevated CFTB in order to create a consistent personal narrative in which there is a logical progression from a feminine childhood to a feminine adulthood. There are, however, many reasons to be skeptical of this hypothesis. First, this explanation would fail to account for why *muxe nguiiu*, who present in a relatively masculine manner in adulthood, also recalled elevated CFTB when compared to gynephilic males. The same could be said of most gay men in Euro-American cultures, many of whom abhor male femininity (Bailey, 2003; Bergling, 2001). Second, no supporting empirical evidence for the selective recall/memory distortion hypothesis has been presented in the literature (for review, see Bailey & Zucker, 1995; Bailey et al., 2016; Zucker et al., 2006). Third, prospective studies, including those conducted in the general population, show strong associations between CSAB in boys and an androphilic orientation in adulthood (see Chapter 2 Introduction). Finally, two studies have demonstrated that androphilic males' elevated levels of CSAB are corroborated by independent raters who examined videos (Rieger et al., 2008) and pictures (Watts et al., 2018) of the participants in childhood, and were unaware of the target's sexual orientation. Taken together, these separate lines of converging evidence challenge the idea that the elevated levels of CSAB recalled by androphilic *muxes* in this study were due to memory distortion or selective recall bias. Nevertheless, prospective studies among the Istmo Zapotec (and other non-Euro-American populations) would be desirable to further elucidate the relationship between CSAB and adult male androphilia outside of a Euro-American cultural context.

A more plausible limitation of this study was that the network sampling procedure utilized could have conceivably produced an unrepresentative sample. However, the representativeness of our study sample was increased by the fact that we interviewed participants not only from the largest urban center in the Istmo region of Oaxaca—the city of Juchitán de Zaragoza—but from 14 other towns and villages throughout the Tehuantepec and Juchitán districts of the Istmo region. As such, we consider our data collection to have been quite comprehensive. It is also worth noting that we collected data on various biographic variables and tested whether they might be confounding the results of our study, which was not the case. Nonetheless, future studies could consider using random sampling procedures to eliminate potential sample bias. Finally, although our sample of *muxe nguiiu* (n = 63) was larger than samples of androphilic males that are commonly utilized in cross-cultural research, it was relatively small when compared to the other groups we compared in this study. As such, it would be valuable if larger groups of *muxe nguiiu* could be recruited for future research.

Conclusion

To the best of our knowledge, this is the first quantitative study outside of a Euro-American context that has compared cisgender and transgender androphilic males' recalled CSTB within the same culture. Our results indicate that both types of androphilic *muxes* recalled being more feminine, and less masculine, than gynephilic men. Furthermore, transgender *muxes* recalled more CSAB than cisgender ones. These findings provide additional evidence from yet another culture—the Istmo Zapotec—that CSAB is a cross-culturally universal aspect of male androphilia, which manifests regardless of whether this trait is expressed in the cisgender or transgender form.

Chapter 3: Occupational Preferences and Recalled Childhood Sex-Atypical Behavior Among Istmo Zapotec Men, Women, and *Muxes*

Abstract

Research has found that both cisgender and transgender androphilic males have female-typical occupational preferences when compared with gynephilic males. Moreover, whereas cisgender androphilic males' occupational preferences tend to be intermediate between those of gynephilic men and androphilic women, transgender androphilic males tend to have occupational preferences that are more similar to androphilic women. No study has directly compared both types of androphilic males within the same culture. The present study investigated occupational preference and its relation to childhood sex-atypical behavior (CSAB), among gynephilic men ($n = 208$), androphilic women ($n = 138$), and cisgender ($n = 132$) and transgender ($n = 129$) androphilic males from the Istmo region of Oaxaca, Mexico, where androphilic males are recognized as third gender, *muxes*. The study found large sex differences in occupational preferences ($d = 2.80$). Furthermore, both cisgender *muxe nguiiu* ($d = 2.36$) and transgender *muxe gunaa* ($d = 3.44$) reported having more sex-atypical occupational preferences compared with men. However, *muxe gunaa* reported higher female-typical occupational preferences than women ($d = 0.59$) and *muxe nguiiu* ($d = 0.57$), whereas *muxe nguiiu* and women did not differ ($d = 0.08$). These findings are consistent with the conclusion that sex-atypical occupational preferences are a cross-culturally universal aspect of male androphilia. Finally, CSAB was associated with sex-atypical occupational preferences among all participants. These findings suggest that a developmental continuity exists between childhood and adulthood sex-atypicality.

Keywords: occupational preferences; childhood sex-atypical behavior; masculinity-femininity; male androphilia; Istmo Zapotec; *muxes*

Introduction

The sex-atypical behavior that characterizes androphilic males in childhood is often manifested as increased female-typical occupational interests in adulthood. On average, males tend to prefer systematizing, thing-orientated occupations which involve understanding and working with physical systems such as machines, equipment, and inanimate objects (e.g., mechanics, carpenters, engineers). In contrast, females usually prefer empathizing, people-orientated occupations which involve managing, thinking about, and frequently interacting with people (e.g., counselors, elementary schoolteachers, nurses) (Archer, 2019; Konrad et al., 2000; Nettle, 2007). Cross-cultural research demonstrates that, on average, gay men from Australia, Brazil, Canada, China, Guatemala, New Zealand, the Philippines, UK, USA, and Western Europe (Ellis et al., 2012; Lippa, 2002, 2005a, 2008a, 2020; Whitam & Mathy, 1986; Zheng et al., 2011), and transgender androphilic males from India, Samoa, and the Philippines (Hart, 1968; Semenyna & Vasey, 2016; Stief, 2017), display sex-atypical occupational preferences.

Research demonstrates that transgender androphilic males, such as Samoan *fa'afafine* tend to exhibit a pattern of behavior and psychology (e.g., occupational preferences, childhood sex-typed behavior, and childhood indicators of separation anxiety) that is similar to androphilic women and thus female-typical (e.g., Semenyna & Vasey, 2016, 2017; VanderLaan, Petterson, & Vasey, 2017; Vasey et al., 2011). In contrast, Euro-American "gay" men demonstrate one that is in between gynephilic men and androphilic women and thus *shifted* in a female-typical direction (e.g., Bailey, 2003; Bailey & Zucker, 1995; Lippa, 2005a, 2008a; VanderLaan et al., 2011a, 2015, 2016). Some studies have directly compared the two types of male androphiles and found that transgender ones have higher female-typical behavior and interests during childhood than cisgender ones (e.g., Chapter 2; Singh et al., 2021; Wallien & Cohen-Kettenis, 2008). In light of this, we sought to determine whether there are significant differences in occupational preferences in adulthood between (1) gynephilic men and androphilic women, (2) gynephilic and androphilic males, and (3) cisgender and transgender androphilic males. This research was conducted in a culture where both forms of male androphilia are prevalent—the Istmo Zapotec.

The research presented in Chapter 2 indicates that relative to gynephilic men, both cisgender ($d = 2.33$) and transgender *muxes* ($d = 4.99$) among the Istmo Zapotec recall having higher levels of childhood sex-atypical behavior during childhood than gynephilic men. The size of these differences are considered to be very large from a statistical standpoint (Cohen, 1988). Moreover, transgender *muxe gunaa* recalled even higher sex-atypical behavior during childhood than cisgender *muxes nguiiu* and did not differ significantly from androphilic women in this regard. It would be surprising if the very large male orientation differences in childhood sex-atypicality disappeared without a trace by adulthood.

In adulthood, *muxes* are known for embracing a variety of occupations within Istmo Zapotec culture. Although many of these occupations are considered stereotypically feminine (e.g., clothing designer, embroidery, sewing, cooking, and event decorators), others have been traditionally held by men (e.g., cab drivers, public officials, and politician) (Céspedes Vargas, 2015; Chiñas, 1992; Mirandé, 2017). A qualitative study of *muxes* in the workplace found that wage labor jobs (e.g., structured labor under a contract of employment) are mostly occupied by relatively masculine *muxes* (i.e., *muxe nguiiu*), whereas self-employment is more common among feminine *muxes* (i.e., *muxe gunaa*) (Céspedes Vargas, 2015). Quantitative data bearing on the extent to which cisgender and transgender *muxes* differ from gynephilic men, and from each other, with respect to their preferences for sex-typed occupations are lacking.

The relatively high presence of both forms of male androphilia among the Istmo Zapotec allowed us to determine whether occupational preferences differ according to sex, male sexual orientation, and male androphilia type within the same culture. Given previous literature, we formulated four separate predictions. First, we predicted that we would find sex differences in occupational preferences between Istmo Zapotec gynephilic men and androphilic women. Second, we expected to find male sexual orientation differences, with both cisgender and transgender *muxes* having more sex-atypical occupational preferences than gynephilic men. Third, we predicted differences in occupational preferences between *muxe* types, with transgender *muxe gunaa* scoring similar to androphilic women, and cisgender *muxe nguiiu* scoring in between gynephilic men and androphilic women.

We also assessed whether a relationship existed between childhood sex-atypical behavior (CSAB) and adult occupational preferences among the Istmo Zapotec. Three studies have found that CSAB is positively associated with sex-atypicality in adulthood occupational preferences (Canada: VanderLaan et al., 2016; Samoa: Semenyna & Vasey, 2016; USA: Lippa, 2008b). Given these findings, we predicted that greater recalled CSAB would be related to greater sex-atypical occupational preferences among both male and female participants. Finally, we predicted that among males, the association between recalled CSAB and occupational preferences would exist independent of sexual orientation and gender identity.

Methods

Participants

All participants were recruited using network sampling procedures which consisted of contacting initial participants who provided referrals for additional participants, and so on. Data were collected during five trips between 2015 and 2019 in the city of Juchitán de Zaragoza, as well as 16 towns and villages in the Juchitán and Tehuantepec districts of the Istmo region of Oaxaca, Mexico. Participants were required to provide informed written consent prior to taking part in the study.

A total of 208 gynephilic men, 138 androphilic women, and 261 *muxes* were interviewed for this study. Among *muxes*, there were 129 who identified as *muxe gunaa* and 132 who identified as *muxe nguiiu*. Participants' sexual orientation was assessed using a 7-point Kinsey scale (Kinsey et al., 1948), which asked about sexual feelings over the previous year. Istmo Zapotecs recognize that *muxes* are biological males, as evidenced by the fact that they possess male genitalia and secondary sex characteristics. Nevertheless, participants were informed that the category "males" included men and/or *muxes*, whereas the category "females" included only women, in order to assess the sex that they are attracted to as opposed to the gender. All men identified as exclusively (Kinsey rating = 0, $n = 202$ men) or predominantly (Kinsey rating = 1, $n = 6$ men) gynephilic. All women identified as exclusively (Kinsey rating = 6, $n = 137$ women) or predominantly (Kinsey rating = 5, $n = 1$ woman) androphilic. All *muxes* identified as exclusively (Kinsey rating = 6, $n = 114$ *muxe nguiiu*; $n = 129$ *muxe gunaa*) or predominantly (Kinsey rating = 5, $n = 18$ *muxe nguiiu*) androphilic.

Procedures and Measures

Participants were interviewed using standardized questionnaires, which were available in Spanish after being translated and back-translated by two fluent Spanish-English speakers. Two of the authors, as well as a Spanish-speaking research assistant, were available to answer participants' questions. A Zapotec-speaking research assistant was also present for interviews when participants were not fully fluent in Spanish. Questions were read aloud by the authors and research assistants in Spanish or Zapotec as necessary. Participants were asked to report information regarding their age (in years), average weekly income, and level of education. Participants were coded as earning either "1000 or less" or "Over 1000" Mexican Pesos and receiving either "Junior high school or lower" or "High school or college" education.

Occupational preferences were evaluated with a version of Lippa's (2010) measure specifically adapted to include occupations relevant to life in the Istmo region of Oaxaca. Participants rated 15 occupations on a seven-point scale (1 = strongly dislike; 7 = strongly like), reporting their interest in doing each of the following jobs: car mechanic, clothing designer, truck driver, primary schoolteacher, carpenter, refrigerator repairperson, fishing boat crew member, florist, nurse, hairdresser, inventor, dance teacher, electrical engineer, social worker, and event decorator. Given the modification to this measurement and that it has not been previously used to assess occupational preferences in the Istmo region of Oaxaca, we conducted an exploratory factor analysis to see how the data clustered together and whether these 15 occupations can reliably be used to assess male-typical and female-typical interest. From this analysis, we were able to obtain two factors which corresponded to male-typical occupational preferences (MTOP) and female-typical occupational preferences (FTOP) (see Statistical Analyses and Results sections for more details). Thus, we calculated a MTOP score by averaging the ratings for the occupations that loaded into the MTOP factor and a FTOP score by averaging the ratings for the occupations that loaded into the FTOP factor.

Cronbach's alpha coefficients were appreciable in this sample for FTOP ($\alpha = 0.82$) and MTOP ($\alpha = 0.85$). A male-versus-female-typical occupational preference (MF-Occ) score was calculated by subtracting the MTOP scores from FTOP (Lippa, 1991, 2005b). As such, positive scores indicate greater female-typical occupational preferences whereas negative scores indicated greater male-typical occupational preferences. Given that some of the group differences in MF-Occ were inconsistent with our predictions (see Results), additional group comparisons were conducted in which *muxe nguiiu* and *muxe gunaa* were combined into a single group of non-binary androphilic males, comparable to the more monolith grouping of Samoan androphilic males, who exhibit a range of gender role presentation yet are classified into the single category of *fa'afafine* (see Semenyna & Vasey, 2016).

The data for the childhood sex-typed behavior used in this study were partially derived from the sample in Chapter 2, although the present sample contains data from an additional 28 gynephilic men, 69 *muxe nguiiu*, and 9 *muxe gunaa*. As in the previous study and others (e.g., Semenyna & Vasey, 2016; VanderLaan et al., 2011a, 2015, 2016; VanderLaan, Petterson, & Vasey, 2017), childhood sex-typed behavior was assessed using the Childhood Gender Identity Scale (Bartlett & Vasey, 2006). This scale is derived from the Gender Identity Questionnaire for Children (Johnson et al., 2004), which is a parent-report questionnaire used to assess children's gender expression. The Childhood Gender Identity Scale consists of a childhood female-typical behavior (CFTB) subscale containing five items and a childhood male-typical behavior (CMTB) subscale containing four items. Participants were asked to recall how often they exhibited female-typical behavior (e.g., "put on girls' makeup or clothes or accessories") and male-typical behavior (e.g., "rough and tumble play") before the age of 12 years using a 5-point Likert-type scale that ranged from 1 = "Never" to 5 = "Always/All the time." Mean scores were calculated from each of the two subscales to obtain recalled CFTB and CMTB subscale scores.

Cronbach's alpha coefficients for CMTB ($\alpha = 0.88$) and CFTB ($\alpha = 0.94$) were appreciable in the present sample. A childhood sex-atypical behavior (CSAB) composite score was created for all males (i.e., gynephilic men, *muxe nguiiu*, and *muxe gunaa*) by subtracting CFTB from CMTB, and for females by subtracting CMTB from CFTB. A constant of 4 was added to all scores so the values for CSAB ranged from 0 to 8. Thus, a score of 0 indicates no sex-atypical behavior whereas higher values indicate greater sex-atypical behavior recalled during childhood for both male and female participants.

Statistical Analyses

Statistical analyses were conducted using JASP, version 0.14.1 (JASP Team, 2020). Group differences in age were assessed using a one-way ANOVA; group differences in weekly income and level of education were assessed using chi-square analyses because of the ordinal nature of these variables. To determine which groups differed, post-hoc pairwise comparisons were conducted following significant chi-square analyses by using *z*-tests comparing the proportion of weekly income and level of education between groups (with alpha adjusted to 0.008).

In order to determine whether the 15 occupations could be accurately categorized as being typically preferred by males or females, we conducted an exploratory factor analysis (EFA). Given that *muxes* constitute about 3–6 % of the Istmo Zapotec male population (Gómez et al., 2018), but 55.7 % of our male sample, they were excluded from the analysis in order to assess the common variance for the occupations measured using a sample representative of the general population (i.e., among gynephilic males and androphilic females). As suggested by Sakaluk and Short (2017), common factors were extracted using maximum likelihood estimation with promax (i.e., oblique) rotation, and a parallel analysis was used to determine the number of factors to retain. Factor loadings for the individual occupations were considered significant if they were greater than 0.4 (Stevens, 2002).

Group differences in the MTOP and FTOP scores, the average MF-Occ score, the average recalled CFTB and CMTB subscale scores, and the CSAB composite score between

Istmo Zapotec gynephilic men, androphilic women, *muxe nguiiu*, and *muxe gunaa* were assessed using one-way ANOVAs. To determine the size and direction of significant omnibus tests, post-hoc pairwise comparisons were conducted using the Games-Howell procedure since groups showed unequal variances for all variables (see Results). Cohen's *d* statistics were calculated for all pairwise comparisons as $\frac{M_1 - M_2}{\sqrt{\frac{(n_1 - 1)SD_1^2 + (n_2 - 1)SD_2^2}{n_1 + n_2 - 2}}}$ and presented with their 95 % confidence intervals.

An additional group analysis was conducted by comparing MF-Occ scores between gynephilic males, androphilic females, and *muxes* combined (*muxe nguiiu* + *muxe gunaa*). Similar to the other omnibus tests, a one-way ANOVA was performed using a Brown-Forsythe test, and all post-hoc pairwise comparisons were conducted using the Games-Howell procedure due to significant scores for Levene's test for equality of variance ($p = .014$). The strength of the group difference was assessed with Cohen's *d* effect sizes and their 95 % confidence intervals.

Pearsons' *r* correlations were conducted to assess the relationship between childhood-sex atypical behavior and occupational preferences among male (gynephilic men, *muxe nguiiu*, and *muxe gunaa* combined) and female participants. A multiple linear regression was also conducted to assess whether the relationship between childhood sex-atypical behavior and occupational preferences among males was independent of sexual orientation and gender identity. To do so, two dummy coded variables labelled Men vs. *Muxe nguiiu* and Men vs. *Muxe gunaa* were created. *Muxe gunaa* were coded as 0 and *muxe nguiiu* as 1 in the former, and vice versa for the latter. For both variables, gynephilic men were coded as 0.

Results

Descriptive statistics for the biographic information are presented in Table 3.1. Significant group differences were found for level of income, $\chi^2(3) = 14.24$, $p = .003$, and level of education, $\chi^2(3) = 63.62$, $p < .001$, but not for age, $F(3, 603) = 0.728$, $p = .536$. A significantly higher proportion of *muxe nguiiu* than androphilic women reported earning more than 1000 Pesos ($p < .001$). A significantly lower proportion of *muxe gunaa* reported receiving high school or college education than all other groups (all $p < .001$). Nonetheless, level of income and level of education were not used as a covariate in further analyses given that the direction and significance of our main variables did not change when controlling for these biographic variables.

Table 3.1

Descriptive statistics for biographic information by group.

	Gynephilic Men (n = 208)	*Muxe Nguiiu* (n = 132)	*Muxe Gunaa* (n = 129)	Androphilic Women (n = 138)
Age (in years) *M* (*SD*)	30.06 (9.59)	29.29 (9.10)	30.77 (9.38)	30.78 (10.38)
Level of Education				
Junior high school or lower	32.69%	25.76%	66.67%	26.81%
High school or college	67.31%	74.24%	33.33%	73.19%
Weekly Income (Mexican Pesos)				
1000 or less	50.00%	38.64%	49.61%	61.59%
Over 1000	50.00%	61.36%	50.39%	38.41%

Adult Occupational Preferences

The EFA revealed that the occupations measured could be significantly grouped into two factors, $\chi^2(76) = 170.24$, $p < .001$, $RMSEA = 0.060$ (95 % CI: 0.048, 0.072). However, three occupations (primary schoolteacher, inventor, and social worker) did not obtain factor loadings above 0.4 (Table 3.2). Thus, a second EFA using similar procedures was run after removing those three occupations (Table 3.3). Once again, we found that two factors fit the data well, $\chi^2(43) = 91.45$, $p < .001$, $RMSEA = 0.058$ (95 % CI: 0.041, 0.073). The occupations that clustered on the same factor suggested that the first factor represents female-typical preferred occupations, and the second factor represents male-typical preferred occupations. Therefore, using occupations that loaded onto these two factors, average FTOP and MTOP scores, and an MF-Occ score were calculated and used in subsequent analysis.

Table 3.2

Estimates for rotated loadings of the two-factor solution with 15 occupations.

Item	Female-typical occupations	Male-typical occupations
	Loading	Loading
Car Mechanic	-0.25	**0.73**
Clothing Designer	**0.76**	-0.15
Truck Driver	-0.26	**0.63**
Primary School Teacher	0.23	0.21
Carpenter	0.01	**0.71**
Fridge Repairperson	-0.09	**0.73**
Fishing Boat Crew Member	0.04	**0.59**
Florist	**0.77**	-0.06
Nurse	**0.52**	-0.01
Hair Dresser	**0.78**	-0.17
Inventor	0.19	0.39
Dance Teacher	**0.69**	-0.04
Electrical Engineer	-0.13	**0.65**
Social Worker	0.27	0.19
Event Decorator	**0.80**	-0.15

Bold numbers represent factor loadings > 0.40.

Table 3.3

Estimates for rotated loadings of the two-factor solution with 12 occupations.

Item	Female-typical occupations	Male-typical occupations
	Loading	Loading
Car Mechanic	-0.14	**0.72**
Clothing Designer	**0.76**	-0.05
Truck Driver	-0.16	**0.63**
Carpenter	0.12	**0.74**
Fridge Repairperson	-0.02	**0.74**
Fishing Boat Crew Member	0.14	**0.62**
Florist	**0.79**	0.05
Nurse	**0.51**	0.04
Hair Dresser	**0.79**	-0.06
Dance Teacher	**0.69**	0.04
Electrical Engineer	-0.05	**0.62**
Event Decorator	**0.80**	-0.04

Bold numbers represent factor loadings > 0.40.

Significant group differences were found for average FTOP, MTOP, and MF-Occ scores (Table 3.4). Androphilic women reported significantly higher FTOP than gynephilic men ($p < .001$, $d = 1.85$ [1.60, 2.11]) and *muxe nguiiu* ($p = .003$, $d = 0.43$ [0.19, 0.68]). *Muxe gunaa* reported significantly higher FTOP than gynephilic men ($p < .001$, $d = 1.79$ [1.53, 2.05]) and *muxe nguiiu* ($p = .007$, $d = 0.40$ [0.15, 0.64]). *Muxe nguiiu* reported significantly higher FTOP than gynephilic men ($p < .001$, $d = 1.18$ [0.95, 1.42]). No significant group differences were found between androphilic women and *muxe gunaa* ($p = .994$, $d = 0.03$ [-0.21, 0.27]).

Gynephilic men reported significantly higher MTOP than androphilic women ($p < .001$, $d = 1.54$ [1.30, 1.79]), *muxe gunaa* ($p < .001$, $d = 2.32$ [2.04, 2.60]), and *muxe nguiu* ($p < .001$, $d = 1.91$ [1.65, 2.18]). Androphilic women reported significantly higher MTOP than *muxe gunaa* ($p < .001$, $d = 0.70$ [0.45, 0.95]), and *muxe nguiiu* ($p = .023$, $d = 0.35$ [0.11, 0.59]). *Muxe nguiiu* reported significantly higher MTOP and *muxe gunaa* ($p = .031$, $d = 0.34$ [0.10, 0.59]).

With respect to MF-Occ scores, gynephilic men scored significantly lower than androphilic women ($p < .001$, $d = 2.80$ [2.50, 3.10]), *muxe gunaa* ($p < .001$, $d = 3.44$ [3.10, 3.78]), and *muxe nguiiu* ($p < .001$, $d = 2.36$ [2.08, 2.65]), indicating greater male-typical and lower female-typical, occupational preferences. In contrast, *muxe gunaa* had significantly higher MF-Occ scores than *muxe nguiiu* ($p < .001$, $d = 0.57$ [0.32, 0.82]) and androphilic women ($p < .001$, $d = 0.59$ [0.35, 0.84]), indicating greater female-typical and lower male-typical occupational preferences. No significant differences in MF-Occ scores were found between *muxe nguiiu* and androphilic women ($p = .919$, $d = 0.08$ [-0.16, 0.32]).

Lastly, significant differences in MF-Occ were found between gynephilic men, androphilic women, and *muxes* combined, $F(2, 569.41) = 545.15$, $p < .001$. *Muxes*' MF-Occ scores ($M = 2.72$, $SD = 1.69$) were significantly higher than those of gynephilic men

($p < .001$, $d = 2.73$ [2.48, 2.98])], but did not significantly differ from those of androphilic women ($p = .096$, $d = 0.21$ [0.00, 0.41]).

Recalled Childhood Sex-Typed Behavior

Significant group differences were found in the average CFTB and CMTB scores, and the composite CSAB score (Table 3.4). Androphilic women recalled significantly more CFTB than gynephilic men ($p < .001$, $d = 5.16$ [4.72, 5.60]) and *muxe nguiiu* ($p < .001$, $d = 1.72$ [1.44, 2.00]). *Muxe gunaa* recalled significantly more CFTB than *muxe nguiiu* ($p < .001$, $d = 1.66$ [1.38, 1.94]) and gynephilic men ($p < .001$, $d = 5.02$ [4.58, 5.46]). *Muxe nguiiu* recalled significantly more CFTB than gynephilic men ($p < .001$, $d = 1.59$ [1.34, 1.84]). No significant difference in recalled CFTB was observed between androphilic women and *muxe gunaa* ($p = .985$, $d = 0.04$ [-0.20, 0.28]).

Gynephilic men recalled significantly more CMTB than androphilic women ($p < .001$, $d = 2.77$ [2.47, 3.07]), *muxe gunaa* ($p < .001$, $d = 3.24$ [2.91, 3.57]), and *muxe nguiiu* ($p < .001$, $d = 1.80$ [1.55, 2.06]). *Muxe nguiiu* recalled significantly more CMTB than androphilic women ($p < .001$, $d = 0.70$ [0.45, 0.95]) and *muxe gunaa* ($p < .001$, $d = 0.97$ [0.71, 1.23]). No significant difference in recalled CMTB was observed between androphilic women and *muxe gunaa* ($p = .161$, $d = 0.25$ [0.01, 0.50]).

Finally, with respect to CSAB composite scores, *muxe gunaa* recalled significantly greater CSAB than gynephilic men ($p < .001$, $d = 5.11$ [4.66, 5.55]), androphilic women ($p < .001$, $d = 3.56$ [3.18, 3.95]), and *muxe nguiiu* ($p < .001$, $d = 1.53$ [1.26, 1.81]). *Muxe nguiiu* also recalled significantly greater CSAB than gynephilic men ($p < .001$, $d = 2.03$ [1.76, 2.29]) and androphilic women ($p < .001$, $d = 1.25$ [0.99, 1.51]). Lastly, androphilic women recalled significantly greater CSAB than gynephilic men ($p < .001$, $d = 0.74$ [0.51, 0.96]).

Table 3.4

Comparison of gynephilic men, muxe nguiiu, muxe gunaa, and androphilic women on occupational preferences and childhood sex-typed behavior scores.

	Gynephilic Men (n = 208)		*Muxe nguiiu* (n = 132)		*Muxe gunaa* (n =129)		Androphilic Women (n = 138)		One-way ANOVA[g]		
	M	SD	M	SD	M	SD	M	SD	F	df	p
Female-typical occupational preferences[a,b,c,d,e]	3.09	1.29	4.73	1.52	5.26	1.06	5.29	1.00	125.98	505.46	< .001
Male-typical occupational preferences[a,b,c,d,e,f]	4.72	1.15	2.47	1.22	2.07	1.14	2.90	1.23	172.90	555.49	< .001
Male-versus-female-typical occupational preferences[a,b,c,d,f]	-1.63	1.47	2.26	1.90	3.19	1.29	2.39	1.39	358.92	494.53	< .001
Childhood female-typical behavior[a,b,c,d,e]	1.39	0.43	2.68	1.18	4.34	0.78	4.38	0.75	489.55	365.88	< .001
Childhood male-typical behavior[a,b,c,d,e]	4.39	0.71	2.83	1.06	1.90	0.85	2.13	0.95	267.73	491.79	< .001
Childhood sex-atypical behavior[a,b,c,d,e,f]	1.00	0.85	3.85	1.98	6.45	1.34	1.77	1.28	426.15	386.42	< .001

Values for the male-versus-female-typical occupational preferences scores ranged from -6 to 6, with positive scores representing higher female-typical behavior and negative scores representing greater male-typical behavior. Values for the childhood sex-atypical behavior scores ranged from 0 to 8, with higher scores representing greater sex-atypical behavior

[a] Statistically significant difference ($p < .001$) between gynephilic men and *muxe nguiiu.*

[b] Statistically significant difference ($p < .001$) between gynephilic men and *muxe gunaa*.

[c] Statistically significant difference ($p < .001$) between gynephilic men and androphilic women.

[d] Statistically significant difference ($p < .05$) between *muxe nguiiu* and *muxe gunaa*.

[e] Statistically significant difference ($p < .05$) between *muxe nguiiu* and androphilic women.

[f] Statistically significant difference ($p < .001$) between *muxe gunaa* and androphilic women.

[g] Due to significant Levene's test for equality of variance ($p < .05$), all one-way ANOVA were performed using Brown-Forsythe tests, and all post-hoc pairwise comparisons were conducted using the Games-Howell procedure.

Recalled Childhood Sex-Atypical Behavior and Adult Occupational Preferences

A significant correlation was found between CSAB and MF-Occ among all male ($r = .770$, $p < .001$) and female ($r = -.203$, $p = .017$) participants. Model 1 of the linear regression analysis (Table 3.5) revealed that among males, CSAB was a significant predictor of adult MF-Occ ($\beta = 0.77$, $p < .001$), accounting for 59 % of the variance. Model 2 revealed that among males, CSAB significantly predicted adult MF-Occ scores independent of sexual orientation ($\beta = 0.38$, $p < .001$). Furthermore, this model revealed that, compared with being a gynephilic male, being a *muxe nguiiu* ($\beta = 0.47$, $p < .001$) or a *muxe gunaa* ($\beta = 0.46$, $p < .001$) independently predicts higher MF-Occ scores. Altogether, the predictors in Model 2 accounted for 70% of the variance in MF-Occ scores. Finally, the significant increase in the variance explained between Model 1 and 2 ($\Delta R^2 = 0.109$, $p < .001$) revealed that the variance in MF-Occ scores explained by male sexual orientation is independent of CSAB.

Table 3.5

Linear regression predicting male-versus-female-typical occupational preferences scores based on gender and childhood sex-atypical behavior scores.

		Male-versus-female-typical occupational preference					
		B	95% CI	SE	β	*t*	*p*
Model	*Predictor*						
1	Childhood sex-atypical behavior	0.78	0.72, 0.84	0.03	0.77	26.03	< .001
2	Childhood sex-atypical behavior	0.38	0.28, 0.48	0.05	0.38	7.72	< .001
	Men vs *Muxe nguiiu*	2.81	2.38, 3.23	0.22	0.47	13.03	< .001
	Men vs *Muxe gunaa*	2.75	2.13, 3.36	0.31	0.46	8.74	< .001

Model 1: $R^2 = 0.593$; Adjusted $R^2 = 0.592$; $F(1, 465) = 677.68$, $p < .001$.
Model 2: $R^2 = 0.702$; Adjusted $R^2 = 0.700$; $F(3, 463) = 364.28$, $p < .001$.
$\Delta R^2 = 0.109$, $p < .001$.
For both dummy variables, gynephilic men were coded as 0. In Men vs *Muxe nguiiu*, *muxe gunaa* were coded as 0 and *muxe nguiiu* as 1. In Men vs *Muxe gunaa*, *muxe nguiiu* were coded as 0 and *muxe gunaa* as 1.

Discussion

This study examined whether sex, male sexual orientation, and androphilic male type (i.e., cisgender, transgender) differences in occupational preferences exist among Istmo Zapotec gynephilic men, androphilic women, cisgender androphilic males (i.e., *muxe nguiiu*), and transgender androphilic males (i.e., *muxe gunaa*). In line with our first prediction, Istmo Zapotec gynephilic men and androphilic women demonstrated very large sex differences in occupational preferences ($d = 2.80$). This finding is consistent with cross-cultural research which has found that the magnitude of the sex differences in occupational preferences is very large across cultures (Archer, 2019), even when controlling for cultural differences in gender equality (Lippa, 2010). These results do not fit with social role theory, which holds that psychological sex differences are a product of different socialization pressures and gender role enforcement to which boys and girls are subjected (Eagly & Wood, 1999; Hyde, 2005; Wood & Eagly, 2002). Instead, the recurrence of consistent sex differences across substantially different cultural contexts suggests that biological factors play some role in the production of men and women's average occupational interests.

Consistent with our second prediction, both cisgender and transgender *muxes* reported having more sex-atypical occupational preferences than gynephilic men. These findings are consistent with previous cross-cultural research (Ellis et al., 2012; Hart, 1968; Lippa, 2002, 2005a, 2008a, 2020; Semenyna & Vasey, 2016; Stief, 2017; Whitam & Mathy, 1986; Zheng et al., 2011) and suggest that sex-atypical occupational preferences are a cross-cultural universal correlate of male androphilia. Furthermore, this documentation of male sexual orientation differences in a growing number of disparate cultures also suggests that biological factors play some role in the average occupational interests of gynephilic and androphilic males.

To the best of our knowledge, this is the first study to look at occupational preferences using both cisgender and transgender androphilic males from within the same culture. Among androphilic males, transgender *muxes* had more sex-atypical occupational preferences than cisgender *muxes*. However, the manner by which these *muxes* types differed from the other groups was not completely consistent with our predictions. Unlike cisgender androphilic males from Euro-American cultures, whose occupational preferences are intermediate to those of men and women (Ellis et al., 2012; Lippa, 2002, 2005a, 2008a, 2020; Whitam & Mathy, 1986; Zheng et al., 2011), *muxe nguiiu's* overall occupational preferences did not differ from those of androphilic women. Furthermore, whereas Semenyna & Vasey (2016) found that Samoan *fa'afafine* had similar occupational preferences to androphilic women, *muxe gunaa* in the present study had a higher MF-Occ score than androphilic women.

A closer examination of male-typical and female-typical occupational preferences scores can provide some insights into the pattern of occupational preferences endorsed by both types of *muxes*. Androphilic women had a greater preference for male-typical occupations than both cisgender and transgender *muxes*. In contrast, androphilic women and *muxe gunaa* did not differ in their preferences for female-typical occupations, whereas *muxe nguiiu's* preferences for female-typical occupations were in between those of gynephilic men and women. These results suggest that discrepancies in MF-Occ group difference scores between this study and previous ones are mostly driven by a greater aversion towards male-typical occupations among our androphilic male groups.

Why would cisgender *muxes* have higher aversion toward male-typical occupations than their gay male counterparts in Euro-American cultures? In Euro-American cultures, it is common for androphilic males to begin identifying as "gay" during adolescence (e.g., Floyd & Bakeman, 2006; Haltom & Ratcliff, 2021) and to make a conscious effort to suppress their female-typical behavior, while presenting in a more male-typical manner (e.g., Barron & Bradford, 2007; Hunt et al., 2016; Taywaditep, 2001; Whitam, 1977). In contrast, among the Istmo Zapotec, *muxes* are commonly identified as such, by family and community members, as early as 3 years of age (Chiñas, 1995; Miano Borruso, 2002). Although cisgender *muxe nguiiu* have a relatively masculine gender presentation, their gender identity is not typical of their sex. Consequently, identification as *muxe nguiiu* involves recognition of oneself as a member of a distinct, third gender composed of males who are more feminine than gynephilic men. These different cultural approaches to cisgender male androphilia may result in Euro-American gay men being somewhat more eager to endorse an interest in male typical occupations and, in doing so, present a masculine persona to the world. In contrast, cisgender *muxe nguiiu* may be less motivated to make similar claims because their identities as feminine males are public knowledge and may have been so since childhood. Future research could explore these possibilities by examining cross-cultural differences in self and public awareness of sexual orientation, gender identity, and degree of sex-atypical behavior.

Why would transgender *muxe gunaa* have higher aversion toward male-typical occupations than their *fa'afafine* counterparts in Samoa? Most *fa'afafine* are markedly feminine, but some are unremarkably masculine, with varying expressions of femininity and masculinity in between these two extremes. Whereas most Samoan androphilic males are categorized as *fa'afafine* by themselves and others, regardless of the degree to which they present in a masculine or feminine manner (Bartlett & Vasey, 2006), Istmo Zapotec *muxes* are often subcategorized, by themselves and others, as masculine (*muxe nguiiu*) or feminine (*muxe gunaa*) depending on their gender presentation (Gómez et al., 2017). However, when *muxe nguiiu* and *muxe gunaa* were combined into a single group, our results were similar to those obtained in Semenyna & Vasey (2016), in that, similar to Samoan *fa'afafine*, the combined group of *muxes* had more sex-atypical occupational preferences than gynephilic men but did not differ significantly from androphilic women. Given these results, it would be interesting to determine whether any differences in occupational preferences exist among Samoan *fa'afafine* depending on the degree to which they present in a female-typical or male-typical manner. It would also be interesting to compare Samoan androphilic males who identify as *fa'afafine* (regardless of their gender role presentation) and those who identify as men.

In line with previous research in Canada (VanderLaan et al., 2016), the USA (Lippa, 2008b), and Samoa (Semenyna & Vasey, 2016), childhood sex-atypical behavior was associated with greater sex-atypical occupational preferences in adulthood among both male and female participants. This association was stronger among males ($r = .770$) than females ($r = -.203$), most likely because, unlike our male sample, our female sample only included opposite-sex-attracted participants. This sexual orientation homogeneity would result in less variance in childhood sex-typed behavior and adulthood occupational preferences, thus reducing the magnitude of the correlation. Among males, both recalled childhood sex-atypical behavior and being androphilic (whether cisgender or transgender) were independently associated with greater sex-atypical adult occupational preferences, accounting for 70 % of the variance. The explanatory power of these variables was somewhat higher than those found in previous studies (Lippa, 2008b; Semenyna & Vasey, 2016), probably because the male sample employed in previous studies only included one type of male androphilia whereas our male sample include both cisgender and transgender androphilic males, allowing for more variance to be explained. Overall, it appears that the degree of sex-atypical behavior displayed during childhood can be a strong predictor of sex-atypical occupational interests during adulthood. These findings suggest the existence of a developmental continuity between childhood and adulthood sex-(a)typicality.

Finally, although not predicted, androphilic women recalled greater childhood sex-atypical behavior than gynephilic men, which is consistent with previous research conducted in Canada (Coome et al., 2018; Peragine et al., 2021) and the USA (Lippa, 2008b; Martin et al., 2017). Clinical research demonstrates that girls usually require greater levels of sex-atypical behavior than boys before their parents seek out clinical assessment, and that parents, teachers, and peers are less tolerant of sex-atypical behavior in boys than in girls (e.g., Zucker & Bradley, 1995). Thus, it is possible that sex differences in childhood sex-atypical behaviors are due to somewhat lower social pressures to act in a sex-typical manner among girls compared with boys. Future research among the Istmo Zapotec should test the extent to which such social pressures during childhood are associated with the development of masculine and feminine expression.

Limitations

This study has two noteworthy limitations. First, retrospective reports of childhood behaviors have been characterized as flawed and prone to selective recall bias and memory distortion (e.g., Fausto-Sterling, 2014). Nonetheless, both retrospective and prospective research show strong associations between CSAB in boys and an androphilic orientation in adulthood (Bailey & Zucker, 1995; Bartlett & Vasey, 2006; Besharat et al., 2016; Cardoso, 2005, 2009; Green, 1987; Li et al., 2017; Petterson et al., 2017; Semenyna & Vasey, 2016, 2017; Semenyna, VanderLaan, & Vasey, 2017; Whitam, 1983). Furthermore, research using childhood home videos (Rieger et al., 2008) and pictures (Watts et al., 2018) demonstrate that androphilic males exhibit sex-atypical behavior at an early age. In contrast, no support for the selective recall/memory distortion hypothesis has ever been presented in the literature (for review, see

Bailey & Zucker, 1995; Bailey et al., 2016; Zucker et al., 2006). Thus, it is likely that *muxes'* recollections of their childhood behaviors are accurate and not the product of memory distortion or selective recall bias.

Finally, the network sampling procedure utilized for this study could have conceivably produced an unrepresentative sample. Efforts to avoid such bias were made by interviewing participants from 17 towns and villages throughout the Tehuantepec and Juchitán districts of the Istmo region of Oaxaca. Nonetheless, future research in the Istmo region could use a random sampling procedure to eliminate potential bias.

Conclusion

This study found that both cisgender and transgender androphilic males (*muxes*) had greater sex-atypical occupational preferences than Istmo Zapotec gynephilic men. Cisgender *muxe nguiiu* had similar patterns of occupational preferences to androphilic women. However, transgender *muxe gunaa* had higher female-typical occupational preferences than both cisgender women and *muxe nguiiu*. Finally, consistent with previous research (Lippa, 2008b; Semenyna & Vasey, 2016; VanderLaan et al., 2016), an association was found between sex-atypical behavior in childhood and sex-atypical occupational preferences in adulthood among all participants. This suggests that a developmental continuity exists between childhood and adulthood sex-(a)typicality. Overall, the present study among the Istmo Zapotec suggests that the preference for sex-atypical occupations is a cross-cultural universal aspect of male androphilia.

Chapter 4: Sex and Male Sexual Orientation Differences in Cognitive Abilities in Samoans and Istmo Zapotec

Abstract

Sex and male sexual orientation differences have been observed in various cognitive abilities. For example, males who are gynephilic tend to outperform males and females who are androphilic in visual-spatial abilities (e.g., mental rotation and judgment of line orientation). In contrast, androphilic males and females tend to outperform gynephilic males in object location memory and verbal fluency. Nevertheless, these male sexual orientation differences have been mostly documented in Euro-American cultures using cisgender gay men. The present study assessed sex and male sexual orientation differences in cognitive abilities in Samoa and the Istmo region of Oaxaca, Mexico, where the transgender form of male androphilia is commonplace. In Samoa, transgender androphilic males identify as *fa'afafine*. In the Istmo region, cisgender and transgender androphilic males identify as *muxes nguiiu* and *muxe gunaa*, respectively. Results demonstrated that in Samoa, gynephilic men (n = 97) outperform androphilic women (n = 102) and *fa'afafine* (n = 99) in judgement of line orientation. In the Istmo region, gynephilic men (n = 95) outperform androphilic women (n = 99), but not *muxe nguiiu* (n = 77) nor *muxe gunaa* (n = 82), in judgement of line orientation and mental rotation. No sex or male sexual orientation differences were found for object location memory or verbal fluency. These findings suggest that the sex and male sexual orientation differences in visual-spatial abilities are slightly more cross-culturally consistent than those for object location memory and verbal fluency.

Keywords: male androphilia; mental rotation; judgement of line orientation; object location memory; verbal fluency; Samoa; Istmo Zapotec.

Introduction

Research on sex differences in cognitive abilities demonstrate that males and females differ in their visual-spatial and verbal abilities. With respect to visual-spatial abilities, males tend to outperform females in tests of spatial navigation (e.g., maze solving), spatial perception (e.g., judging orientation of lines), and mental rotation (e.g., mentally rotating three-dimensional objects) (e.g., Archer, 2019; Coluccia & Louse, 2004; Halpern et al., 2007; Kimura, 2002; Sneider et al., 2015; Voyer et al., 2017). In contrast, females tend to outperform males in tests of spatial location which involve remembering objects and their locations (e.g., Silverman et al., 2007; Voyer et al., 2007). With respect to verbal abilities, females tend to outperform males in reading comprehension and writing test as well as verbal fluency tests which involve generating as many words as possible that belong to a certain category, that begin with a specific letter, or that are synonym of a familiar word (e.g., Acevedo et al., 2000; Archer, 2019; Reilly et al., 2019; Maylor et al., 2007). Moreover, sex differences in mental rotation, judgment of line orientation, object location memory, reading comprehension, and writing proficiency, have been found across dozens of cultures (e.g., Halpern et al., 2007; Lippa et al., 2010; Silverman et al., 2007; Stoet & Geary, 2013) and emerge in childhood (e.g., Lauer et al., 2015, 2019; Quinn & Liben, 2014; Reilly et al., 2019; Voyer et al., 1995, 2017).

In addition to these sex differences, research has also found male sexual orientation differences in cognitive abilities. A recent meta-analysis comprised of 30 research articles and 244,434 participants from primarily Euro-American cultures assessed male sexual orientation differences in male-favoring spatial-related tasks (e.g., mental rotation and spatial perception and navigation), female-favoring spatial-related tasks (e.g., object location memory), and female-favoring verbal-related tasks (e.g., letter, category, and synonymy fluency) (Xu et al., 2017;

2020). The meta-analysis found that androphilic men scored higher in female-favoring spatial-related tasks (Hedges' g = .38) and lower in male-favoring spatial-related tasks (Hedges' g = .54) than gynephilic men. In contrast, while the scores for female-favoring verbal-related tasks were higher for androphilic compared to gynephilic men (Hedges' g = .36), the differences did not reach statistical significance (p = .057). This research suggests that the visual-spatial and, to a lesser degree, the verbal abilities of androphilic males are shifted in a female-typical direction.

One explanation for the consistency of the sex differences in cognitive abilities, particularly those related to visual-spatial abilities, and why similar differences emerge between androphilic and gynephilic males is provided by the neuroendocrine organizational hypothesis. This hypothesis suggests that exposure to female-typical levels of sex-steroid hormones during critical developmental periods will "feminize" areas of the brain that regulate sexual orientation and its correlated behaviors (including those involved in visual-spatial and verbal cognitive abilities), whereas male-typical hormonal exposure will "masculinize" these same areas (e.g., Balthazart, 2016; Bao & Swaab, 2011; Berenbaum & Beltz, 2011, 2016; Ellis & Ames, 1987; Hines et al., 2015). In this manner, sexual orientation and cognitive abilities are similarly influenced by the effects of prenatal and/or neonatal hormones on the developing brain. Consistent with this hypothesis, genetic males with complete androgen insensitivity syndrome—whose body does not respond to androgens due to a lack of androgen receptors—have decreased visual-spatial abilities and are more likely to be androphilic than males without this condition (e.g., Hamann et al., 2014; Hines et al., 2003; Imperato-McGlnley et al., 1991; Wisniewski et al., 2000). Furthermore, genetic females with congenital adrenal hyperplasia—who are exposed to high levels of testosterone in utero—have elevated (i.e., more male-typical) visual-spatial abilities and are more likely to have non-heterosexual orientations compared to females without this condition (e.g., Berenbaum et al., 2012; Meyer-Bahlburg et al., 2008; Puts et al., 2008). Altogether, this research suggests that the sex and sexual orientation differences in cognitive abilities are partially due to differences in hormone exposure during critical periods of brain development.

While sex differences in cognitive abilities have been observed across multiple cultures, the male sexual orientation differences have mostly been documented in Euro-America (e.g., Canada, Spain, USA, UK) (Xu et al., 2017; 2020). Furthermore, most of this research has focused on androphilic males with masculine gender presentations (i.e., cisgender) whereas only a few studies have looked at the cognitive abilities of androphilic males with feminine gender presentations (i.e., transgender/transexual/gender non-binary). One of these studies found that gynephilic men had higher mental rotation and judgment of line orientation test scores than androphilic male-to female (MtF) transexuals (van Goozen et al., 2002). Similarly, Carrillo et al. (2010) found that gynephilic men had higher mental rotation test scores than androphilic MtF transexuals, although the differences were not statistically significant. With respect verbal abilities, Soleman et al. (2013) found that androphilic MtF transexual adolescents had higher letter fluency scores than cisgender adolescent males and females, whereas no group differences were found for category fluency. Nevertheless, these studies are limited by their low androphilic MtF transexual sample size (all $n \leq 22$).

To our knowledge, only one study has explored whether the female-shifted cognitive abilities observed among cisgender androphilic males in Euro-America also applies to both cisgender and transgender androphilic males outside of Euro-America. This study found that gynephilic men ($n = 210$) from Thailand had significantly higher mental rotation scores than both cisgender ($n = 144$) and transgender androphilic males ($n = 113$), whereas no differences were found between the two androphilic male groups (Thurston et al., 2021). Furthermore, the supplementary material in Thurston et al. (2021) demonstrates that cisgender and transgender androphilic males did not differ significantly in verbal fluency. Thus, the available research suggests that androphilic males' cognitive abilities are shifted in a female-typical pattern regardless of gender presentation. Nevertheless, further cross-cultural research is needed to corroborate this conclusion.

The present study assessed sex and male sexual orientation differences in mental rotation, judgement of line orientation, and object location memory in Samoa and the Istmo region of Oaxaca, Mexico (hereafter the Istmo region), where the indigenous Istmo Zapotec people predominate. We also assessed sex and male sexual orientation differences in verbal fluency in the Istmo region. Conducting the present study in these locations allowed us to address the following three questions: 1) Do the male sexual orientation differences in visual-spatial and verbal abilities that exist in Euro-America cultures also exist in non-Euro-American cultures?; 2) Are the visual-spatial and verbal abilities of transgender androphilic males in Samoa (i.e., *fa'afafine*) and the Istmo region (i.e., *muxe gunaa*) shifted in a female-direction similar to their cisgender counterparts (i.e., gay men) in Euro-America?; 3) Do cisgender (i.e., *muxe nguiiu*) and transgender (i.e., *muxe gunaa*) androphilic males differ with respect to their cognitive abilities?

Given previous literature, we predicted that in Samoa and the Istmo region, gynephilic males will score higher than androphilic males (both cisgender and transgender) and females in tests of mental rotation and judgement of line orientation, whereas androphilic males and females will score higher than gynephilic males in tests of object location memory and verbal fluency. Furthermore, given that Thurston et al. (2021) did not find any significant differences in visual-spatial and verbal abilities scores between cisgender and transgender androphilic males, we predicted that *muxe nguiiu* and *muxe gunaa* will have similar scores in all tests.

Method

Participants

A total of 120 men, 100 women, 78 *muxe nguiiu*, and 82 *muxe gunaa* from the Istmo region and 109 men, 102 women, and 100 *fa'afafine* from Samoa were recruited to participate in the study. Participants' sexual orientation was assessed using a 7-point Kinsey scale (Kinsey et al., 1948), which asked about sexual feelings over the previous year. In the Istmo region, 15 men, 92 women, 68 *muxe nguiiu*, and 81 *muxe gunaa* identified as exclusively androphilic (Kinsey 6), 5 men, 7 women, 9 *muxe nguiiu*, and 1 *muxe gunaa* identified as predominantly androphilic (Kinsey 5), 5 men and 1 *muxe nguiiu* identified as ambiphilic (i.e., sexually attracted to both men and women; Kinsey 2-4), 4 men and 1 woman identified as predominantly gynephilic (Kinsey 1), and 91 men identified as exclusively gynephilic (Kinsey 0). In Samoa, 3 men, 101 women, and 96 *fa'afafine* identified as exclusively androphilic, 3 men, 1 woman, and 3 *fa'afafine* identified as predominantly androphilic, 6 men and 1 *fa'afafine* identified as ambiphilic, and 98 men identified as exclusively gynephilic. Given the limited numbers of cases, ambiphilic males and (cisgender) androphilic men from the Istmo region and Samoa were excluded from the study. Thus, the final sample size consisted of 95 gynephilic men, 77 *muxe nguiiu*, 82 *muxe gunaa*, and 99 androphilic women from the Istmo region, and 97 gynephilic men, 99 *fa'afafine*, and 102 androphilic women from Samoa.

Procedure

Data were collected from Istmo Zapotec participants from November 2018 to March 2019 in the city of Juchitán de Zaragoza, as well as other towns and villages within the Juchitán and Tehuantepec districts of the Istmo region of Oaxaca, and from Samoan participants in October to December 2018 in Upolu. All procedures utilized in the study were approved by the Human Subject Research Committee at the University of Lethbridge. Canadian foreign nationals, and USA Citizens, are permitted to conduct research in Mexico for a period of 180 days if they have a valid passport (Consulado General de México en Toronto, 2022). In addition, a letter endorsing our research was obtained from the Office of the Municipal President in Juchitán, Mexico. Samoan data were collected under a research visa obtained from the Samoan Immigration Office, with the support of the Samoan *Fa'afafine* Association.

All participants were recruited using a network sampling procedure that consisted of contacting initial participants, who gave referrals for additional participants, who in turn provided further referrals, and so on. Participants were required to provide informed written consent prior to taking part in the study and received an honorarium of 20 Tala in Samoa and 150 Pesos in Mexico. In Samoa and the Istmo region, participants were interviewed using standardized questionnaires. In Samoa, questionnaires were available in English or Samoan after being translated and back-translated by fluent Samoan-English speakers. The last author, as well as Samoan-speaking research assistants, were available to answer participants' questions. In the Istmo region, questionnaires were available in Spanish after being translated and back-translated by fluent Spanish-English speakers. The first author, as well as Spanish-speaking research assistants, were available to answer participants' questions.

Measures

Participants were asked to report information regarding their age (in years), level of education, and level of income. Level of education was reported by stating the highest level of education achieved (1 = "None," 2 = "Primary school," 3 = "Junior high school," 4 = "High school or college," 5 = "Post-secondary school," 6 = "Graduate school"). Level of income was based on an average weekly income scale that ranged from 1 (0–250 Mexican Pesos) to 9 (more than 2000 Mexican Pesos) in the Istmo region, and from 1 (0-100 Tala) to 9 (more than 1000 Tala) in Samoa.

Judgment of line orientation was assessed using a shortened version of the Benton Judgement of Line Orientation test (Benton et al., 1983) which consisted of 15 items. For each item, participants had to judge which lines from an array of numbered lines were in the same spatial orientation as two fragment lines in the space above. Participants were given 1 point if they correctly assessed the spatial orientation of the two fragment lines and 0 points for any other response. Thus, the maximum score that participants could achieve was 15 points. Before conducting the test, participants had to complete 5 practice items so that they could familiarize themselves with the test.

Mental rotation abilities were assessed by using a 20-item Mental Rotation Task (Vandenberg & Kuse, 1978), adapted from the same test described by Shepard & Metzler (1971). For this test, participants had to look at a line drawing of a three-dimensional cuboid model made up of 10 cubes and decide which two of four other models displayed below it corresponded to the target model. Participants were made aware that two of the four models were the same as the target model, but oriented differently, whereas the remaining two other models were completely different from the target model. Participants were given two points if they selected both correct choices, one point if they only selected one of the two correct choices, and 0 points if the selected both incorrect choices. Thus, the maximum score that participants could achieve was 40 points. Before conducting the test, participants had to complete 3 practice items so that they could familiarize themselves with the task. Participants were given 10 minutes to complete the test, after which, they were not allowed to continue. The total run time was recorded to control for this variable when conducting group comparisons.

Participants' object location memory was assessed with the Object Array Task (Levy et al., 2005), which is a paper-and-pencil task consisting of a stimulus array of 31 black and white drawings of familiar objects arranged randomly. Participants were asked to look and study the stimulus array for one minute. Following this, the original stimulus array was removed, and participants had to conduct two recall tasks with different conditions. The first task consisted of an *object exchange* condition in which the position of seven pairs of objects were exchanged. The exchanged objects were either adjacent to each other or on opposite sides of the stimulus array. Participants had one minute to circle with a pen all objects that exchanged positions. The second task consisted of a *novel object* condition in which 14 objects were replaced with new objects. Participants had one minute to circle with a pen all novel objects. For both tasks, the number of correctly and wrongly circled objects were counted. Participants scores consisted of number of correctly circled objects minus the number of wrongly circled objects. Thus, the highest and lowest score that participants could achieve was 14 and -17, respectively.

Finally, verbal fluency was assessed among participants from the Istmo region using tests that measure category (Acevedo et al., 2000; Benton & Hamsher, 1978), letter (Benton & Hamsher, 1978), and synonym fluency (Hines, 1990). For each test, participants were given 60 seconds to generate as many words as possible that belong to a certain category (category fluency), begin with a specific letter (letter fluency), or are synonyms of a familiar Spanish word (synonym fluency). The categories used to assess category fluency were *Animals* and *Fruits & Vegetables* (60 seconds per category) and the score was the sum of all acceptable words generated from both categories excluding proper nouns and repetitions. The test letters used to assess letter fluency were *T* and *A* (60 seconds per letter) and the score was the sum of all correctly generated words starting with both letters excluding proper nouns and repetitions. The familiar words that were used to assess synonym fluency were *Andar* and *Hablar*, which are Spanish for *Walk* and *Talk* (60 seconds per word), and the score was the sum of all acceptable words excluding nonsynonyms or word associations and repetitions. Two fluent Spanish speakers rated the responses for each test and consulted a thesaurus and/or dictionary when in doubt.

Statistical Analyses

Statistical analyses were conducted using jamovi, version 2.3 (The jamovi project, 2022). Data transformations were used for various variables to correct for skewness. For the Istmo region data, age, mental rotation run times and scores, and object location memory scores in the novel object condition were transformed using a log transformation, and judgment of line orientation scores, object location memory scores in the object exchange condition, and letter fluency scores were transformed using a square root transformation. For the Samoan data, age and mental rotation run times were transformed using log transformation, level of education and object location memory scores in the novel object condition were transformed using square root transformation, and judgement of line orientation scores were transformed using a reciprocal transformation. The transformed variables were used for all statistical analyses. Pearson's *r* and Kendall's tau-B[4] correlation analyses were first conducted to assess whether age, level of education, and level of income, were associated with cognitive test performances. Pearson's *r* correlation analyses were also used to assess the association between mental rotation scores and

[4] Kendall's tau-B correlations analyses were only used to assess correlations between level of income and cognitive test performances in Samoa given that data transformation could not correct for significant skewness in level of income.

the test run times. Given significant correlations, covariates were used when assessing group differences in some cognitive test performances.

Assessing cognitive tests performances in the Istmo region

In the Istmo region, group differences in age, level of education, level of income, judgement of line orientation, and mental rotation test run times were assessed using one-way ANOVA. Since groups show unequal variances for level of education and level of income using Levene's tests (both $p < .001$), the F statistics for both variables were reported using Welch tests. To determine the direction of significant omnibus tests, post-hoc pairwise comparisons were conducted using the Tukey procedure for age and judgment of line orientation, and the Games-Howell procedure for level of education and level of income given the unequal variances. Cohen's d effect sizes were also calculated as $\frac{M_1 - M_2}{\sqrt{\frac{(n_1 - 1)SD_1^2 + (n_2 - 1)SD_2^2}{n_1 + n_2 - 2}}}$ and presented with their 95% confidence intervals to assess the strength of group differences.

Group differences in mental rotation scores, object exchange scores in both the object exchange and novel object conditions, and category, letter, and synonym fluency scores were assessed using analyses of covariance (ANCOVA) to control for the influences of covariates. For mental rotation scores, participants' age, level of education, and test run times were used as covariates. For object location scores in the object exchange condition and the category and synonym fluency scores, participant's level of education was used as a covariate. For object location scores in the novel object condition, participants' age, level of education, and level of income were used as covariates. Finally, for letter fluency scores, participant's level of education and level of income were used as covariates. To determine the size and direction of significant omnibus tests, all pairwise comparisons were conducted using the Tukey procedure. Cohen's d

effect sizes and their 95% confidence intervals were also calculated for all pairwise comparisons using estimated marginal means.

Assessing cognitive tests performances in Samoa

In Samoa, group differences in level of income were assessed using a Kruskal-Wallis *H* test due to significant skewness. With respect to age, level of education, and mental rotation scores and test run times, group differences were assessed using one-way ANOVAs. With respect to judgment of line orientation scores, and object location memory scores in both object exchange and novel object conditions, group differences were assessed using one-way ANCOVAs to control for the effects of level of education. To determine the direction of significant omnibus tests, all pairwise comparisons were conducted using the Tukey procedure, and Cohen's *d* effect sizes and their 95% confidence intervals were calculated as outlined above to assess the strength of group differences. Estimated marginal means were used to calculate Cohen's *d* effect sizes and their 95% confidence intervals when covariates were used in the omnibus test.

Results

Cognitive tests performance in the Istmo region

Descriptive statistics for Istmo Zapotec gynephilic men, *muxe nguiiu*, *muxe gunaa*, and androphilic women are reported in Table 4.1. Significant group differences were found for age, $F(3, 349) = 5.51$, $p = .001$, level of education, $F(3, 184.72) = 13.01$, $p < .001$, and level of income, $F(3, 189.31) = 5.50$, $p = .001$. Gynephilic men were significantly younger than *muxe gunaa* ($p = .002$) and androphilic women ($p = .006$), *muxe gunaa* had significantly lower levels of education than gynephilic men, *muxe nguiiu*, and androphilic women (all $p < .001$), and androphilic women had lower levels of income than *muxe nguiiu* ($p = .003$) and *muxe gunaa* ($p =$

.020). Pearson's *r* correlations between the biographic variables and the cognitive test performances among Istmo Zapotec participants are reported in Table 4.2. Age was negatively correlated with mental rotation scores and object location memory scores in the novel object condition. Level of education was positively correlated with mental rotation scores, object location memory scores from both the object exchange and novel object conditions, and the category, letter, synonym fluency scores. Level of income was positively correlated with object location memory score in the novel object condition and letter fluency. Thus, age, level of education, and level of income were used as covariates when conducting group comparisons for their respective correlated variables. Furthermore, participants' mental rotation test run time was significantly correlated with their mental rotation test scores, $N = 347$, $r = .356$, $p < .001$. Thus, mental rotation run time was also used as a covariate when conducting group differences in mental rotation scores.

Group comparisons for the visual-spatial ability tests revealed that there were significant group differences for judgment of line orientation scores, $F(3, 348) = 8.69$, $p < .001$, mental rotation test run time, $F(3, 343) = 8.69$, $p < .001$, and mental rotation scores, $F(3, 340) = 3.64$, $p = .013$ (covariates: age, level of education, and mental rotation run time). For judgment of line orientation scores, androphilic women scores significantly lower than gynephilic men ($p = .022$, $d = .41$ [.13, .70]), *muxe nguiiu* ($p < .001$, $d = .63$ [.33, .94]), and *muxe gunaa* ($p < .001$, $d = .67$ [.38, .97]). No significant differences in judgement of line orientation scores were found between gynephilic men and *muxe nguiiu* ($p = .480$, $d = .22$ [-.08, .52]), gynephilic men and *muxe gunaa* ($p = .316$, $d = .26$ [-.04, .56]), nor between the two types of *muxes* ($p = .995$, $d = .04$ [-.27, .35]).

Table 4.1

Descriptive statistics for biographic information and cognitive test scores by group among Istmo Zapotec participants

	Gynephilic Men (n = 95)		*Muxe Nguiiu* (n = 77)		*Muxe Gunaa* (n = 82)		Androphilic Women (n = 99)	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Age (in years)	26.52	7.46	28.69	7.63	30.74	8.12	30.41	9.1
Level of education	4.07	3.70	4.13	3.47	3.27	2.73	3.88	2.96
Level of income	6.04	0.64	7.13	0.82	6.83	1.10	5.42	0.92
Judgment of line orientation score[a]	9.54	2.83	10.14	2.95	10.32	2.68	8.19	3.40
Mental rotation test run time (in seconds)[b]	351.56	161.77	324.95	154.44	240.79	117.46	298.37	144.76
Mental rotation score[b]	21.79	4.92	20.75	3.39	19.09	2.80	19.40	3.14
Object location memory score								
Object exchange condition[c]	7.47	3.00	7.38	3.10	6.40	3.29	8.22	2.78
Novel object condition	11.81	1.91	11.73	1.88	10.91	2.51	11.82	1.76
Category fluency score[d]	37.65	7.74	39.24	8.71	34.70	7.96	39.09	9.24
Letter fluency score[e]	22.63	7.35	23.00	8.12	19.48	8.29	22.35	8.65
Synonym fluency score[e]	8.49	2.32	8.87	3.05	7.11	2.63	7.79	2.73

Abbreviations: *M* = means; *SD* = standard deviation.

[a] Androphilic women: n = 98

[b] Gynephilic men: n = 94; *muxe nguiiu*: n = 76; androphilic women: n = 95

[c] *Muxe gunaa*: n = 81

[d] Gynephilic men: n = 93; *muxe nguiiu*: n = 76; androphilic women: n = 98

[e] Gynephilic men: n = 94; *muxe nguiiu*: n = 76; androphilic women: n = 98

Table 4.2

Pearson's r correlations between cognitive tests scores and age, level of education, and level of income among Istmo Zapotec participants

Cognitive tests scores		Biographic variables					
		Age		Level of education		Level of income	
	N	Pearson's *r*	*p*-value	Pearson's *r*	*p*-value	Pearson's *r*	*p*-value
Judgment of line orientation score	352	-.011	.833	.093	.080	.087	.102
Mental rotation score	347	-.129	**.016**	.172	**.001**	-.039	.473
Object location memory score							
Object exchange condition	352	-.005	.924	.127	**.017**	-.079	-.140
Novel object condition	353	-.131	**.014**	.172	**.001**	-.131	**.014**
Category fluency score	349	.026	.632	.320	**< .001**	-.019	.719
Letter fluency score	350	.078	.145	.360	**< .001**	.116	**.031**
Synonym fluency score	350	.006	.909	.230	**< .001**	.020	.714

Bold numbers represent *p*-values below .05.

With respect to mental rotation test run times, *muxe gunaa* had shorter run times than gynephilic men ($p < .001$, $d = .74$ [.43, 1.04]), *muxe nguiiu* ($p = .003$, $d = .56$ [.24, .88]), and androphilic women ($p = .049$, $d = .39$ [.09, .69]). No significant differences in mental rotation test run times were found between gynephilic men and *muxe nguiiu* ($p = .670$, $d = .17$ [-.13, .47]), gynephilic men and androphilic women ($p = .085$, $d = .34$ [.06, .63]), nor between *muxe nguiiu* and androphilic women ($p = .687$, $d = .17$ [-.13, .47]). Finally, for mental rotation scores, gynephilic men had significantly higher scores than androphilic women ($p = .010$, $d = .47$ [.17, .76]). No significant differences in mental rotation scores were found between gynephilic men and *muxe nguiiu* ($p = .751$, $d = .15$ [-.15, .46]), gynephilic men and *muxe gunaa* ($p = .137$, $d = .36$ [.03, .68]), androphilic women and *muxe nguiiu* ($p = .185$, $d = .31$ [.01, .62]), androphilic women and *muxe gunaa* ($p = .895$, $d = .11$ [-.20, .42]), and the two types of *muxes* ($p = .637$, $d = .20$ [-.13, .54]).

Group comparisons for the object location memory tests revealed significant group differences for object location memory scores in the object exchange condition, $F(3, 347) = 3.84$, $p = .010$ (covariate: level of education), but not in novel object condition $F(3, 346) = 1.71$, $p = .165$ (covariates: age, level of education, and level of income). Within the object exchange condition, androphilic women had significantly higher object location memory scores than *muxe gunaa* ($p = .005$, $d = .51$ [.21, .82]). No significant group differences in object location memory scores were found between gynephilic men and *muxe nguiiu*, ($p = .998$, $d = .03$ [-.33, .28]), gynephilic men and *muxe gunaa* ($p = .391$, $d = .25$ [-.06, .56]), gynephilic men and androphilic women ($p = .263$, $d = .26$ [-.02, .55]), *muxe nguiiu* and *muxe gunaa* ($p = .536$, $d = .22$ [-.11, .55]), and *muxe nguiiu* and androphilic women ($p = .232$, $d = .29$ [-.01, .59]).

Group comparisons for the verbal fluency test revealed significant group differences in synonym fluency scores, $F(3, 345) = 3.73$, $p = .012$ (covariate: level of education), but not for category fluency, $F(3, 344) = 2.01$, $p = .112$ (covariate: level of education), and letter fluency, $F(3, 344) = .68$, $p = .564$ (covariates: level of education and level of income). *Muxe nguiiu* had significantly higher synonym fluency scores than *muxe gunaa* ($p = .016$, $d = .50$ [.17, .83]). No significant differences in synonym fluency scores were found between gynephilic men and *muxe nguiiu*, ($p = .826$, $d = .13$ [-.17, .44]), gynephilic men and *muxe gunaa* ($p = .096$, $d = .37$ [.05, .68]), gynephilic men and androphilic women ($p = .392$, $d = .23$ [-.06, .51]), *muxe nguiiu* and androphilic women ($p = .089$, $d = .36$ [.06, .66]), and *muxe gunaa* and androphilic women ($p = .802$, $d = .14$ [-.16, .44]).

Cognitive tests performance in Samoa

Descriptive statistics for Samoan gynephilic men, *fa'afafine*, and androphilic women are reported in Table 4.3. Significant group differences were found for level of education, $F(2, 295) = 6.97$, $p = .001$, but not for age, $F(2, 295) = 2.72$, $p = .068$, or level of income, $H(2) = 1.39$, $p = .498$. Gynephilic men had significantly lower levels of education than *fa'afafine* ($p < .001$, $d = .53$ [.24, .81]), and androphilic women ($p = .049$, $d = .33$ [.05, .62]). Pearson's r and Kendall's tau-B correlations between the biographic variables and the cognitive test performances among Samoan participants are reported in Table 4.4. Age was negatively correlated with object location memory scores in the novel object condition, and level of income was positively correlated with judgment of line orientation scores and both object location memory scores. Nevertheless, age and level of income were not used as covariates when conducting group comparisons for the cognitive test performances given that they did not differ between groups and because the direction and significance of the results did not change when they were used as

Table 4.3

Descriptive statistics for biographic information and cognitive test scores by group among Samoan participants.

	Gynephilic Men (n = 97)		*Fa'afafine* (n = 99)		Androphilic Women (n = 102)	
	M	*SD*	*M*	*SD*	*M*	*SD*
Age (in years)	34.87	10.01	32.13	10.48	34.59	9.90
Level of education	4.03	0.81	4.41	0.76	4.29	0.64
Judgment of line orientation score	10.55	3.19	9.29	3.59	8.10	3.72
Mental rotation test run time (in seconds)	214.89	99.66	192.38	90.51	192.58	87.39
Mental rotation score	18.70	2.56	19.09	3.04	18.60	2.30
Object location memory score						
Object exchange condition	3.60	2.98	4.65	3.46	4.58	3.00
Novel object condition	7.15	3.28	8.62	3.03	8.25	3.49
	Mdn	*IQR*	*Mdn*	*IQR*	*Mdn*	*IQR*
Level of income	1.00	2.00	1.00	2.00	1.00	2.00

Abbreviations: *M* = means; *SD* = standard deviation; *Mdn* = median; *IQR* = interquartile range.

Table 4.4

Pearson's r and Kendall's tau-B correlations between cognitive tests scores and age, level of education, and level of income among Samoan participants

Cognitive tests scores		Biographic variables					
		Age		Level of education		Level of income	
	N	Pearson's *r*	*p*-value	Pearson's *r*	*p*-value	Kendall's tau-b	*p*-value
Judgment of line orientation score	298	-.096	.099	.255	**<.001**	.138	**.002**
Mental rotation score	298	-.073	.209	.068	.240	.015	.748
Object location memory score							
Object exchange condition	298	-.015	.796	.276	**<.001**	.139	**.002**
Novel object condition	298	-.156	**.007**	.423	**<.001**	.212	**<.001**

Bold numbers represent *p*-values below .05.

covariates. Level of education was positively correlated with judgment of line orientation scores and object location memory scores from both the object exchange and novel object conditions. Therefore, level of education was used as a covariate when comparing groups for judgement of line orientation scores and for both object location memory scores. Contrary to the Istmo Zapotec data, participants' mental rotation test run time in Samoa was not correlated with their mental rotation score, $N = 298$, $r = .10$, $p = .078$. Thus, mental rotation test run time was not used as a covariate when conducting group comparisons in mental rotation scores.

Group comparison for the cognitive tests performances revealed that there were significant group differences for judgment of line orientation scores, $F(2, 294) = 18.03$, $p < .001$ (covariate: level of education), but not for mental rotation test run times, $F(2, 295) = 2.17$, $p = .116$, mental rotation scores, $F(2, 295) = .96$, $p = .383$, or the object location memory scores in the object exchange condition, $F(2, 294) = 1.54$, $p = .217$ (covariate: level of education) and novel object condition $F(2, 294) = 1.91$, $p = .150$ (covariate: level of education). Gynephilic men had significantly higher judgement of line orientation scores than *fa'afafine* ($p < .001$, $d = .57$ [.28, .86]) and androphilic women ($p < .001$, $d = .85$ [.56, 1.14]), whereas *fa'afafine* and androphilic women did not differ from each other ($p = .119$, $d = .28$ [.00, .56]).

Discussion

The present study examined whether sex and male sexual orientation differences in cognitive abilities exist among gynephilic men, androphilic women, and androphilic males in Samoa and the Istmo region. The study also assessed whether there were differences in cognitive abilities between androphilic male sub-types (i.e., cisgender and transgender) in the Istmo region. Consistent with our predictions and previous studies, sex differences in visual-spatial abilities were found in the Istmo region and Samoa. Specifically, gynephilic men outperform women in tests of judgement of line orientation in both the Istmo region and Samoa, and in tests of mental rotation in the Istmo region. While it is unclear why no sex differences were found in mental rotation abilities in Samoa, it is worthwhile noting that the averages and standard deviations for mental rotation test run times for all groups in Samoa (see Table 4.3) were lower than those of all groups in the Istmo region (see Table 4.1) regardless of sex and sexual orientation. Thus, it is possible that the average participant in Samoa was not as focused or interested in excelling in the test relative to those in the Istmo region. This could also explain why the average mental rotation score in Samoa (M = 18.80, SD = 2.65, N = 298) was lower than the average score in the Istmo region (M = 20.27, SD = 3.84, N = 347).

Inconsistently with our predictions, no sex differences in female-favoring spatial (i.e., object location memory) and verbal abilities (i.e., verbal fluency) were found in Samoa, nor in the Istmo region. It is possible that the present study was not sufficiently powered to detect small sex differences in these cognitive abilities. For example, with a sample size of 109,612 men and 88,509 women, Maylor al. (2007) found a significant sex difference of d = .25 (converted from η^2 = .015) for object location memory and significant sex differences of d = .14 (converted from η^2 = .005) and d = .13 (converted from η^2 = .004) for category and synonym fluency, respectively. Based on these effect sizes, a total of 199 participants per group would be required to have sufficient power to detect significant sex differences in object location memory, and 632-733 per group to detect significant differences in verbal fluency (category and synonym fluency respectively).[5] Thus, it is possible that the predicted sex differences might emerge if the present study had a greater number of gynephilic men and androphilic women.

[5]A priori power analyses were conducted using G*Power 3.1.9.6 (see Faul et al., 2007) with statistical power set at the recommended .80 level (Cohen, 1988) and alpha set to .05.

With respect to male sexual orientation, Samoan gynephilic men outperform *fa'afafine* in tests of judgement of line orientation. This finding is consistent with our prediction and suggests that male sexual orientation differences in visual-spatial abilities are not limited Euro-American cultures. Inconsistent with our predictions, however, no male sexual orientation differences in judgement of line orientation were found in the Istmo region. Moreover, while a trend in the differences in mental rotation scores between gynephilic men and *muxe gunaa* was observed (d = .36 [.03, .68]), this difference was not statistically significant (p = .137). A power analysis demonstrates that 97 participants per group would be required to detect a significant group difference of this size.[5] Thus, it is possible that this null finding is a result of a Type 2 error due to our relatively lower sample size of *muxe gunaa* (n = 82). With respect to the female-favoring cognitive abilities, however, no male sexual orientation differences were found for verbal fluency in the Istmo region nor in object location memory in Samoa and Istmo region.

The results highlighted thus far suggest that the sex and male sexual orientation differences in male-favoring visual-spatial abilities are somewhat more consistent and reliable than those for female-favoring visual-spatial and verbal abilities. This speculation is consistent with meta-analyses which find medium to large sex differences in mental rotation (d = .66) and line angle judgement (d = .49) favoring males, and small sex differences in object location memory (d = .31) and overall verbal abilities (d = .27) favoring females (reviewed in Archer, 2019). It is also consistent with results from Xu's et al. (2020) meta-analysis which found that the male sexual orientation differences in male-favoring spatial-related tasks (Hedges' g = .54) are larger than those for female-favoring spatial-related (Hedges' g = .38) and verbal-related tasks (Hedges' g = .36).

With respect to androphilic male type differences in the Istmo region, the present study only found one significant difference. Namely, *muxe nguiiu* had greater synonym fluency than *muxe gunaa*. Previous qualitative research in the Istmo region has found that masculine-presenting *muxes* are more likely to have wage-labor jobs which are characterized by structured labor under formal contracts (e.g., lawyer, teacher, salesperson) whereas feminine-presenting *muxes* are more likely to be self-employed (e.g., embroiders, event decorator, hairstylist) (Céspedes Vargas, 2015). Thus, it is possible that, due to these occupational differences, *muxe nguiiu* are trained to have more expansive vocabulary than *muxe gunaa*, which would explain why they demonstrate greater synonym fluency. Future research could explore this possibility by collecting data on, and controlling for, occupational history when assessing group differences in verbal fluency.

Overall, the sex and male sexual orientation differences in visual-spatial abilities found in the present study provide some, albeit limited, support for the neuroendocrine organizational hypothesis—that is, female-/male-typical hormonal exposure during critical periods of development leads to female-/male-typical sexual orientations and cognitive abilities. Nevertheless, the abundance of null results in our group comparisons warrants alternate etiological explanations. One of these explanations is provided by social role theory, which suggest that psychological sex differences are due to differences in socialization and gender-role enforcement between males and females (e.g., Eagly & Wood, 1999, 2011). For example, it is possible that boys are socialized to play more sports and video games, which have been shown to improve spatial performance regardless of sex (e.g., Uttal et al., 2013). At the same time, developmental research demonstrates that the sex differences in visual-spatial abilities (e.g., mental rotation) emerge in early infancy (Quin & Liben, 2014). With respect to verbal abilities, Kung et al. (2016) showed that boys' higher levels of testosterone at 1-3 months of age mediated their lower expressive vocabulary size at 18-30 months of age relative to girls of the same age. Thus, while it is possible that socialization factors can modify the size of the sex differences in visual-spatial and verbal abilities, the cross-cultural consistency and the early life onset of these differences suggest that biological factors likely play a role.

Perhaps a better explanation for the lack of sex and male sexual orientation differences in the present study is provided by the condition-dependant trait expression model proposed by Geary (2021). This model suggests that sexually differentiated traits that confer competitive advantages, such as height or visual-spatial abilities, are costly to produce and maintain and are, therefore, susceptible to environmental stressors. Consequently, any biologically influenced sex differences in cognitive abilities would only be observed under optimal environmental conditions. Consistent with this model, one longitudinal study found that boys prenatally exposed to polychlorinated biphenyls (PCB)—a highly toxic contaminant—scored significantly lower than control boys in tests of spatial reasoning (Guo et al., 1995). In contrast, girls prenatally exposed to PCB did not significantly differ from control girls. Furthermore, cross-cultural research demonstrates that men's advantages in visuo-spatial abilities and women's advantages in verbal episodic memory are greater in cultures with optimal social and economic conditions such as greater gender equity, life expectancy, and per capita income (Asperholm et al., 2019; Lippa et al., 2010).

Thus, it is possible that gynephilic men and androphilic women in the present study did not show the predicted cognitive advantages because their local environments were not characterized by the optimal conditions in which their cognitive potential could fully develop. Indeed, both Samoa and the state of Oaxaca are characterized as low-income locations with limited financial resources. For example, Samoa's gross domestic product is ranked 203rd out of 228 countries (Central Intelligence Agency, 2022b). Similarly, the state of Oaxaca has one of the largest poverty rates in Mexico, with 61.7% of the population living in conditions of poverty and 20.6% living in conditions of extreme poverty (Consejo Nacional de Evaluación de la Política de Desarrollo Social, 2022).

This rationale could also be used to explain why no male sexual orientation differences were observed in any of our cognitive measures in the Istmo region, and the mental rotation and object location memory tasks in Samoa. That is, androphilic males in these locations might not have demonstrated the predicted elevated spatial memory and verbal abilities because they were exposed to suboptimal environmental conditions (e.g., poverty, malnourishment, or limited educational resources) that hindered the development of these abilities. Moreover, these stressors might have had more noticeable effects in the expression of elevated spatial memory and verbal abilities among androphilic males and females in the present study because, as mentioned earlier, the group differences for these cognitive abilities tend to be smaller than those for the male-favoring visual-spatial abilities. Furthermore, relative to cisgender *muxe nguiiu*, transgender *muxe gunaa* tend to come from bigger families with lower socioeconomic status, which increases the chances of malnutrition (e.g., see Chapter 6; Miano Borruso, 2001; Mirandé, 2017). It is possible, then, that the transgender androphilic males from our Istmo Zapotec sample experienced greater social stressors and chronic malnutrition during development than all other groups. This could explain why they had the lowest score averages in those tests in which they were predicted to show an advantage (i.e., object location memory and verbal fluency) (see Table 4.1), and why their synonym fluency was significantly lower than those of cisgender androphilic males. Future research should further explore the extent to which socio-economic factors can influence sex and sexual orientation differences in cognitive abilities.

Limitations

The present study had several noteworthy limitations. First, as stated in the Discussion, some of our group sample sizes might not have been large enough to detect small differences in cognitive abilities. Second, some of the figures in the object location memory tasks (e.g., snowflake, snowman, rectangular-dome shaped mailbox) might not have been immediately recognizable to participants in Samoa and the Istmo region, particularly to those who have limited access to television and the internet, which could decrease their ability to memorize/recall the object during the task. It is worth pointing out, however, that Silverman et al. (2007) found sex difference in object location memory in 35 out of 40 countries which included both Euro-American and non-Euro-American cultures.

Finally, the standardized pen-and-paper method of assessing cognitive abilities utilized in the present study could have limited the participants ability to demonstrate their full cognitive capabilities, which could have reduced the size of our group differences. As stated earlier, Samoa and the Istmo region are characterized by having low financial resources (Central Intelligence Agency, 2022b; Consejo Nacional de Evaluación de la Política de Desarrollo Social, 2022), which limits the resources available to invest in education, and, consequently, participants' familiarity with standardized, paper-based tasks developed in Euro-America. Future research could circumvent this limitation by evaluating cognitive abilities using real-world, hands-on tasks. For example, instead of assessing visual-spatial abilities using the paper-based tasks utilized here, future studies could use the Brick Building Task, which also shows sex differences, and consists of duplicating brick models from an assortment of Lego® bricks (Aguilar et al., 2020).

Conclusion

The present study provides further cross-cultural evidence confirming the existence of sex differences in visual-spatial abilities. Specifically, gynephilic men outperform androphilic women in a judgement of line orientation task in Samoa, and in judgement of line orientation and mental rotation tasks in the Istmo region of Oaxaca, Mexico. Furthermore, we also replicated the male sexual orientation differences in visual-spatial abilities in a novel, non-Euro-American culture by demonstrating that Samoan gynephilic men outperform *fa'afafine* in the judgement of line orientation task. Nevertheless, unlike previous studies from Euro-American cultures, we did not find any evidence of sex and male sexual orientation differences in object location memory nor verbal fluency in Samoa or the Istmo region. Overall, the cross-cultural evidence accrued from the present study and the literature in general suggest that the sex and, to a lesser extent, male sexual orientation differences in visual-spatial abilities could have a similar biological etiology, as indicated by the neurohormonal organization hypothesis. In contrast, the cross-cultural inconsistencies in the sex and male sexual orientation differences in object location memory and verbal fluency suggest that these cognitive abilities could be more socially malleable.

Chapter 5: Kin-directed Altruism and the Evolution of Male Androphilia Among Istmo Zapotec *Muxes*

Abstract

Male androphilia is considered an evolutionary puzzle because it reduces direct reproduction, but is influenced by genetic factors, reliably occurs across cultures, and has persisted over evolutionary time. The kin selection hypothesis states that genes for male androphilia can be maintained in a population if the costs of not reproducing directly are offset by enhancing the reproduction of kin. We tested this hypothesis among the Istmo Zapotec of Oaxaca, Mexico, where transgender and cisgender androphilic males are known as *muxe gunaa* and *muxe nguiiu*, respectively. We compared altruistic tendencies towards kin and non-kin children between *muxe nguiiu* (n = 106), *muxe gunaa* (n = 106), gynephilic men (n = 172), and androphilic women (n = 130). We also assessed whether the sisters of *muxes* (n = 96) reported receiving more childcare support from their *muxe* sibling compared to women with only gynephilic brothers (n = 65). The results showed that cisgender and transgender *muxes* reported more kin-directed altruistic tendencies than men. *Muxe nguiiu* also reported more kin-directed altruistic tendencies than women. When controlling for altruistic tendencies towards non-kin children, both *muxe* types exhibited more kin-directed altruistic tendencies than men and women. Women with *muxe* siblings reported receiving more childcare support from these relatives compared to women with only gynephilic brothers. These findings provide support for the kin selection hypothesis and highlight its potential role in elucidating the evolutionary paradox of male androphilia.

Keywords: kin altruism; male androphilia; Istmo Zapotec; *muxes*; transgender

Introduction

The existence of male androphilia has been described as one of the outstanding paradoxes in evolutionary biology (Bailey & Zuk, 2009). This trait is influenced by genetic factors (e.g., Alanko et al., 2010; Gómez et al., 2018; Gómez-Gil et al., 2010; Hamer, 2002; Långström et al., 2010; Sanders et al., 2015; Schwartz et al., 2010; Semenyna, VanderLaan, et al., 2017; VanderLaan, Forrester, et al., 2013), reliably occurs across human cultures (e.g., Hames et al., 2017), and has persisted over evolutionary time (e.g., Larco Hoyle, 1998; Nash, 2001), yet it has deleterious effect on reproduction (e.g., Coome et al., 2020; Ganna et al., 2019; Schwartz et al., 2010; Vasey et al., 2014). If reproduction is the engine that drives evolution, how have genes for male androphilia endured the selective pressure of sexual selection (Darwin, 1871) and avoided becoming extinct?

One of the hypotheses that has been proposed as a solution to the evolutionary paradox of male androphilia, regardless of the form it takes, 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 offsets 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 immediate descent) weighted by the degree of relatedness (Hamilton, 1963). Theoretically speaking, androphilic males could increase their indirect fitness by channeling altruistic behavior towards kin, which, in turn, would facilitate survival and increased reproductive success by those kin. As such, one prediction of the kin selection hypothesis is that androphilic males should be more willing to behave altruistically towards their close relatives (e.g., nieces and nephews) when compared to gynephilic males. However, research conducted on cisgender androphilic males in Euro-American (i.e., USA: Bobrow & Bailey, 2001; Canada: Abild et al., 2014;

Forrester et al., 2011; UK: Rahman & Hull, 2005; Spain and Italy: Camperio Ciani et al., 2016) and non-Euro-American (Japan: Vasey & VanderLaan, 2012) industrialized cultures has not found evidence of a significant difference between androphilic and gynephilic males' willingness to engage in kin-directed altruism.

In contrast, a program of research conducted on transgender male androphiles in Samoa has repeatedly found support for the kin selection hypothesis. This research demonstrates that transgender androphilic males, known locally as *fa'afafine*, report being more willing to invest time and resources towards their nieces and nephews when compared to gynephilic males and androphilic women (VanderLaan, Petterson, & Vasey, 2017; VanderLaan & Vasey, 2012; Vasey & VanderLaan, 2009, 2010a, 2010b). These tendencies appear to manifest as actual behavior given that *fa'afafine* report investing more money towards their nieces when compared to Samoan men and women (Vasey & VanderLaan, 2010c).

Several studies have tested more refined predictions derived from the kin selection hypothesis to assess whether the cognition of *fa'afafine* shows evidence of having been shaped by kin selection. These studies have produced various findings consistent with the conclusion that *fa'afafine's* cognition exhibits hallmarks of adaptive design. First, while Samoan men and women tend to be less willing to invest in nieces and nephews when engaged in sexual/romantic relationships, *fa'afafine's* kin-directed altruistic tendencies remain elevated regardless of their relationship status (VanderLaan & Vasey, 2012). Second, while male paternity is not always certain, a mother's genetic relatedness to her offspring is always guaranteed. Therefore, androphilic males should favor investing in their sisters' offspring to maximize indirect fitness. Consistent with this prediction, when compared to Samoan men and women, *fa'afafine* tend to invest in their sisters' children more often, particularly when the consequences of investment are non-trivial (e.g., paying for medical expenses) (VanderLaan & Vasey, 2014). Moreover, *fa'afafine's* avuncular tendencies are higher when they have more older sisters rather than when they have more older brothers (VanderLaan & Vasey, 2013). Third, compared to Samoan men and women, *fa'afafine* prefer investing more heavily in younger relatives who tend to be more susceptible to mortality (VanderLaan & Vasey, 2014). Finally, *fa'afafine* are less likely to redirect altruistic tendencies towards non-kin children compared to Samoan men and women, thus, maximizing their indirect fitness (Vasey & VanderLaan, 2010a).

The adaptive feminine phenotype model is an evolutionary developmental framework thought to reconcile and explain the cross-cultural inconsistencies in empirical support for the kin selection hypothesis (VanderLaan et al., 2011b, 2016; VanderLaan, Petterson, & Vasey, 2017; Vasey et al., 2020). Specifically, it suggests that cisgender androphilic males do not exhibit elevated kin-directed altruism because they become more masculine and less feminine as they transition from childhood to adulthood (Bailey, 2003). Consistent with this model, VanderLaan, Petterson, & Vasey (2017) demonstrated that Samoan *fa'afafine's* elevated kin-directed altruism in adulthood emerges in childhood in the form of elevated concern for kin's wellbeing, which is associated with childhood measures of femininity. Further, VanderLaan et al. (2016) found that adulthood female-typical behavior was associated with kin-directed altruism among Canadian androphilic men and women and mediated the group differences found in kin-directed altruism, in which androphilic women scored higher than androphilic and gynephilic men.

Based on this body of research, Vasey et al. (2020) suggested that the expression of elevated kin-directed altruistic tendencies is contingent on a feminine expression of male androphilia as characterized by the transgender form. This speculation was further informed by research which suggests that the transgender form of male androphilia is ancestral to the cisgender form. Specifically, VanderLaan, Ren, & Vasey (2013) found that cultures in which transgender androphilic males occurred were characterized by a significantly greater presence of ancestral socio-cultural conditions compared to societies in which this form of male androphilia was not reported. On the basis of this work, VanderLaan, Ren, & Vasey (2013) concluded that transgender male androphilia was likely to be the form in which this trait was expressed ancestrally. Consequently, they argued that transgender male androphiles may represent more optimal models when testing evolutionary hypotheses. In contrast, the cisgender form of male androphilia appears to reflect recent cultural and historical influences that may obscure the outcome of evolutionary processes.

Non-Samoan research that might speak to this speculation is sparse and characterized by several limitations. Camperio Ciani et al. (2016) tested the kin selection hypothesis among the Urak Lawoi people inhabiting Ko Lipe island in the Andaman sea off the coast of Thailand. In that population, transgender androphilic males are known locally as a third gender: *na-ning* (Vasey et al., 2016). Camperio Ciani et al. (2016) found no evidence that *na-ning*—whom the authors referred to using the Thai term, *kathoey*—exhibited elevated altruism towards nieces and nephews when compared to Urak Lawoi gynephilic men. Unfortunately, Camperio Ciani et al.'s (2016) study of the Urak Lawoi is compromised by the fact that the sample sizes were small (19 *na-ning* and 19 men) and consequently, the statistical analyses were underpowered (Vasey et al., 2016).

Research conducted by Nila et al. (2018) tested the kin selection hypothesis in Java, Indonesia, and found that compared to gynephilic males, androphilic males expressed elevated altruistic tendencies towards nieces and nephews while also receiving less financial and emotional support from their families. These tendencies manifested behaviorally in the form of increased transfer of money from androphilic males to their nieces and nephews. Nila et al.'s (2018) sample consisted of 82 androphilic males, some of whom (n = 11) declared themselves to be members of a traditional third gender, *waria*, and the rest were presumably cisgender. Therefore, this is the first study to provide evidence of elevated kin-directed altruism among a sample of predominantly cisgender androphilic males. This finding, however, remains to be replicated.

To more fully test the idea that elevated kin-directed altruism is contingent on a transgender expression of male androphilia, we initiated a test of the kin selection hypothesis among the Istmo Zapotec. Research conducted among the Istmo Zapotec demonstrates that *muxes* recall elevated indicators of childhood separation anxiety (Gómez et al., 2017), which has been argued to be a developmental precursor to kin-directed altruism in adulthood (VanderLaan et al., 2011a; VanderLaan et al., 2015, 2016; VanderLaan, Petterson, & Vasey, 2017). Among the Istmo Zapotec, it is believed that while sons and daughters will eventually get married and move out, *muxes* will stay with their parents and take care of them during old age (Miano Borruso, 2002; Mirandé, 2017).

The present study sought to undertake three tests of the kin selection hypothesis. First, we sought to test the kin selection hypothesis in a novel non-European culture—the Istmo Zapotec—where both transgender and cisgender androphilic males are prevalent. Specifically, we tested whether avuncular tendencies towards nieces and nephews differed between Istmo Zapotec gynephilic men, androphilic women, and cisgender and transgender *muxes*. We predicted that transgender *muxes* (i.e., *muxe gunaa*) would exhibit higher altruistic tendencies towards nieces and nephews when compared to gynephilic men and androphilic women (Study

1, Prediction 1), similar to Samoan *fa'afafine* (e.g., VanderLaan, Petterson, & Vasey, 2017; VanderLaan & Vasey, 2012; Vasey & VanderLaan, 2009, 2010a, 2010b). In contrast, we predicted that cisgender *muxes* (i.e., *muxe nguiiu*) would not exhibit higher altruistic tendencies towards nieces and nephews when compared to gynephilic men and androphilic women (Study 1, Prediction 2). This prediction was formulated due to the scant evidence for elevated kin-directed altruism among cisgender androphilic males (consistent evidence: Nila et al., 2018; inconsistent evidence: Abild et al., 2014; Bobrow & Bailey, 2001; Camperio Ciani et al., 2016; Forrester et al., 2011; Rahman & Hull, 2005; Vasey & VanderLaan, 2012). In addition, previous research demonstrates that adult femininity is associated with kin-directed altruism (e.g., VanderLaan et al., 2016; VanderLaan, Petterson, & Vasey, 2017), but *muxe nguiiu*, like Euro-American gay men, have a relatively male-typical gender presentation and an interest for female-typical occupations that is intermediate between those of men and women (e.g., see Chapter 3; Lippa, 2005a, 2008a, 2020; Whitam & Mathy, 1986).

Second, we aimed to test whether Istmo Zapotec *muxes'* altruistic tendencies evinced hallmarks of adaptive design by being maximally focused towards kin children. To do this, we first assessed within group differences in altruistic tendencies towards kin versus non-kin children. Similar to previous research (Forrester et al., 2011; Vasey and VanderLaan, 2010a, 2012), we expected all groups to exhibit greater willingness to behave altruistically towards kin rather than non-kin children (Study 1, Prediction 3). In addition, we compared whether the association between altruistic tendences towards kin and non-kin children differed between groups. Previous research has found that both transgender (Vasey & VanderLaan, 2010a) and cisgender (Forrester et al., 2011; but see Vasey & VanderLaan, 2012) androphilic males exhibit greater cognitive dissociations (i.e., weaker correlations) between these tendencies compared to gynephilic men and androphilic women. Thus, we predicted that both cisgender and transgender *muxes* would exhibit weaker correlations between their willingness to direct altruism towards kin and non-kin children compared to gynephilic men and androphilic women (Study 1, Prediction 4). Finally, we assessed whether *muxes'* elevated kin-directed altruism, if present, is a by-product of a generalized tendency to express altruism towards all children. Similar to Samoan *fa'afafine* (Vasey & VanderLaan, 2010a), we predicted that *muxe gunaa's* elevated altruistic tendencies towards kin children would be significantly higher than those of gynephilic men and androphilic women even after controlling for altruistic tendencies towards non-kin children (Study 1, Prediction 5). In contrast, following the same rationale provided for Prediction 2, we predicted that cisgender *muxe nguiiu* would direct altruistic tendencies towards kin children in a manner that was comparable to gynephilic men and androphilic women after controlling for altruistic tendencies towards non-kin children (Study 1, Prediction 6).

Previous tests of the kin-selection hypothesis have relied on assessing participants' kin-directed altruism via self-reported data. While informative, this type of data is limited given that it is prone to various types of biases such as selective recall, memory distortion, and socially desirable responding (e.g., Ross, 1980). Thus, in order to circumvent these limitations, we conducted a separate study where we interviewed Istmo Zapotec women with gynephilic brothers but no *muxe* siblings and women with at least one *muxe* sibling and assessed how much their male sibling assisted with childcare. This study allowed us to corroborate and validate whether any potential male sexual orientation differences in willingness to engage in kin-directed altruism from Study 1 translated into actual behavior. Following the same rationale for Study 1, we predicted that the sisters of *muxe gunaa* would report higher childcare support from those siblings, compared to sisters who had gynephilic brothers but no *muxe* siblings (Study 2, Prediction 7). Finally, we predicted that women with *muxe nguiiu* siblings and those with only gynephilic brothers would report similar levels of childcare support from both (Study 2, Prediction 8).

Study 1: Materials and Methods

Participants

All participants were recruited using a network sampling procedure that consisted of contacting initial participants, who gave referrals for additional participants, who in turn provided further referrals, and so on. Written consent was required prior to participating in the study. A total of 172 cisgender gynephilic men, 130 cisgender androphilic women, 106 transgender *muxe gunaa*, and 106 cisgender *muxe nguiiu* were analyzed for Study 1. Participants' sexual orientation was assessed using a Kinsey scale (Kinsey et al., 1948) for sexual feelings over the previous year. Istmo Zapotec, including *muxes* themselves, recognize that *muxes* are biological males, as evidenced by the fact that they possess male genitalia and secondary sexual characteristics. Nevertheless, participants were informed that the category "males" included men and/or *muxes*, whereas the category "females" only included women, in order to assess the sex that they are attracted to as opposed to the gender. All men identified as exclusively (Kinsey rating = 0, n = 168) or predominantly gynephilic (Kinsey rating = 1, n = 4). All women identified as exclusively (Kinsey rating = 6, n = 129) or predominantly androphilic (Kinsey rating = 5, n = 1). All *muxe gunaa* identified as exclusively androphilic (Kinsey rating = 6, n = 106). All *muxe nguiiu* identified as predominantly (Kinsey rating = 5, n = 15) or exclusively androphilic (Kinsey rating = 6, n = 91).

Procedure

Data were collected in the city of Juchitán de Zaragoza, as well as 14 towns and villages within both the Juchitán and Tehuantepec districts of the Istmo region of Oaxaca, Mexico. Four field trips took place between November–December 2015, February–March 2016, November–December 2016, and February 2018. All participants were interviewed using standardized questionnaires, which were available in Spanish after being translated and back-translated by fluent Spanish-English speakers. The first author, as well as Spanish-speaking research assistants, were available to answer participants' questions. A Zapotec-speaking research assistant was also present for interviews involving participants who were not fully fluent in Spanish. Questions were read out loud by research assistants in Spanish or Zapotec as necessary.

Measures

Participants were asked to report information regarding their age (in years), level of education, and level of income. Level of education was reported by stating the highest level of education achieved (1 = "None," 2 = "Primary school," 3 = "Junior high school," 4 = "High school or college"). Level of income was based on an average weekly income scale that ranged from 1 (0–250 Mexican Pesos) to 9 (more than 2000 Mexican Pesos).

Altruistic tendencies towards kin children were assessed using a modified version of the Avuncular/Materteral Tendencies Subscale (Vasey et al., 2007), which is a measurement instrument containing nine items used to quantify willingness to invest time and resources towards nieces and nephews, with three additional items (see Appendix 1). These three items were added to expand the range of altruistic tendencies assessed by including items on providing protection (item 10) and allocating money to provisioning clothing (item 11) and food (item 12) for nieces and nephews. For each item, participants were asked to rate their willingness to exhibit a particular altruistic behavior towards nieces and nephews who were the children of a sibling with whom they were emotionally closest. Responses to these items were based on a 7-point Likert-type scale that ranged from 1 = “Very Unwilling” to 7 = “Very Willing.” Altruistic tendencies towards kin children scores were calculated as the mean rating given to the twelve items.

Willingness to invest time and resources towards non-kin children was assessed using a modified version of the Altruistic Tendencies Towards Non-Kin Children Subscale (Vasey & VanderLaan, 2010a). This subscale was identical to the Avuncular/Materteral Tendencies subscale used in this study except that instead of nieces and nephews, the participants were asked to rate their willingness to direct altruistic behaviors towards a child in their neighborhood who is not a member of their family (see Appendix 2). Responses to these items were based on a 7-point Likert-type scale that ranged from 1 = “Very Unwilling” to 7 = “Very Willing.” Altruistic tendencies towards non-kin children scores were calculated as the mean rating given to the twelve items.

Study 1: Results

Table 5.1 summarizes the descriptive statistics for level of education, level of income, age, altruistic tendencies towards kin children scores, altruistic tendencies towards non-kin children scores, and scale reliabilities (i.e., Cronbach α) for the last two variables. A one-way ANOVA revealed no significant group difference for age, $F(3, 510) = 0.378$, $p = .769$. Kruskal-Wallis H tests demonstrated that there were significant group differences in level of income, $H(3) = 16.85$, $p < .001$, and level of education, $H(3) = 61.65$, $p < .001$. Post hoc pairwise comparisons using Dunn’s tests with Bonferroni correction revealed that androphilic women had significantly lower income than *muxe nguiiu* ($p < .001$) and gynephilic men ($p = .014$), and that *muxe gunaa* had a lower level of education than all other groups (all $p < .001$) who did not differ from each other. Nonetheless, level of education and income were not used as covariates in subsequent analyses given that the direction and significance of our group comparisons for altruistic tendencies towards kin children scores and altruistic tendencies towards non-kin children scores did not change when controlling for these biographic variables.

Table 5.1

Descriptive statistics for biographic information and altruistic tendencies towards kin and non-kin children by group

	Gynephilic Men (*n* = 172)	*Muxe Nguiiu* (*n* = 106)	*Muxe Gunaa* (*n* = 106)	Androphilic Women (*n* = 130)
Level of education				
None (%)	1.16	0.00	4.72	2.31
Primary (%)	6.40	6.60	21.70	4.61
Junior high school (%)	25.00	19.81	41.50	19.23
High school or college (%)	67.44	73.59	32.08	73.85
Level of income				
0–250 Pesos (%)	8.14	7.55	3.77	20.00
251–500 Pesos (%)	8.14	7.55	10.38	7.69
501–750 Pesos (%)	12.79	10.38	19.81	20.00
751–1000 Pesos (%)	15.70	10.38	17.93	15.39
1001–1250 Pesos (%)	15.70	12.26	19.81	6.15
1251–1500 Pesos (%)	9.88	14.15	6.60	7.69
1501–1750 Pesos (%)	8.72	8.49	4.72	0.77
1751–2000 Pesos (%)	6.98	7.55	1.89	9.23
More than 2000 Pesos (%)	13.95	21.70	15.09	13.08
Age *M*	30.96	30.19	31.58	30.75
(*SD*)	(9.38)	(9.00)	(9.51)	(10.48)
Altruistic tendencies towards kin children				
Reliability (α)	0.81	0.64	0.79	0.85
Score *M*	5.73	6.33	6.14	6.04
(*SD*)	(0.84)	(0.53)	(0.76)	(0.76)
Altruistic tendencies towards non-kin children				
Reliability (α)	0.91	0.89	0.90	0.91
Score *M*	4.54	5.09	4.88	5.11
(*SD*)	(1.30)	(1.14)	(1.35)	(1.11)

The scales for both altruistic tendencies scores ranged from 1 to 7.

A two-way mixed model repeated measures ANOVA was performed on altruistic tendencies towards kin children scores and altruistic tendencies towards non-kin children scores in which groups were used as a between-subject factor and score type as a within-subject factor. Statistically significant main effects were observed for group, $F(3, 510) = 10.97$, $p < .001$, score type, $F(1, 510) = 660.52$, $p < .001$, and the interaction between group and score type, $F(3, 510) = 2.98$, $p = .030$. Within-group comparisons using two-tailed, paired sampled *t*-tests demonstrated that the altruistic tendencies towards kin children scores were significantly greater than the altruistic tendencies towards non-kin children scores for gynephilic men, $t(171) = 16.18$, $p < .001$, $d = 1.23$ (1.03, 1.43) [6], *muxe nguiiu*, $t(105) = 12.25$, $p < .001$, $d = 1.19$ (0.94, 1.44), *muxe gunaa*, $t(105) = 11.47$, $p < .001$, $d = 1.11$ (0.87, 1.36), and androphilic women, $t(129) = 11.95$, $p < .001$, $d = 1.05$ (0.83, 1.26).

The within-group magnitude of difference between altruistic tendencies towards kin children scores and altruistic tendencies towards non-kin children scores were compared between groups. This was done by conducting Pearson's *r* correlations for the two score types within each group, and then comparing these correlations between groups using Fisher's *r*-to-*Z* transformation. These analyses demonstrated that the two scores were significantly positively correlated for gynephilic men ($n = 171$, $r = 0.67$, $p < .001$), *muxe nguiiu* ($n = 106$, $r = 0.41$, $p < .001$), *muxe gunaa* ($n = 106$, $r = 0.55$, $p < .001$), and androphilic women ($n = 130$, $r = 0.61$, $p < .001$) (see Figure 5.1). The correlation between score types was significantly weaker among *muxe nguiiu* when compared to gynephilic men ($z = 3.00$, $p = .001$) and androphilic women ($z = 2.61$, $p = .020$). No significant differences were found in the magnitude of the score type correlations between gynephilic men and *muxe gunaa* ($z = 1.54$, $p = .062$), gynephilic men and

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[6] Cohen's *d* effect sizes for paired-sampled *t*-tests were calculated for each group as $\frac{t}{\sqrt{n}}$ and presented with their 95% confidence intervals.

androphilic women ($z = 0.87$, $p = .193$), *muxe nguiiu* and *muxe gunaa* ($z = 1.31$, $p = .095$), or *muxe gunaa* and androphilic women ($z = 0.68$, $p = .200$).

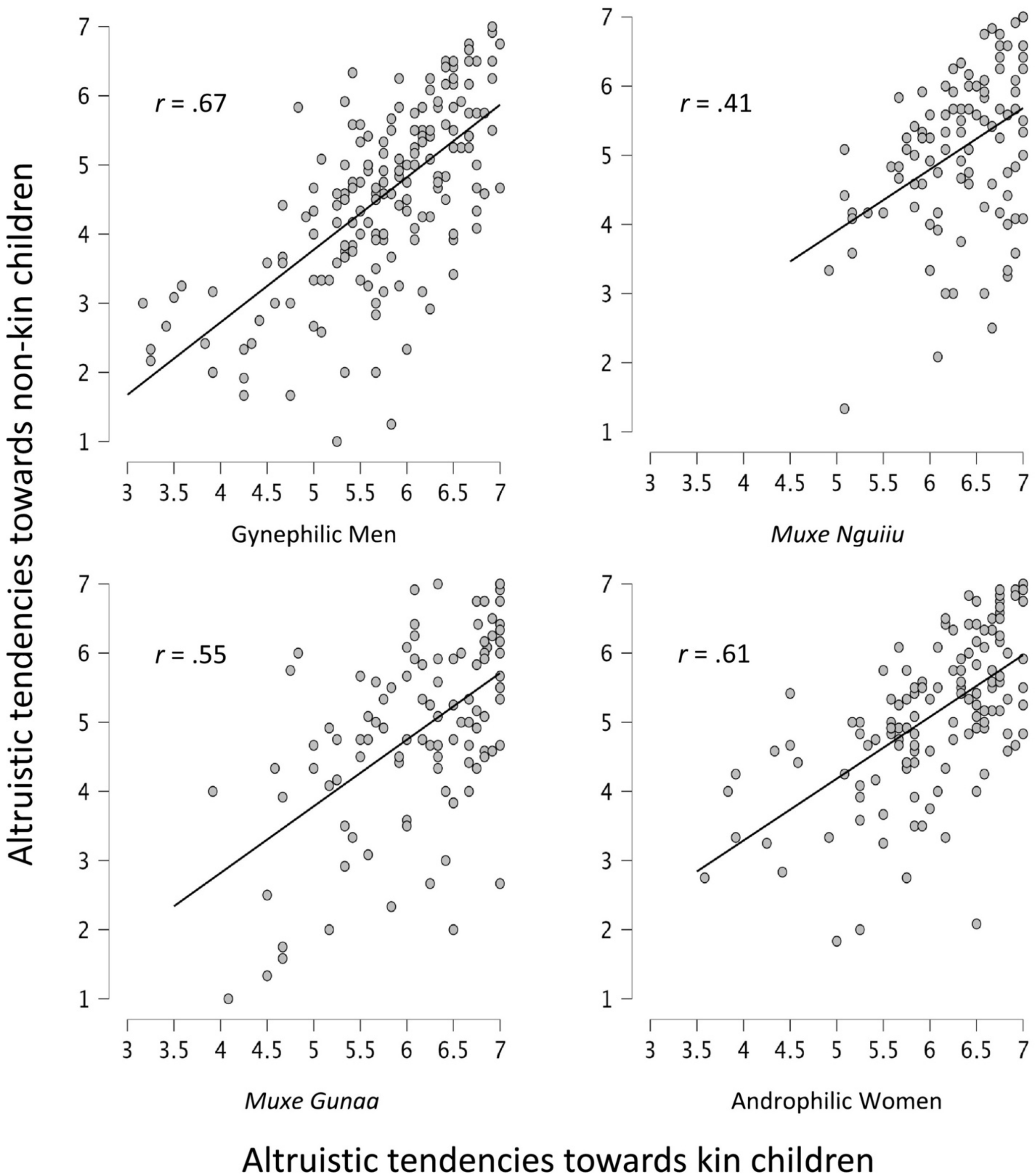

Figure 5.1. Pearson's *r* correlations between altruistic tendencies towards kin children and altruistic tendencies towards non-kin children scores among Istmo Zapotec gynephilic men (top left), *muxe nguiiu* (top right), *muxe gunaa* (bottom left), and androphilic women (bottom right). The scales for both altruistic tendencies scores ranged from 1 to 7.

A one-way ANOVA was conducted to compare altruistic tendencies towards kin children scores between groups. A significant Levene's test demonstrated that there were unequal variances between groups ($p < .001$). As such, the F statistic and degrees of freedom for the omnibus test were reported using Brown-Forsythe, and the Games-Howell procedure was used for all post hoc pairwise comparisons. A one-way ANOVA demonstrated a significant main effect for group in altruistic tendencies towards kin children scores [Brown-Forsythe $F(3, 479.48) = 16.19$, $p < .001$]. Post hoc pairwise comparisons demonstrated that gynephilic men scored significantly lower than *muxe nguiiu* ($p < .001$, $d = 0.81$ [0.56, 1.06][7]), *muxe gunaa* ($p < .001$, $d = 0.50$ [0.26, 0.75]), and androphilic women ($p = .006$, $d = 0.38$ [0.15, 0.61]), and that *muxe nguiiu* score significantly higher than androphilic women ($p = .004$, $d = 0.43$ [0.17, 0.69]). No significant differences were found between androphilic women and *muxe gunaa* ($p = .736$, $d = 0.13$ [-0.12, 0.39]), or between *muxe nguiiu* and *muxe gunaa* ($p = .170$, $d = 0.28$ [0.01, 0.55]).

A one-way ANOVA comparing altruistic tendencies towards non-kin children scores also demonstrated a significant main effect for group [$F(3, 510) = 6.78$, $p < .001$]. Post hoc pairwise comparisons using Fisher's Least Significant Differences (LSD) demonstrated that gynephilic men scored significantly lower than *muxe nguiiu* ($p < .001$, $d = 0.44$ [0.19, 0.68]), *muxe gunaa* ($p = .026$, $d = 0.26$ [0.01, 0.50]), and androphilic women ($p < .001$, $d = 0.47$ [0.23, 0.70]). No significant differences were found between androphilic women and *muxe nguiiu* ($p = .864$, $d = 0.02$ [-0.23, 0.28]), androphilic women and *muxe gunaa* ($p = .156$, $d = 0.19$ [-0.07, 0.44]), or between *muxe nguiiu* and *muxe gunaa* ($p = .234$, $d = 0.16$ [-0.11, 0.43]).

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[7] Cohen's d for all *post hoc* pairwise comparisons were calculated as $d = \frac{M_1 - M_2}{\sqrt{\frac{(n_1 - 1)SD_1^2 + (n_2 - 1)SD_2^2}{n_1 + n_2 - 2}}}$. All effect sizes were reported with their 95% confidence intervals.

Finally, a between group comparison was performed for altruistic tendencies towards kin children scores using a one-way ANCOVA, controlling for altruistic tendencies towards non-kin children scores (see Figure 5.2). This analysis revealed a significant main effect for group, $F(3, 509) = 11.29$, $p < .001$. Post hoc pairwise comparisons using Fisher's LSD demonstrated that *muxe nguiiu* scored higher than gynephilic men ($p < .001$, $d = 0.66$ [0.41, 0.91]) and androphilic women ($p < .001$, $d = 0.49$ [0.23, 0.75]), and that *muxe gunaa* also scored higher than gynephilic men ($p < .001$, $d = 0.47$ [0.23, 0.72]), and androphilic women ($p = .021$, $d = 0.30$ [0.05, 0.56]). No significant differences were observed between gynephilic men and androphilic women ($p = .157$, $d = 0.17$ [-0.06, 0.40]), or between *muxe nguiiu* and *muxe gunaa* ($p = .169$, $d = 0.19$ [-0.08, 0.46]).

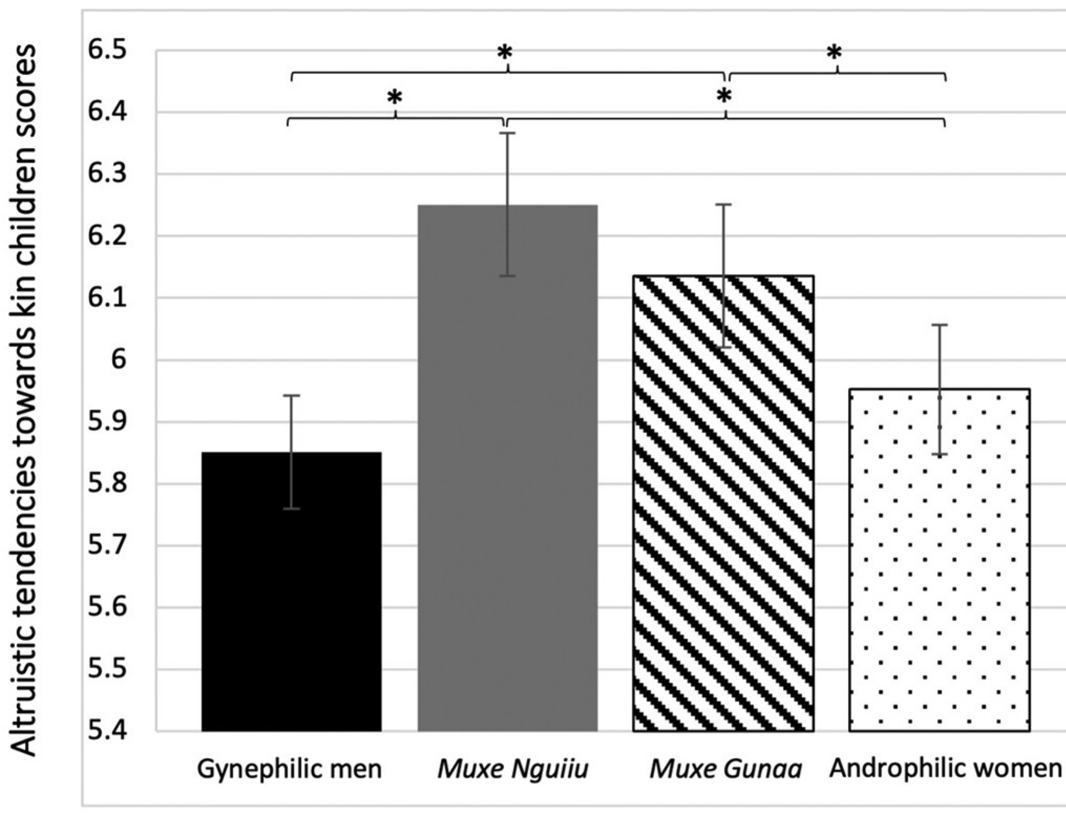

Figure 5.2: Group differences in the estimated marginal means for altruistic tendencies towards kin children scores. Values are adjusted for the covariate (i.e., avuncular tendencies towards non-kin children scores). Error bars represent 95% confidence intervals. Significant group differences are flagged by an asterisk (*) denoting $p < .05$. The scale for the altruistic tendencies towards kin children scores ranged from 1 to 7.

Study 2: Materials and Methods

Participants

Similar to Study 1, all participants were recruited using a network sampling procedure. Written consent was required prior to participating in the study. A total of 65 sisters of gynephilic men, 57 sisters of *muxe nguiiu*, and 39 sisters of *muxe gunaa* (96 sisters of *muxes* combined) were analyzed for Study 2.

Procedures

Data were collected in the city of Juchitán de Zaragoza, as well as other towns and villages within both the Juchitán and Tehuantepec districts of the Istmo region of Oaxaca, Mexico. Two field trips took place between June–August 2018 and May–June 2019. All participants were fluent in Spanish and interviewed using the same procedure described for Study 1.

Measures

Participants were asked to report information regarding their age (in years) and their number of offspring. Women's ages ranged from 18 to 58 and they all had at least one offspring. Childcare support received by male siblings was assessed using a modified version of the Avuncular/Materteral Tendencies Subscale, where women were asked how often their *muxe* sibling or gynephilic brother participated in twelve activities related to childcare. These activities were identical to those found in the Avuncular/Materteral Tendencies Subscale from Study 1 but framed from the sister's perspective (see Appendix 3). Women with a *muxe* sibling were asked to report on that sibling. Women without a *muxe* sibling were asked to report on the gynephilic brother with whom they felt the closest emotionally. Responses to the 12 items were based on a

5-point Likert-type scale that ranged from 1 = "Never" to 5 = "Always." Siblings' altruism towards nieces and nephews were calculated as the mean rating for the twelve subscale items

Study 2: Results

Descriptive statistics for age, number of offspring, siblings' altruism towards nieces and nephews scores, and scale reliabilities (i.e., Cronbach α) for this measure are summarized in Table 5.2 for sisters of gynephilic men, sisters of *muxe nguiiu*, sisters of *muxe gunaa*, and sisters of *muxes* combined. A significant Levene's test demonstrated that there were unequal variances in number of offspring between groups (p = .015). As such, the F statistic and degrees of freedom for the omnibus test were reported using Brown-Forsythe. One-way ANOVAs revealed no significant group differences for sisters' age, $F(2, 158) = 1.35$, $p = .261$, nor sisters' number of offspring, $F(2, 130.56) = 1.34$, $p = .266$. An independent samples t-test also showed that there were no age differences between the sisters of *muxes* combined and the sisters of gynephilic men, $t(159) = 1.58$, $p = .115$. Moreover, an independent samples Welch's t-test demonstrated no significant differences in the number of offspring between the sisters of *muxes* combined and the sisters of gynephilic men, $t(156.28) = 1.74$, $p = .084$. Finally, siblings' altruism towards nieces and nephews scores were not significantly correlated with sisters' age (Pearson's $r = -.056$, $p = .483$), nor with sisters' number of offspring (Pearson's $r = -.030$, $p = .703$). Therefore, sister's age and number of offspring were not included as covariates in subsequent analyses.

A one-way ANOVA comparing siblings' altruism towards nieces and nephews scores did not find a significant main effect for group, $F(2, 158) = 2.94$, $p = .056$. A priori power analyses based on the results from the post hoc pairwise comparisons for altruistic tendencies towards kin children scores in Study 1 revealed that a sample size of $n = 24$ for *muxe nguiiu* and $n = 28$ for gynephilic is needed in order to detect an effect size of $d = 0.81$, whereas a sample size of $n = 52$

for *muxe gunaa* and n = 84 for gynephilic men is needed in order to detect an effect size of d = 0.50.[8] Given that Study 2 only included 39 sisters of *muxe gunaa*, it is possible that the non-significant result from the omnibus test reflects a Type II error due to this low sample size. In order to increase power, the sisters of transgender *muxe gunaa* and cisgender *muxe nguiiu* were combined to a single group. An independent sample t-test revealed that sisters of *muxes* (*muxe nguiiu* and *muxe gun*aa combined) had significantly higher siblings' altruism towards nieces and nephews scores than the sisters of gynephilic men, $t(159) = 2.41$, $p = .017$, $d = 0.39$ (0.07, 0.70)[9] (see Figure 5.3).

Table 5.2

Descriptive statistics for age, number of offspring, and sibling's altruism towards nieces and nephews by group

	Sisters of Gynephilic Men (n = 65)	Sisters of *Muxe Nguiiu* (n = 57)	Sisters of *Muxe Gunaa* (n = 39)	Sisters of *Muxes* combined (n = 96)
Age *M* (*SD*)	34.71 (8.70)	37.35 (8.67)	36.49 (10.05)	37.00 (9.22)
Number of offspring *M* (*SD*)	1.98 (0.87)	2.28 (1.18)	2.23 (1.09)	2.26 (1.14)
Siblings' altruism towards nieces and nephews				
Reliability (α)	0.87	0.88	0.90	0.88
Score *M* (*SD*)	2.37 (0.86)	2.74 (0.93)	2.68 (0.92)	2.72 (0.92)

The scale for siblings' altruism towards nieces and nephews scores ranged from 1 to 5.

[8] Two a priori power analyses were conducted using G*Power 3.1.9.2 (see Faul et al., 2007) with statistical power set at the recommended 0.80 level (Cohen, 1988). The "Means: Difference between two independent means (two groups)" statistical test was used with the sample size allocation ratio set to 0.61 (i.e., $\frac{n \text{ for sisters of } \textit{muxe gunaa}}{n \text{ for sisters of gynephilic men}}$) and 0.88 (i.e., $\frac{n \text{ for sisters of } \textit{muxe nguiiu}}{n \text{ for sister of gynephilic men}}$).

[9] Cohen's d was calculated as $d = \frac{M_1 - M_2}{\sqrt{\frac{(n_1 - 1)SD_1^2 + (n_2 - 1)SD_2^2}{n_1 + n_2 - 2}}}$ with its 95% confidence intervals.

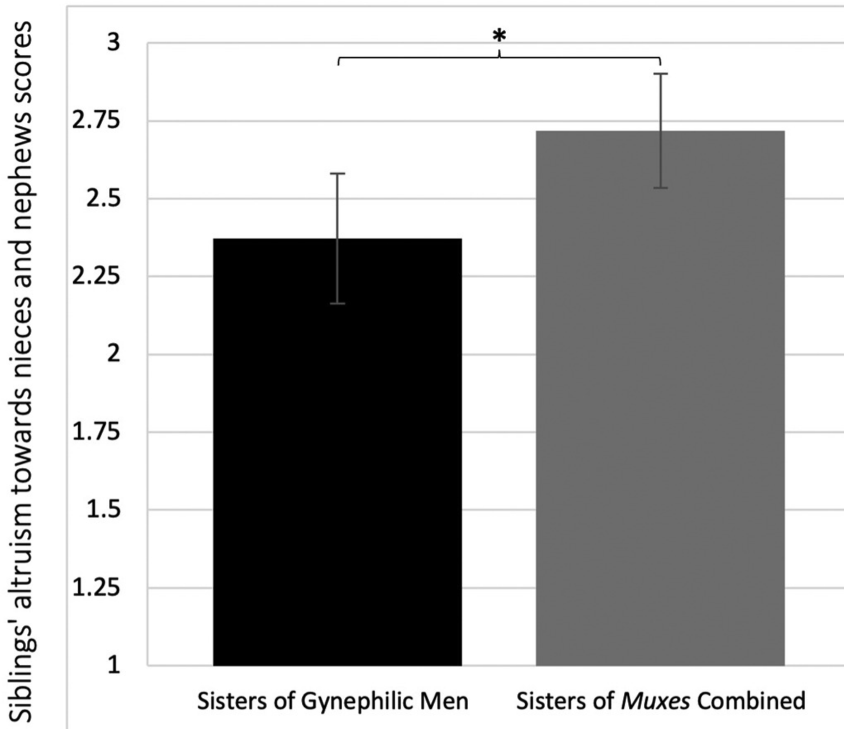

Figure 5.3: Group difference in mean siblings' altruism towards nieces and nephews scores. Error bars represent 95% confidence intervals. The significant group difference is flagged by an asterisk (*) denoting $p < .05$. The scale for the siblings' altruism towards nieces and nephews scores ranged from 1 to 5.

Discussion

To test the kin selection hypothesis, Study 1 compared the altruistic tendencies of Istmo Zapotec *muxes*, gynephilic men, and androphilic women towards kin and non-kin children. Data were collected for two types of androphilic *muxes*: cisgender *muxes nguiiu* and transgender *muxes gunaa*. All groups reported being more willing to take care of their nieces and nephews compared to non-kin children. These results are similar to findings from Canada (Forrester et al., 2011), Japan (Vasey & VanderLaan, 2012) and Samoa (Vasey & VanderLaan, 2010a) and suggest that all individuals, regardless of their gender or sexual orientation, have evolved via kin selection to bias altruism towards close relatives (Daly et al., 1997).

To offset the reproductive cost of male androphilia, the kin selection hypothesis predicts that androphilic males should exhibit elevated altruistic tendencies towards close kin compared to gynephilic men and androphilic women. Moreover, on the basis of previous research, Vasey et al. (2020) suggested that the expression of elevated kin-directed altruism is contingent on the transgender form of male androphilia being expressed. Therefore, it was predicted that only transgender *muxe gunaa* would exhibit elevated altruistic tendencies towards kin.

Consistent with prediction 1, *muxe gunaa* reported greater altruistic tendencies towards their nieces and nephews than gynephilic men. In contrast with prediction 2, however, *muxe nguiiu* also exhibited greater kin-directed altruism than gynephilic men and the two *muxe* types did not differ from each other for this measure. Furthermore, cisgender *muxes* reported greater altruistic tendencies towards their nieces and nephews than androphilic women, but transgender *muxes* did not.

With respect to the issue of adaptive design, if the psychology of androphilic males evolved to allocate resources towards kin in a more precise and efficient manner, then one would expect altruistic tendencies towards kin and altruistic tendencies towards non-kin to be more dissociated in these individuals compared to others. Previous research indicates that this cognitive dissociation is present among transgender androphilic males in Samoa (Vasey & VanderLaan, 2010a) and cisgender androphilic males in Canada (Forrester et al., 2011) but not in Japan (Vasey & VanderLaan, 2012). In the present study, we found that the correlation between altruistic tendencies towards kin children and altruistic tendencies towards non-kin children were significantly weaker among cisgender *muxe nguiiu* when compared to gynephilic men and androphilic women, whereas this was not the case for transgender *muxe gunaa*. This suggest that compared to gynephilic men and androphilic women, *muxe nguiiu's* altruistic tendencies towards kin and non-kin are adaptively dissociated in a manner that would maximize their altruism towards kin. In contrast, the findings for *muxe gunaa* were more equivocal given that they were simultaneously on par with the greater dissociation seen among *muxe nguiiu* and the lesser dissociation seen among androphilic women and gynephilic men. That said, it is worth noting that the differences in the magnitude of the score type correlations between gynephilic men and *muxe gunaa* came close to significance in the expected direction (p = .062).

Nevertheless, further analysis indicated that both types of *muxes* exhibited elevated altruistic tendencies towards kin compared to gynephilic men and androphilic women even when controlling for more generalized altruism towards non-kin. This provides further evidence that androphilic males elevated altruism is adaptively designed to be focused on kin and not a by-product of general interest in helping all children. Nonetheless, this finding was contrary to our predictions that only transgender *muxe gunaa* would exhibit a willingness to maximize altruism towards kin.

Although the elevated kin-directed altruistic tendencies exhibited by *muxe nguiiu* were inconsistent with predictions 2 and 6 and with most other studies that have tested the kin selection hypothesis using cisgender androphilic males (Abild et al., 2014; Bobrow & Bailey, 2001; Camperio Ciani et al., 2016; Forrester et al., 2011; Rahman & Hull, 2005; Vasey & VanderLaan, 2012; but see Nila et al., 2018), they are consistent with the general predictions of the kin selection hypothesis, which hold that elevated kin-directed altruism is linked to male same-sex sexual orientation, not with a transgender identity and presentation. Nevertheless, the present study did not implement direct measures of sex-typed behavior and cannot, thus, disregard the possibility that the expression of elevated kin-directed altruism among *muxes* is partially contingent on the expression of elevated femininity, as predicted by the adaptive phenotype model (VanderLaan et al., 2011a, 2016; VanderLaan, Petterson, & Vasey, 2017;

Vasey et al., 2020). Future studies among the Istmo Zapotec could specifically test this model by looking at the association between childhood and adulthood femininity and kin-directed altruism.

Study 2 employed a novel test of the kin selection hypothesis by assessing whether the elevated kin-directed altruism reported by androphilic males is confirmed by their sister. Contrary to our predictions, the omnibus test comparing the amount of childcare support received from the male siblings of sisters of gynephilic men, *muxe nguiiu*, and *muxe gunaa* was not significant. To control for the possibility of a Type II error due to low sample sizes (see power analyses in Study 2: Results), the sisters of *muxe gunaa* and *muxe nguiiu* were combined into a single group to increase statistical power. This decision was justified by the fact that there were no significant differences in kin-directed altruistic tendencies between the two types of *muxes* in Study 1.

Consistent with the kin selection hypothesis, the amount of childcare support from *muxe* siblings (*muxe nguiiu* and *muxe gunaa* combined) that sisters reported receiving was greater than the amount of childcare support that women without *muxe* siblings reported receiving from their gynephilic brothers to whom they were emotionally close. Furthermore, there was no significant difference in number of offspring between sister groups nor a significant correlation between sisters' number of offspring and their male siblings' kin-directed altruism. These findings suggest that *muxes'* elevated kin-directed altruism are not a result of a greater need for childcare support among their sisters because of a greater number of children.[10] Overall, these findings

[10] One of the interpretations of the kin selection hypothesis is that *muxes*' elevated willingness to assist with childcare would allow their female siblings to have additional time and resources to produce more offspring than women without *muxe sib*lings. Nevertheless, the present study does not provide a proper test of this prediction given that the majority of women in our sample (87.6%) were below the average national age at natural menopause (i.e., 47.9 years-old) (Legorreta et al., 2013) and have, therefore, not completed their reproductive careers.

corroborate those obtained from Study 1 and from previous studies conducted in Samoa (VanderLaan, Petterson, & Vasey, 2017; VanderLaan & Vasey, 2012; Vasey and VanderLaan, 2009, 2010a, 2010b). In addition, these findings suggest that androphilic males' elevated willingness to engage in kin-directed altruism translate into actual behavior as suggested by previous research on monetary exchange in Samoa (Vasey & VanderLaan, 2010c) and Java (Nila et al., 2018).

The fact that our cisgender androphilic male group exhibited elevated kin-direct altruistic tendencies challenges the idea that such predispositions are contingent on a transgender expression of male androphilia as previously suggested by Vasey et al. (2020). Although the continued expression of female-typical behavior from childhood to adulthood remains a possible factor that regulates the expression of elevated kin-directed altruistic tendencies among androphilic males, there are other factors that could also play a role. These include a collectivistic cultural context, geographic proximity to family, and social acceptance/tolerance of male androphilia. However, previous research conducted in Canada and Japan has found that these variables, on their own, do not facilitate the expression of kin-directed altruism in cisgender androphilic males (Abild et al., 2014; Forrester et al., 2011; Vasey & VanderLaan, 2012). It is possible, however, that when these variables co-occur, the resulting synergy facilitates the expression of elevated altruism towards nieces and nephews. If so, this could help explain why evidence for the kin selection hypothesis has been consistently found in Samoa—a collectivistic culture where extended family often live in close proximity and *fa'afafine* enjoy high levels of social acceptance (Vasey et al., 2007).

It is noteworthy, however, that evidence for the kin selection hypothesis has also been found in Java, Indonesia—a non-Euro American, collectivistic culture where individuals live in extended kin networks but male androphilia is not widely accepted (Nila et al., 2018). Moreover, these social factors are unlikely to explain the hallmarks of adaptive design exhibited by Canadian gay men and Samoan *fa'afafine* in previous studies (Forrester et al., 2011; VanderLaan & Vasey, 2012, 2013, 2014; Vasey & VanderLaan, 2010a) and the Istmo Zapotec *muxes* in the present study. Instead, it could be that some social factors (e.g., geographic proximity to family and collectivistic cultural contexts) facilitate the expression of an evolved predisposition towards elevated kin-directed altruism among androphilic males more than others (e.g., social acceptance of male androphilia).

With respect to our sample, previous qualitative research has described the Istmo Zapotec as a family-oriented culture, where households are usually composed of three kin generations, with a local economy that is partially based on acts of reciprocity and solidarity, and where androphilic males enjoy a relatively high degree of acceptance (e.g., Bennhold-Thomsen, 1997; Céspedes Vargas, 2015; Miano Borruso, 2002; Mirandé, 2017). Therefore, it is possible that the expression of *muxes'* elevated altruistic tendencies towards kin is facilitated in part by their proximity to kin, the social tolerance they experience, and the Istmo Zapotec culture's tendency to prioritize the group versus the individual, or a specific combination of these factors. Future tests of the kin selection hypothesis should attempt to control for these variables in combination to assess whether their interaction can help predict elevated kin-directed altruism among androphilic males.

Limitations

The present study had several noteworthy limitations. First, there are multiple social explanations for why gynephilic men and androphilic women demonstrated lower kin-directed altruistic tendencies compared to *muxes*. For example, it is possible that Istmo Zapotec men and women were less willing to take care of nieces and nephews because they have to devote more of their time towards taking care of their own children or towards sexual/romantic relationship partners, both of which the *muxes* might be lacking. Furthermore, *muxes* might have greater social expectations for themselves, or from others, to contribute more to the care of nieces and nephews than other family members. Although previous quantitative research in Samoa has found that *fa'afafine's* elevated kin-directed altruistic tendencies are not explained by a lack of parental responsibilities, lower sexual/romantic involvements, and greater social expectations (discussed in Chapter 5 Introduction), it remains to be seen whether the same can be said for Istmo Zapotec *muxes*.

Second, although the sample sizes for both *muxe* types in Study 1 were fairly large by the standards of cross-cultural research, the sample size utilized in Study 2, especially for the sisters of *muxe gunaa*, was rather small for statistical purposes. While significant time and energy was invested in trying to locate additional sisters of *muxes* who were willing to participate in this study, this task proved quite difficult even after several months of fieldwork. Nevertheless, it would be more optimal if future studies among the Istmo Zapotec employ adequate sample sizes for statistical comparisons involving both types of *muxes*.

Finally, the network sampling procedure we utilized could have conceivably produced an unrepresentative sample. Efforts were made to avoid such bias by interviewing participants throughout the city of Juchitán de Zaragoza—the largest urban center in the Istmo region—as well as 14 towns and villages throughout the Istmo region of Oaxaca. Nonetheless, future research conducted among the Istmo Zapotec could consider using random sampling procedures.

Conclusion

The present study found that both cisgender and transgender *muxes* were more willing to invest time and resources towards their nieces and nephews when compared to Istmo Zapotec gynephilic men. Furthermore, cisgender *muxe nguiiu's* altruistic tendencies towards nieces and nephews were more dissociated from their altruistic tendencies towards non-kin children, compared to gynephilic men and androphilic women. When controlling for altruism towards non-kin children, both cisgender and transgender *muxes* demonstrated elevated willingness to take care of kin children compared to gynephilic men and androphilic women. Taken together, these results are consistent with the conclusion that *muxes'* elevated kin-directed altruistic tendencies are adaptively designed to maximize their inclusive fitness. Finally, the sisters of *muxes* reported receiving more childcare support from their *muxe* siblings compared to the amount of childcare support that women without *muxe* siblings reported receiving from their gynephilic brothers.

This study is noteworthy for several reasons. First, it replicates and triangulates findings in support of the kin selection hypothesis previously found in Samoa and Java. Second, it is the first study to test this hypothesis using discrete groups of transgender and cisgender androphilic males from the same culture. Third, it is the first study to assess androphilic males' kin-directed altruism via their sisters' reports. Beyond validating the *muxe* siblings' self-reports, these data from sisters help confirm that the altruistic tendencies in question actually manifests in terms of real-world behavior. In conclusion, the findings from Studies 1 and 2 are consistent with the kin selection hypothesis for the evolution of male androphilia.

Chapter 6: Offspring Production Among the Relatives of Istmo Zapotec Men and *Muxes*

Abstract

Male androphilia is influenced by biological factors, reliably occurs across diverse cultures, and has persisted over evolutionary time despite the fact that it reduces reproduction. One possible solution to this evolutionary paradox is the sexually antagonistic genes hypothesis (SAGH), which states that genes associated with male androphilia reduce reproduction when present in males but increase reproduction when present in their female relatives. The present study tested the SAGH among the Istmo Zapotec—a non-Euro-American culture in Oaxaca, Mexico, where transgender and cisgender androphilic males are known as *muxe gunaa* and *muxe nguiiu*, respectively. To test the SAGH, we compared offspring production by the biological relatives of *muxe gunaa* ($n = 115$), *muxe nguiiu* ($n = 112$), and gynephilic men ($n = 171$). The mothers and paternal aunts of *muxe gunaa* had higher offspring production than those of *muxe nguiiu*. Additionally, the relatives of *muxe gunaa* had more offspring than those of gynephilic men, whereas no such differences were found between the families of gynephilic men and *muxe nguiiu*. Elevated reproduction by the mothers and, particularly the aunts, of *muxe gunaa* is consistent with the SAGH. However, the absence of group differences between gynephilic men and *muxe nguiiu*, and the group differences between the two types of *muxes* are not predicted by the SAGH. This is the first study to demonstrate reproductive differences between kin of transgender and cisgender androphilic males within the same non-Euro-American culture.

Keywords: sexual antagonism; fecundity; sexual orientation; male androphilia; transgender; *muxes*; Istmo Zapotec

Introduction

One of the hypothesis that attempts to account for the persistence of genes for male androphilia throughout evolutionary time is the sexually antagonistic genes hypothesis (SAGH). A sexually antagonistic gene is one that produces fitness costs in one sex but provides fitness benefits when present in the opposite sex (e.g., Berger et al., 2016). Because kin share genetic material, androphilic males and their female kin could both possess sexually antagonistic genes. According to the hypothesis, sexually antagonistic genes associated with the development of androphilia inhibit reproduction in male carriers, but enhance reproduction when carried by females (Camperio Ciani et al., 2004). Consequently, the female relatives of androphilic males should have more offspring than those of gynephilic males. Elevated reproductive output exhibited by the female relatives of androphilic males is thought to offset the lack of (or reduced) reproduction exhibited by the androphilic male themselves, and thereby allow genes for male androphilia to persist across generations.

Artificial selection experiments on cowpea seed beetles (*Callosobruchus maculatus*) and fruit flies (*Drosophila melanogaster*) confirm that same-sex sexual behavior is partly heritable, and selection for this trait in males leads to an increase in their female relatives' lifetime reproductive success (Berger et al., 2016; Hoskins et al., 2015). Furthermore, molecular genetic research on *Drosophila melanogaster* demonstrates that the X-chromosome is highly susceptible to sexually antagonistic fitness variation (Gibson et al., 2002; but see Fry, 2010). When coupled with human molecular genetic research demonstrating that Xq28—a region located at the tip of the X-chromosome—is linked to male androphilia (e.g., Hamer, 2002; Sanders et al., 2015; but see Ganna et al., 2019), these studies suggest that if sexually antagonistic genes for male androphilia exist, they are likely present on the X-chromosome.

Support for an X-chromosome linked version of the SAGH could be found if the maternal female relatives of androphilic males exhibited elevated reproduction when compared to those of gynephilic males, given that the X-chromosome can only be shared with maternal relatives. Because androphilic males share genes with their mothers and maternal grandmothers, as well as their fathers and maternal grandfathers, any elevated offspring production observed among these female relatives could be attributable to genetic contributions from their male partners as opposed to sexually antagonistic genes. Therefore, elevated reproduction among the mothers and maternal grandmothers of androphilic males does not offer definitive support for the X-linked version of the SAGH. Conversely, androphilic males do not share genes with the reproductive partners of their maternal aunts. As such, while elevated reproductive output by the mothers and maternal grandmothers of androphilic males would be consistent with the X-chromosome-linked version of the SAGH, the most robust demonstration of this hypothesis involves documenting elevated reproduction by androphilic males' maternal aunts alongside that of their mothers or maternal grandmothers.

Studies conducted in various Euro-American cultures have tested the SAGH. Samples drawn from Italy, France, and Spain demonstrated that the mothers and maternal aunts of androphilic males had more children than those of gynephilic males (Camperio Ciani et al., 2004; Camperio Ciani & Pellizzari, 2012; Iemmola & Camperio Ciani, 2009). Similarly, a study conducted in Britain found elevated reproduction among the maternal aunts of White androphilic males, but not among other ethnicities (Rahman et al., 2008). Another British sample showed that the paternal grandmothers of androphilic males had more offspring than those of gynephilic males (King et al., 2005). Finally, a study using samples from the U.S. found elevated reproduction among the sisters and paternal grandmothers of androphilic males compared to those of gynephilic males (Schwartz et al., 2010). Overall, these findings suggest that the female relatives of androphilic males may exhibit elevated reproductive output. Nonetheless, support for the X-chromosome-linked version of the SAGH among Euro-American cultures remains equivocal given that some of these studies did not show elevated reproduction among the maternal relatives of androphilic males, and several studies did not show this elevated reproduction among the key kin category of maternal aunts.

Test of the SAGH in Euro-American cultures is limited by the fact that such populations often exhibit relatively low-fertility rates (Central Intelligence Agency, 2022a). Contemporary families in Euro-American societies tend to cease reproduction after obtaining a certain number of children, or after having one child of each sex. It has been suggested that these so called “stopping rules” obscure well-established biodemographic correlates of male androphilia such as the fraternal birth order effect (Blanchard & Lippa, 2007; Xu & Zheng, 2017; Zucker et al., 2007). A decision to produce fewer children could similarly prevent the female relatives of androphilic males from exhibiting the elevated reproduction that the SAGH predicts.

One way to circumvent the aforementioned limitation would be to conduct tests of the SAGH in populations where females are more likely to reproduce at, or closer to, their maximum capacity. Samoa is a Polynesian island nation in which women have high-fertility rates (Central Intelligence Agency, 2022a) and androphilic males, who are predominantly transgender, are known locally as a “third” gender, *fa’afafine*. Studies have repeatedly demonstrated that the mothers of *fa’afafine* have more offspring than those of gynephilic males (Semenyna, Petterson, et al., 2017; VanderLaan & Vasey, 2011; Vasey & VanderLaan, 2007). In addition, studies have repeatedly demonstrated that the maternal grandmothers of *fa’afafine* have elevated reproductive output compared to those of gynephilic males (Semenyna, Petterson, et al., 2017; VanderLaan et al., 2012). These results are consistent with the X-chromosome-linked version of the SAGH, but do not provide definitive support for the hypothesis because elevated reproduction has not been documented among the maternal aunts of *fa'afafine*.

Support for the SAGH would be greatly bolstered if additional evidence from high-fertility populations could be garnered. To date, no study has directly compared offspring production between the families of cisgender androphilic males, transgender androphilic males, and cisgender gynephilic males within the same culture. With these considerations in mind, the present study tested the SAGH in a high-fertility, non-Euro-American population where both forms of male androphilia exist at appreciable rates—the Istmo Zapotec.

The Zapotec are an indigenous group found primarily in the southern Mexican state of Oaxaca (Danver, 2013; Instituto Nacional de Estadística y Geografía, 2009). Fertility rates in Oaxaca are estimated to be higher than those of most Euro-American cultures (Consejo Nacional de Población, 2018). The relatively high prevalence of both cisgender and transgender *muxes* among the Istmo Zapotec allows for tests of the SAGH using both expressions of male androphilia within the same culture. The current study compared the reproductive output of maternal and paternal line male and female extended relatives (i.e., grandmothers, aunts, and uncles), as well as the mothers of gynephilic males, cisgender *muxe nguiiu*, and transgender *muxe gunaa*. The two *muxe* groups were first compared to each other and then each was individually compared with gynephilic males. In light of the SAGH and given that previous research has shown elevated reproduction among the relatives of Euro-American cisgender androphilic males, as well as non-Euro-American transgender androphilic males (see above), we predicted that offspring production by the relatives of *muxe gunaa* and *muxe nguiiu* would not differ. Furthermore, in line with the X-chromosome-linked version of the SAGH, we predicted that the maternal female relatives of both *muxe gunaa* and *muxe nguiiu* would have higher offspring production when compared to the maternal female relatives of gynephilic males.

Method

Participants

Data were collected in the city of Juchitán de Zaragoza, as well as 14 towns and villages within both the Juchitán and Tehuantepec districts of the Istmo region of Oaxaca, Mexico. Four field trips took place between November and December 2015, February–March 2016, November–December 2016, and February 2018. All participants were recruited using a network sampling procedure that consisted of contacting initial participants, who gave referrals for additional participants, who in turn provided further referrals, and so on. Written consent was required prior to participating in the study.

A total of 171 cisgender gynephilic men, 115 transgender *muxe gunaa*, and 112 cisgender *muxe nguiiu* were interviewed for this study. Participants' sexual orientation was assessed using a Kinsey scale (Kinsey et al., 1948) for sexual feelings over the previous year. Istmo Zapotec, including *muxes* themselves, recognize that *muxes* are biological males, as evidenced by the fact that they possess male genitalia and secondary sexual characteristics. Nevertheless, participants were informed that the category "males" included men and/or *muxes*, whereas the category "females" only included women. All men identified as exclusively (Kinsey rating = 0, $n = 165$) or predominantly gynephilic (Kinsey rating = 1, $n = 6$). All *muxe gunaa* identified as exclusively androphilic (Kinsey rating = 6, $n = 115$). All *muxe nguiiu* identified as exclusively (Kinsey rating = 6, $n = 96$) or predominantly androphilic (Kinsey rating = 5, $n = 16$).

Biographic Information

Participants were asked to report their age in years. A one-way ANOVA revealed that the average age of gynephilic men ($M = 30.33$, $SD = 9.18$), *muxe gunaa* ($M = 30.39$, $SD = 9.29$), and *muxe nguiiu* ($M = 29.79$, $SD = 9.46$) did not differ significantly ($F[2, 395] = .151$, $p = .860$). Participants were also asked to report their average weekly income with a scale ranging from 1 (0–250 Mexican Pesos) to 9 (more than 2000 Mexican Pesos). A one-way ANOVA revealed that the average level of income for gynephilic men ($M = 4.98$, $SD = 2.48$), *muxe gunaa* ($M = 4.77$, $SD = 2.24$), and *muxe nguiiu* ($M = 5.36$, $SD = 2.58$), did not differ significantly ($F[2, 395] = 1.67$, $p = .190$). As such, neither of these biographic variables were used as covariates when conducting further analysis.

Procedure and Measures

Participants were interviewed using standardized questionnaires, which were available in Spanish after being translated and back-translated by fluent Spanish–English speakers. The first author, as well as Spanish-speaking research assistants, were available to answer participants' questions. A Zapotec-speaking research assistant was also present for interviews involving participants who were not fully fluent in Spanish. Questions were read out loud by research assistants in Spanish or Zapotec as necessary.

Participants were asked to report the total number of offspring produced by their biological mothers, their paternal and maternal biological grandmothers, and each of their paternal and maternal biological aunts and uncles. Non-biological children were excluded from the analysis. The mean number of children produced by each kin category was calculated for each group and used to conduct group comparisons. Some of the participants had relatives who moved outside of the Istmo to different areas within Mexico or to different countries that are known to have lower fertility rates (e.g., Mexico City, United States). Since the primary aim of this study was to analyze the offspring production of the families of *muxes* and gynephilic men within the Istmo region of Oaxaca, only relatives who spent their entire reproductive history within the Istmo were included in the analysis.

Results

The offspring production of each kin category was compared among Istmo Zapotec gynephilic men, *muxe gunaa*, and *muxe nguiiu* using independent samples *t*-tests, as well as Cohen's *d* effect sizes with 99% CI. Given the numerous statistical comparisons carried out, a more conservative critical alpha of .01 was used to control the Type I error rate. Using a more conservative critical alpha of .01 reduces the probability of Type I errors due to multiple comparisons, while also preventing the Type II error rate from being unacceptably high, as would be the case if a more conservative correction (e.g., Bonferroni correction) was employed (see Nakagawa, 2004).

Comparison between the two types of *muxes* demonstrated that the mothers and paternal aunts of transgender *muxe gunaa* had significantly more offspring than those of cisgender *muxe nguiiu* (Table 6.1). With respect to the transgender form of male androphilia, the mothers, paternal aunts, maternal aunts, and maternal uncles of *muxe gunaa* had a significantly elevated reproduction relative to those of gynephilic men (Table 6.2). Finally, no significant group differences were found in the average number of offspring produced by the kin of *muxe nguiiu* and gynephilic men (Table 6.3).

Discussion

The present study compared the number of offspring produced by the relatives of Istmo Zapotec *muxes* and gynephilic men. Given that previous research on the SAGH has never directly compared both forms of male androphilia within the same cultures, we first compared

Table 6.1

Average offspring production of paternal and maternal-line relatives of muxe gunaa and muxe nguiiu

	Muxe Gunaa			*Muxe Nguiiu*			*t*	*df*	*p*[a]	Cohen's *d*
	n	*M*	*SD*	*n*	*M*	*SD*				[99% CI]
Paternal line										
Grandmothers	111	6.57	2.54	109	6.37	2.32	.612	218	.541	.08 [-.27, .43]
Aunts[b]	92	3.35	1.87	89	2.58	1.49	3.09	172.6	.002	.45 [.06, .84]
Uncles[c]	89	3.05	2.00	92	2.69	1.36	1.40	154.7	.163	.21 [-.17, .59]
Maternal line										
Grandmothers	112	6.83	3.10	108	6.19	2.56	1.65	218	.099	.22 [-.12, .57]
Aunts	96	3.60	1.88	89	3.19	2.35	1.32	183	.190	.19 [-.19, .57]
Uncles	91	3.29	1.64	89	2.87	1.40	1.86	178	.065	.27 [-.11, .66]
Mothers[d]	114	5.11	2.55	112	3.94	1.87	3.96	207.2	< .001	.52 [.17, .87]

[a] Two-tailed *p*-value

[b] Degrees of freedom and *t*-statistic were adjusted based on Levene's test for equality of variances: $F = 3.98$, $p = .047$

[c] Degrees of freedom and *t*-statistic were adjusted based on Levene's test for equality of variances: $F = 7.02$, $p = .009$

[d] Degrees of freedom and *t*-statistic were adjusted based on Levene's test for equality of variances: $F = 14.65$, $p = < .001$

Table 6.2

Average offspring production of paternal and maternal-line relatives of muxe gunaa and gynephilic men

	Muxe Gunaa			Gynephilic Men			*t*	*df*	*p*[a]	Cohen's *d*
	n	*M*	*SD*	*n*	*M*	*SD*				[99% CI]
Paternal line										
Grandmothers	111	6.57	2.54	167	5.76	2.72	2.49	276	.013	.31 [-.01, .62]
Aunts[b]	92	3.35	1.87	128	2.69	1.39	2.86	159.2	.005	.41 [.05, .76]
Uncles[c]	89	3.05	2.00	137	2.49	1.39	2.28	143.2	.024	.34 [-.02, .69]
Maternal line										
Grandmothers	112	6.83	3.10	167	6.14	2.57	2.03	277	.044	.25 [-.07, .56]
Aunts[d]	96	3.60	1.88	138	2.95	1.50	2.83	174.6	.005	.39 [.04, .73]
Uncles	91	3.29	1.64	145	2.51	1.92	3.24	234	.001	.43 [.08, .78]
Mothers[e]	114	5.11	2.55	170	3.89	2.04	4.29	205.2	<.001	.54 [.22, .86]

[a] Two-tailed *p*-value

[b] Degrees of freedom and *t*-statistic were adjusted based on Levene's test for equality of variances: $F = 10.81$, $p = .001$

[c] Degrees of freedom and *t*-statistic were adjusted based on Levene's test for equality of variances: $F = 7.73$, $p = .006$

[d] Degrees of freedom and *t*-statistic were adjusted based on Levene's test for equality of variances: $F = 4.05$, $p = .045$

[e] Degrees of freedom and *t*-statistic were adjusted based on Levene's test for equality of variances: $F = 10.38$, $p = .001$

Table 6.3

Average offspring production of paternal and maternal-line relatives of muxe nguiiu and gynephilic men

	Muxe Nguiiu			Gynephilic Men			*t*	*df*	p^a	Cohen's *d*
	n	*M*	*SD*	*n*	*M*	*SD*				[99% CI]
Paternal line										
Grandmothers	109	6.37	2.32	167	5.76	2.72	1.92	274	.056	.24 [-.08, .55]
Aunts	89	2.58	1.49	128	2.69	1.39	-.586	215	.559	-.08 [-.43, .28]
Uncles	92	2.69	1.36	137	2.49	1.39	1.05	227	.294	.15 [-.20, .49]
Maternal line										
Grandmothers	108	6.19	2.56	167	6.14	2.57	.179	273	.858	.02 [-.30, .34]
Aunts[b]	89	3.19	2.35	138	2.95	1.50	.865	134.7	.389	.13 [-.22, 48]
Uncles	89	2.87	1.40	145	2.51	1.92	1.56	232	.121	.21 [-.14, .55]
Mothers	112	3.94	1.87	170	3.89	2.04	.205	280	.838	.03 [-.29, .34]

[a] Two-tailed *p*-value

[b] Degrees of freedom adjusted based on Levene's test for equality of variances: $F = 9.50$, $p = .002$

transgender and cisgender *muxes* to determine whether their relatives' offspring production differed. Contrary to our predictions, the mothers and paternal aunts of *muxe gunaa* had significantly more offspring than those of *muxe nguiiu*.

Unlike previous Samoan studies (Semenyna, Petterson, et al., 2017; VanderLaan et al., 2012), this study did not find significantly higher offspring production among the maternal grandmothers of our transgender androphilic male sample when compared to the maternal grandmothers of gynephilic men. Nonetheless, the mothers of *muxe gunaa* reported having more children than those of gynephilic men, making this the fourth study that has found a significantly elevated pattern of reproduction among the mothers of transgender androphilic males (Semenyna, Petterson, et al., 2017; VanderLaan & Vasey, 2011; Vasey & VanderLaan, 2007). Furthermore, this is the first study to show elevated reproductive output among the maternal aunts of transgender androphilic males, which is consistent with the maternal aunt effect found among the families of cisgender androphilic males in various Euro-American populations (Camperio Ciani et al., 2004; Camperio Ciani & Pellizzari, 2012; Iemmola & Camperio Ciani, 2009). This is an important replication of the finding that androphilic males' maternal aunts exhibit elevated reproduction, given that this kin category alone is typified by X-linked relatedness that is not confounded by a simultaneous genetic relationship between study participants and their female kin's reproductive partner (i.e., fathers and grandfathers).

Two patterns were observed that one would not predict based on an X-chromosome linked version of the SAGH. First, the paternal aunts of *muxe gunaa* exhibited higher reproduction than the paternal aunts of gynephilic men. As mentioned in the Introduction, some studies have previously reported elevated reproductive output among the paternal female kin of male androphiles. For example, King et al. (2005) and Schwartz et al. (2010) found that the paternal grandmothers of androphilic males had more offspring than those of gynephilic males, although the effect sizes for these differences were small (Cohen's $d = .17$ and .15, respectively). Furthermore, VanderLaan et al. (2012) reported elevated reproductive output among the paternal grandmothers of Samoan *fa'afafine* compared to those of gynephilic men, but the same group failed to replicate this effect using a much larger sample (Semenyna, Petterson, et al., 2017). This suggests that the initial paternal grandmother effect reported by VanderLaan et al. (2012) might have represented a Type I error. The samples employed for the current study are large by the standards of cross-cultural research, but the paternal aunt effect for *muxe gunaa* should nonetheless be viewed with caution until such time that a replication study is possible. If, however, this effect is real, then it raises the possibility that elevated reproduction among the female kin of male androphiles could be influenced by sexually antagonistic autosomal genes alone, or in combination with, sexually antagonistic X-chromosome linked genes. Lending further credence to this possibility, molecular genetic research demonstrates that the centromeric region of the autosomal chromosome 8 is associated with the expression of male androphilia (Mustanski et al., 2005; Sanders et al., 2015), and that single-nucleotide polymorphisms (SNPs) in the 11th (rs34730029-11q12.1) and 15th (rs28371400-15q21.3) chromosome are associated with same-sex sexual behavior in males (Ganna et al., 2019).

Second, the maternal uncles of *muxe gunaa* exhibited elevated reproductive output compared to those of gynephilic men. The SAGH makes no predictions regarding reproduction by the male kin of male androphiles, but an alternate hypothesis for the evolution of male androphilia, known as the Overdominance Hypothesis (OH), might inform this result. The OH states that genes associated with male androphilia increase reproduction when in the heterozygous state (i.e., two different alleles exist at a single locus, one of which is a gene influencing male androphilia and the other is not) and increase the probability of male androphilia when in the homozygous state (i.e., two copies of the same allele influencing male androphilia are present) (e.g., Camperio Ciani & Pellizzari, 2012; Gavrilets & Rice, 2006; Miller, 2000; Zietsch et al., 2008). Mathematical models demonstrate that overdominance could maintain genes for male androphilia in a population if such genes were over-represented in autosomal chromosomes (Gavrilets & Rice, 2006) such as the 8th, 11th, and 15th chromosome (Ganna et al., 2019; Mustanski et al., 2005; Sanders et al., 2015). Furthermore, some familial clustering studies conducted in Euro-American (Bailey et al., 1999; Schwartz et al., 2010) and non-Euro-American cultures (Gómez et al., 2018; Semenyna, VanderLaan, et al., 2017; VanderLaan, Forrester, et al., 2013; VanderLaan, Vokey, & Vasey, 2013) have found that androphilic males exhibit a preponderance of androphilic male relatives in both the maternal and paternal lines, suggesting that autosomal-linkage factors are important for the inheritance of male androphilia (but see Camperio Ciani et al., 2004; Hamer et al., 1993; Rahman et al., 2008). This is the first study to report elevated reproductive output by the uncles of male androphiles[11] and, as with the paternal aunt effect described above, may represent a Type I error rather than a meaningful group difference. As such, this finding should be viewed with caution until such time that a replication study is possible.

Contrary to our predictions, the present study found that the female relatives of cisgender *muxe nguiiu* did not have more offspring than those of gynephilic men. This finding is inconsistent with some studies in Euro-American cultures, which demonstrate that the female relatives of gay men have elevated reproduction relative to those of gynephilic men (Camperio

[11] King et al. (2005) and Schwartz et al. (2010) reported elevated reproductive output by paternal aunts and uncles combined and, as such, it is not possible to isolate whether aunts, uncles, or both were responsible for this effect.

Ciani et al., 2004; Camperio Ciani & Pellizzari, 2012; Iemmola & Camperio Ciani, 2009; King et al., 2005; Rahman et al., 2008; Schwartz et al., 2010). One explanation for the lack of group differences between *muxe nguiiu* and gynephilic men, as well as the differences observed between the families of transgender and cisgender *muxes*, would be that the female relatives of *muxe gunaa* are more likely to possess sexually antagonistic genes that increase reproduction than the female relatives of *muxe nguiiu*. Consistent with this argument, Gómez et al. (2018) demonstrated that the maternal aunts of *muxe gunaa* had a higher proportion of *muxe* sons than the maternal aunts of *muxe nguiiu*. This suggests that maternal aunts of *muxe gunaa* might have a higher proportion of sexually antagonistic genes that are responsible for both their elevated reproduction and their higher proportion of *muxe* sons. This possibility must be viewed with caution, however, since the differences in proportion of *muxe* sons found between the maternal aunts of *muxe gunaa* and *muxe nguiiu* could represent a Type I error due to the relatively low sample sizes employed (Gómez et al., 2018).

An alternate explanation for the group differences observed between the two types of *muxes* is that there are social factors suppressing reproduction among the families of *muxe nguiiu*, but these same social factors do not exist among the families of *muxe gunaa*. One relevant social factor, in this regard, could be socioeconomic status. Throughout recent history (i.e., mid-18th century to present), families from lower socioeconomic classes, especially those that have lower education, tend to have increased reproduction, and hence larger family sizes, than those from higher socioeconomic classes (e.g., Dribe et al., 2014; Skirbekk, 2008). Furthermore, research across a number of cultures, including among the Istmo Zapotec, suggests that androphilic males with a more feminine gender expression (e.g., *muxe gunaa*) tend to come from lower socioeconomic classes, whereas those with a more masculine presentation (e.g., *muxe* *nguiiu*) come from higher ones (e.g., Blanchard et al., 1987; Harry, 1985; MacFarlane, 1984; Miano Borruso, 2002; Mirandé, 2017; Prieur, 1998; Singh et al., 2021). As such, it could be that the female relatives of cisgender *muxes* did not exhibit elevated offspring production because their higher socioeconomic position restricts their reproductive potential in some manner. For example, women with higher socioeconomic status may have had greater access to birth control, been more motivated to limit their family size for socioeconomic reasons, and thus have been greater users of this technology. Accordingly, it is plausible that the female relatives of both types of androphilic males possess sexually antagonistic genes, but the reproductive benefits associated with such genes are only expressed under conditions that approximate the genes' environment of evolutionary adaptiveness (i.e., absence of birth control and socioeconomic considerations that limit women's peak reproductive capacity) (Irons, 1998).

Conversely, it is possible that the families of transgender and cisgender *muxes* differ in their reproductive output solely for social reasons (i.e., they come from lower socioeconomic classes; see above) and not because of sexually antagonistic genes that increase reproduction. If correct, this possibility would help explain why the grandmothers of all three groups did not differ from each other. Poverty rates in Mexico during the mid-20th century were higher than currently is the case, meaning that a higher proportion of the population previously occupied a lower socioeconomic position (Consejo Nacional de Evaluación de la Política de Desarrollo Social, 2022; Székely, 2005). This suggests that there may have been less variation in socioeconomic status among all the participant's grandmothers (i.e., lower socioeconomic status among all grandmothers). For the social reasons outlined above, this, in turn, could have resulted in higher offspring production among all grandmothers and no significant group differences in this regard. Future research should assess the extent to which socioeconomic factors influence offspring production among families of Istmo Zapotec gynephilic males, *muxe gunaa*, and *muxe nguiiu*.

Although socioeconomic status is one possible proximate factor influencing group differences in reproductive output, other factors are worth considering. These include variations in females' physiology, morphology, sexual behaviors, sexual attitudes, religiosity, and fraternal birth order effects. With respect to physiological factors, menarche represents the beginning of females' reproductive lifespan, and variation in the onset of this physiological milestone can lead to inter-individual discrepancies in women's offspring production. Indeed, studies examining age of menarche effects on fertility show that girls who mature early have a longer reproductive lifespan, earlier age of first sexual intercourse, earlier age of first conception, and shorter inter-birth intervals compared to later maturing girls (e.g., Mulder, 1989; Sandler et al., 1984). As such, an earlier age of menarche (along with its reproductive correlates) among the female kin of androphilic males may lead to elevated reproduction compared to the female kin gynephilic males. Future research should examine this possibility.

With respect to morphological factors, research demonstrates that women who are judged to be more facially attractive have more children, more pregnancies, and higher facial femininity and symmetry—the last of which is associated with a healthy reproductive physiology—compared to women who are judged to be less facially attractive (e.g., Grammer & Thornhill, 1994; Jasienka et al., 2006; Jokela, 2009; Little, 2014; Perrett et al., 1999; Pflüger et al., 2012). This suggests that facial attractiveness is a useful proxy for female fertility. Furthermore, given that androphilic males are judged to have more feminine faces than gynephilic males (e.g., González-Álvarez, 2017; Skorska et al., 2015), it could be that sexually antagonistic genes related to male androphilia, if such genes exist, increases facial femininity in both male and female carriers. Future research should determine the relationship between facial femininity, facial attractiveness, and offspring production among the female relatives of androphilic and gynephilic males.

Alongside physiological and morphological factors, females' sociosexuality—that is, their willingness and desire to engage in uncommitted sexual relations (Simpson & Gangestad, 1991)—can also contribute to their reproductive potential. Individuals who score higher on sociosexuality are characterized by increased interest in casual sex and a greater number of sexual partners when compared to those who are lower in sociosexuality. Although increased sociosexuality is associated with a greater number of sexual partners, cross-cultural research demonstrates that it is negatively correlated with fertility rates across countries (e.g., Lippa, 2009; Schmitt, 2005). It is possible that the nature of this association is partially mediated by the availability and usage of contraceptives in modern times. Indeed, contraceptive usage is positively correlated with sociosexuality across countries (e.g., Lippa, 2009; Schmitt, 2005), and its increased effectiveness and availability over the past century is one of the main explanations for what has been termed the "historical fertility transition" (i.e., the decrease in fertility rates) in developed countries (e.g., Bongaarts, 1982). As such, it is worth considering whether the female relatives of androphilic and gynephilic males differ with respect to their sociosexuality and use of contraceptives, and whether such differences can account for variations in their reproductive output.

Both sociosexuality and contraceptive use can be moderated by social factors such as religion. In a cross-cultural study on the association between religious behavior and human mating strategies, Schmitt & Fuller (2015) found that higher personal religiosity was associated with lower sociosexuality. Nonetheless, research demonstrates that the strength of involvement in religious groups that encourage large family sizes and discourage the uses of contraceptives and abortion—such as Roman Catholics, fundamentalist Protestants, and Latter-Day Saints (Mormons)—is positively correlated to offspring production (e.g., Heaton, 1986; Zhang, 2008). Although religiosity is associated with a decrease in uncommitted sexual relations, it can still increase female fertility by promoting within-pair, procreative copulation. Future cross-cultural research should look at the association between religiosity, sociosexuality, contraceptive use, and offspring production, among the families of both androphilic and gynephilic males.

A large body of research indicates that androphilic males tend to have more older biological brothers than gynephilic males. This finding is referred to as the fraternal birth order effect (FBOE) (e.g., Blanchard, 2018a; Bozkurt et al., 2015; Semenyna, VanderLaan, & Vasey, 2017; VanderLaan, Blanchard, et al., 2017). The FBOE presents a confound in studies of reproductive output, because it is unclear whether the female relatives of androphiles display elevated reproduction due to the effect of sexually antagonistic genes, or if these differences appear precisely because larger families are more likely to produce androphilic males (Khovanova, 2019). The leading explanation for the FBOE is the maternal immune hypothesis, which posits that every gestation of a male fetus increases the probability that a mother will be exposed to male-specific antigens (i.e., Y-linked) which influence sexual differentiation of the fetal brain (Bogaert & Skorska, 2011; Bogaert et al., 2018). Over a succession of such pregnancies, the mother's immune system becomes increasingly proficient at recognizing these antigens and responding to them with antibodies that compromises male-typical development. As such, women with higher fertility may produce more androphilic sons because they experience increased immunological reaction to male fetuses and not because they possess sexually antagonistic genes.

Some past studies have attempted to control for this possibility by looking at the reproductive output of the relatives of firstborn androphilic males, whose sexual orientation should not be due to the FBOE. For example, Camperio Ciani et al. (2004) found that firstborn androphilic males had a (non-significant) elevation in the number of siblings compared to firstborn gynephilic males. Using a larger sample, Iemmola and Camperio Ciani (2009) found a significant difference in the same direction. In another study that combined samples from six data sets, Blanchard (2012) found that firstborn gynephilic males had more siblings than firstborn androphilic males in four of the six data samples, which is inconsistent with the SAGH. Finally, in a study that reanalyzed data from Schwartz et al. (2010), Rieger et al. (2012) not only found that firstborn androphilic males had more siblings than firstborn gynephilic males, but also that the mothers of firstborn androphilic males had about the same number of grandchildren as those of firstborn gynephilic males. In other words, the reproductive cost associated with male androphilia were completely offset by the second generation. It is important to note that all these studies were conducted using data from Euro-American countries where fertility rates are relatively low, which increases the possibility that any potential fraternal birth order and sexually antagonistic genes effects will be obscured. As such, future studies should test the SAGH using similar procedures in places with relatively higher fertility rates, such as in Samoa or in the Istmo region of Oaxaca, Mexico.

Finally, another manner by which the maternal immune response could be associated with the reproductive differences between the female relatives of androphilic and gynephilic males is through differences in the rate of miscarriages. Namely, it is possible that immunological reactions to male fetuses increase the rate of miscarriages among some women, whereas in others who are less prone to miscarriages and, thus, more fecund, it increases the rate of androphilia among the surviving male offspring. If so, the mothers of androphilic males should have fewer miscarriages than those of gynephilic males. Contradicting this possibility, however, is a study reporting that mothers of androphilic males had more miscarriages than mothers of gynephilic males (Skorska et al., 2017). Nonetheless, this increase in fetal loss was specific to mothers of androphilic male only-children, whereas the same was not true for mothers of androphilic males with siblings. More research is needed to understand the relationship between the FBOE, rates of miscarriages, and male sexual orientation.

Limitations

Two noteworthy limitations characterized the current study. First, the reproductive histories of the participants' relatives were not systematically corroborated with the relatives themselves. However, no test of the SAGH has independently corroborated the family pedigree with the relatives of participants. That being said, the Istmo Zapotec are characterized by being a collectivistic culture where individuals often live with, or in close proximity to, their families. Consequently, participants' family members were often nearby to verify family pedigrees as data were being collected. Thus, the information provided by participants was often corroborated, corrected, or elaborated upon by their relatives until a consensus was reached.

The second limitation of this study relates to the fact that we did not assess the reproductive output of participants' sisters. Although such data would be informative, it is highly likely that the sisters of participants would not have finished their reproductive careers at the time of data collection. Nonetheless, future research comparing the offspring production of the sisters of androphilic and gynephilic males would be potentially informative.

Conclusion

The findings of this study among the Istmo Zapotec are broadly consistent with those conducted in Samoa (Semenyna, Petterson, et al., 2017; VanderLaan & Vasey, 2011; VanderLaan et al., 2012; Vasey & VanderLaan, 2007) in that they show elevated reproduction among the mothers of transgender androphilic males, as predicted by the SAGH. Moreover, this is the first study to demonstrate that the maternal aunts of transgender androphilic males exhibit elevated reproduction, a pattern that is consistent with the maternal aunt effect found among the families of cisgender androphilic males in various Euro-American populations (Camperio Ciani et al., 2004; Camperio Ciani & Pellizzari, 2012; Iemmola & Camperio Ciani, 2009). However, inconsistent with the SAGH, the female kin of cisgender androphilic males (*muxe nguiiu*) did not differ in terms of their reproductive output from those of gynephilic males. Moreover, the mothers and paternal aunts of transgender androphilic males had higher offspring production than those of cisgender androphilic males—a pattern that is also inconsistent with the predictions of the SAGH. These group differences may be attributable to social factors such as socioeconomic status that could vary between the families of *muxe gunaa*, *muxe nguiiu*, and gynephilic males in the Istmo Zapotec. Future research should determine whether biological or social factors, or both, are responsible for the differences in offspring production among the families of gynephilic males and both forms of androphilic males in the Istmo Zapotec.

Chapter 7: Facial Attractiveness of the Sisters of Istmo Zapotec Men and *Muxes*: Implications for the Evolution of Male Androphilia

Abstract

Research shows that the female relatives of androphilic males have more children than the female relatives of gynephilic males. The mechanisms by which this occurs are unclear. The hypergyny hypothesis suggests that the female relatives of androphilic males have elevated attractiveness which allows them to obtain male partners with higher socioeconomic status, which in turn, provide them with more resources to produce and sustain multiple offspring. We tested whether the female kin of male androphiles are characterized by elevated attractiveness compared to the female kin of male gynephiles. The research was conducted among the Istmo Zapotec from Oaxaca, Mexico, where androphilic males are recognized as a third gender, *muxes*. We recruited 115 gynephilic men who rated the facial attractiveness of 27 women with at least one *muxe* sibling and 27 women with gynephilic male siblings but not *muxe* siblings (i.e., control sisters). The results showed that gynephilic men found the faces of control sisters more attractive than the faces of *muxe* sisters. This finding is inconsistent with the hypergyny hypothesis and suggests that elevated facial attractiveness is not the mechanism by which the female relatives of androphilic males achieve elevated reproduction.

Keywords: male androphilia; hypergyny; facial attractiveness; *muxes*; Istmo Zapotec.

Introduction

Camperio Ciani et al. (2004) proposed the sexually antagonistic genes hypothesis (SAGH) to resolve the evolutionary paradox of male androphilia. As discussed in the previous chapter, the SAGH holds that genes associated with androphilia in males can persist across generations if the same genes lead to elevated reproduction when present in females. In this way, the fitness costs associated with male androphilia are offset by the fitness benefits experienced by their female kin. Barthes et al. (2013) extended this SAGH with the hypergyny hypothesis. This hypothesis holds that the female relatives of androphilic males signal high fertility through elevated attractiveness, which allows them to obtain male sexual partners of high social-economic status. Such high-status males are able to provide abundant resources, which allows their female partners to produce and support a greater number of offspring when compared to women with no androphilic male relatives. Barthes et al. (2013) used a mathematical model to demonstrate that within stratified societies, this hypergyny could theoretically allow for the selection of sexually antagonistic genes promoting androphilia in males and elevated fertility in females.

Consistent with both of these hypotheses, studies conducted across multiple cultures have found that the female relatives of androphilic males have more offspring than those of gynephilic males (e.g., Camperio Ciani et al., 2004; Camperio Ciani & Pellizzari, 2012; Iemmola & Camperio Ciani, 2009; King et al., 2005; Rahman et al., 2008; Schwartz et al., 2010; Semenyna, Petterson, et al., 2017; VanderLaan & Vasey, 2011; Vasey & VanderLaan, 2007). Moreover, some studies have found that facial attractiveness is positively associated with health and number of children and pregnancies, suggesting that facial attractiveness is an accurate cue of female fertility (e.g., de Jager et al., 2018; Jokela, 2009; Pflüger et al., 2012; Thornhill & Gangestad, 1999; but see Silva et al., 2012). Nonetheless, a test of the hypergyny hypothesis in Thailand found that the sisters of androphilic males were rated by gynephilic men as having lower facial attractiveness than control women with no androphilic male relatives (Skorska et al., 2020). This finding is in direct contrast to Barthes et al.'s (2013) premise that the female relatives of androphilic males have elevated attractiveness. Similar tests in other cultures would be instructive.

In the present study, we tested one of the premises of the hypergyny hypothesis by comparing gynephilic men's ratings of facial attractiveness for: (1) women with at least one androphilic male sibling versus (2) women with gynephilic male siblings but no androphilic male siblings. The research was conducted among the Istmo Zapotec—the people of Mesoamerican origins who inhabit the Istmo region of Oaxaca, Mexico. Previous research conducted in this region has found that the female relatives of *muxes* have more offspring than those of gynephilic men (see Chapter 6). This finding, coupled with Barthes et al.'s (2013) hypergyny hypothesis, led us to predict that Istmo Zapotec gynephilic men would rate the sisters of *muxes* as more attractive than women who only had gynephilic male siblings.

Method

Participants

Potential female participants were asked if they had biological male siblings. Only those who had male siblings were interviewed. Data from 54 Istmo Zapotec women were utilized to conduct the present study. Of these, 27 reported having at least one *muxe* sibling, and 27 reported having gynephilic male siblings but no *muxe* siblings. The latter group was therefore used as control sisters. Female participants reported their sexual orientation using a 7-point Kinsey scale

(Kinsey et al., 1948). All women identified as exclusively (Kinsey 6; $n = 52$) or predominantly androphilic (Kinsey 5; $n = 2$).

A total of 120 males were recruited to rate the facial attractiveness of the female images. Male participants' sexual orientation was also assessed using a 7-point Kinsey scale. Out of the 120 males, 107 responded as Kinsey 0, 8 as Kinsey 1, 1 as Kinsey 2, 3 as Kinsey 3, and 1 as Kinsey 5. Only those who identified as exclusively (Kinsey 0) or predominantly gynephilic (Kinsey 1) were selected to conduct the present study ($N = 115$).

Materials and Measures

Standardized, frontal facial pictures of female participants were taken using a Nikon D3400 DSLR Camera with the aid of a tripod. Participants were asked to remove any facial ornamentation (e.g., glasses, makeup, earrings), tie their hair up, and wear a disposable hairnet above the hairline and behind the ears so that the hairline was clearly visible. Participants stood in front of a white cardboard background and looked directly at the camera while maintaining a neutral expression (i.e., with their mandible relaxed, teeth not touching, and lips closed in a relaxed manner) with their eyes open and chin slightly up. Photographs were taken two meters from the participant with the flash setting on. Participants' faces were framed as tightly as possible. The frame was focused on the participant's nose. A total of 94 pictures were taken out of which 27 were from *muxe* sisters and 67 were from potential control sisters. Women's height (in meters) and weight (in kilograms) were also measured using a measuring tape and a scale. Women's body mass index (BMI) was then calculated $\frac{kg}{m^2}$. The BMI for two *muxe* sisters could not be obtained.

From the pool of 67 images of control sisters, we randomly selected 27 that were within the same age range as the 27 *muxe* sisters (i.e., 18–46) to create the stimuli for male raters. This was done so that the two sister groups would not differ significantly in age (see Results). Thus, 54 images composed of 27 *muxe* sisters and 27 control sisters were selected for males to rate. The order of the 54 images was randomized for placement into a flipbook. The images were then divided into 4 blocks (two with 13 pictures and two with 14 pictures), and the block order was randomized for each male rater.

Procedure

Data from female participants were collected during two trips between June-August 2018 and May 2019 in the city of Juchitán de Zaragoza, as well as other towns and villages within the Juchitán and Tehuantepec districts of the Istmo region of Oaxaca, Mexico. Female participants were recruited using a network sampling procedure that consisted of contacting initial participants, who gave referrals for additional participants, who in turn provided further referrals, and so on. Female participants were required to provide informed written consent prior to participation and provided with 150 Mexican Pesos for their participation. The participants reported their age (in years), had a standardized facial image taken, and had their BMI measured. Female participants' ages ranged from 18 to 46.

Data from male participants were collected in November 2019 in different towns from those in which the photos were taken to reduce the possibility of raters recognizing the women in the photos. Male participants were recruited using a network sampling procedure, required to provide informed written consent prior to participation, and provided with 150 Mexican Pesos for their participation. Male participants were presented with a flipbook containing 54 images of women's faces and were asked to rate how attractive they found each image using a 7-point Likert scale that ranged from 1 = very unattractive to 7 = very attractive. Participants viewed each image in the flipbook and stated their rating aloud. Their responses were recorded by a member of the research group, who did not respond or comment. Male participants then reported their age (in years) which ranged from 18 to 62.

All procedures were approved by the Human Participant Research Committee at the authors' institution. Canadian foreign nationals, and USA Citizens, are permitted to conduct research in Mexico for a period of 180 days if they have a valid passport (Consulado General de México en Toronto, 2022). In addition, however, we obtained a letter endorsing our research from the Office of the Municipal President in Juchitán, Mexico. Our research was also endorsed by some of the leaders of the *muxe* community.

Statistical Analyses

Mean facial attractiveness scores were calculated for each female by averaging the ratings they received from all male raters. Additionally, for each male rater, three mean facial attractiveness ratings were calculated by averaging the ratings given to the 27 images of *muxe* sisters, the 27 images of control sisters, and across all 54 images. Two independent sample *t*-tests were conducted to assess differences in age and BMI between the two sister groups. Pearson's *r* correlation analyses were conducted to assess the relationship between women's age, BMI, and their mean facial attractiveness score, and between men's age and the mean facial attractiveness rating of all the 54 images.

Given that significant correlations were found between women's age and mean facial attractiveness scores and between men's age and mean facial attractiveness ratings (see Results), separate analyses were conducted to control for women's and men's age. For the female data, we conducted a one-way ANCOVA to assess differences in mean facial attractiveness scores between *muxe* sisters and control sisters using women's age as a covariate. The strength of the between-group difference was assessed with a Cohen's *d* effect size controlling for age, calculated as $\frac{M_1 - M_2}{\sqrt{\frac{(n_1-1)SD_1^2 + (n_2-1)SD_2^2}{n_1+n_2-2}}\ (1 - r_{xy}^2)^{1/2}}$ where r_{xy}^2 was the squared correlation between women's mean facial attractiveness scores and their age (Arvey et al., 1985; Cohen, 1977; Cortina & Nouri, 2000).

For the male data, the effects of the repeated measured factor (i.e., ratings given to the images of *muxe* sisters versus control sisters) were assessed separately from the influence of the covariate (i.e., age), which was centered around the mean (see Delaney & Maxwell, 1981; Schneider et al., 2015). Therefore, a repeated measures ANOVA was conducted to assess the differences between men's mean facial attractiveness ratings given to *muxe* sisters and control sisters, and a repeated measures ANCOVA was conducted to determine whether there was an interaction between men's age and the image group. Since there was a significant interaction (see Results), two age groups were created by splitting men below and above the median age (24 years), and the analyses were repeated for both age groups. The strength of the within-group differences were assessed with Cohen's *d* effect sizes for paired samples calculated as $\frac{M_1 - M_2}{\sqrt{\frac{SD_1^2 + SD_2^2}{2}}}$ (Cumming, 2012; Lakens, 2013).

Results

Descriptive statistics for *muxe* sisters and control sisters are reported in Table 7.1. No differences in age, $t(52) = 0.19$, $p = .854$, and BMI, $t(50) = -1.00$, $p = .324$, were found between *muxe* sisters and control sisters. However, significant negative correlations were found between age and mean facial attractiveness scores among all women combined ($n = 54$, $r = -0.60$, $p < .001$), and among *muxe* sisters ($n = 27$, $r = -0.55$, $p = .003$) and control sisters ($n = 27$, $r = -0.70$, $p < .001$). Furthermore, BMI was negatively related with mean facial attractiveness scores among all women, but not among *muxe* sisters ($n = 25$, $r = -0.39$, $p = .053$), nor control sisters (*n*

= 27, r = -0.33, p = .098). Given the lack of significant within-group correlations and given that the direction and significance of the group comparison for mean facial attractiveness scores did not change when controlling for women's BMI, this variable was not used as a covariate in the subsequent analysis. Control sisters had significantly higher mean facial attractiveness scores than *muxe* sisters, $F(1, 51) = 5.35$, $p = .025$, Cohen's $d = .58$ (95% CI: .04, 1.13). There was no significant interaction between sister group and women's age, $F(1, 50) = 1.72$, $p = .196$.

Table 7.1

Descriptive statistics for age, body mass index, and the mean facial attractiveness scores of muxe sisters and control sisters.

	Muxe sisters (n = 27)		Control sisters (n = 27)	
	M	*SD*	*M*	*SD*
Age	29.78	8.02	30.19	8.13
Body mass index	31.82	8.15	29.89	5.63
Mean facial attractiveness score	2.65	0.52	2.93	0.66

Values for the mean facial attractiveness scores ranged from 1 to 7.

Descriptive statistics for male raters are reported in Table 7.2. A significant positive correlation was found between men's age and the mean facial attractiveness ratings (r = 0.33, p < .001). Control sisters were rated as significantly more attractive than *muxe* sisters among all men, $F(1, 114) = 108.80$, $p < .001$, Cohen's $d = .27$ (95% CI: .21, .34). A significant interaction between image group and men's age was found, $F(1, 113) = 7.78$, $p = .006$. However, this interaction disappeared once the men were separated by the median age into those who were younger than 24, $F(1, 54) = 0.11$, $p = .738$, and those who were 24 and older, $F(1, 57) = 1.69$, p = .199. Control sisters were rated as significantly more attractive by both men who were younger than 24 years of age, $F(1, 55) = 57.70$, $p < .001$, Cohen's $d = .24$ (95% CI: .17, .32), and those who were 24 years of age and older, $F(1, 58) = 60.61$, $p < .001$, Cohen's $d = .34$ (95% CI: .23, .44).

Table 7.2

Descriptive statistics for age and the mean facial attractiveness ratings given by male raters combined and separated by age.

	Male raters					
	All ages (n = 115)		< 24 years of age (n = 56)		≥ 24 years of age (n = 59)	
	M	*SD*	*M*	*SD*	*M*	*SD*
Age	29.16	11.33	20.30	1.61	37.56	10.11
Mean facial attractiveness ratings						
All images	2.79	0.99	2.39	0.87	3.16	0.97
Muxe sisters	2.65	0.97	2.28	0.85	2.99	0.95
Control sisters	2.92	1.04	2.50	0.89	3.33	1.01

Values for the mean facial attractiveness ratings ranged from 1 to 7.

Discussion

The present study was conducted in the Istmo region of Oaxaca, Mexico, and examined whether the sisters of androphilic males (i.e., *muxes*) were rated as having higher facial attractiveness than control sisters with gynephilic male siblings but no androphilic male siblings. In direct contrast to our prediction, gynephilic men rated control sisters as more facially attractive than the sisters of *muxes*. These results are remarkably consistent with those found in the previous test of the hypergyny hypothesis conducted in Thailand (Skorska et al., 2020). Altogether, these findings are inconsistent with key elements of Barthes et al.'s (2013) hypergyny hypothesis and suggests that elevated facial attractiveness is not one of the proximate mechanisms underlying the elevated fertility observed among androphilic males' female relatives.

Although the findings from the present study are inconsistent with Barthes et al.'s (2013) hypergyny hypothesis, there are other ways of assessing female attractiveness that were not considered. These include assessment of skin smoothness, hair quality, fluctuation asymmetry, movement patterns (e.g., sprightly gait), waist-to-hip ratio, and breast size (see Sugiyama, 2005, 2015 for review). As a way of further testing the hypergyny hypothesis, future research could investigate whether these characteristics differ between women with androphilic male siblings versus those without.

Alternatively, it could be that factors other than attractiveness are responsible for the elevated reproduction observed among the female relatives of androphilic males. For example, Camperio Ciani et al. (2012) found that the female relatives of androphilic males had more offspring and fewer gynecological disorders and complicated pregnancies than those of gynephilic males. Thus, future studies should assess the extent to which potential differences in reproductive health between the female relatives of androphilic and gynephilic males can help explain the differences in fertility found between the two groups.

Finally, it is possible that the elevated reproduction observed among androphilic males' female relatives is not a consequence of sexually antagonistic genes but is, instead, a by-product of the fraternal birth order effect (FBOE). The FBOE is the finding that older brothers increase the odds of androphilia in later-born males (Blanchard, 2018a, 2018b, 2019; Gómez Jiménez et al., 2020b; Nila et al., 2019). Research indicates the FBOE results from maternal immunological reactions to male-specific antigens which intensifies with successive gestations of male fetuses (Bogaert & Skorska, 2011; Bogaert et al., 2018). In a meta-analysis aimed at parsing the FBOE from any female fecundity effect that might be owing to sexually antagonistic selection, Blanchard et al. (2020) found that among two-son families, the odds of male androphilia were greater in second born males compared to first born ones, a pattern that is consistent with the FBOE. In contrast, the odds of male androphilia did not differ between first born males with one younger brother and males without brothers, a pattern that is inconsistent with the sexually antagonistic genes hypothesis (SAGH). These findings suggest that women with high fertility may produce more androphilic sons because they experience increased immunological reaction to male fetuses and not because they possess sexually antagonistic genes. Thus, future tests of the SAGH (a foundational aspect of the hypergyny hypothesis) should attempt to parse apart female fecundity effects from the FBOE. This could be done by examining whether elevated reproduction is observed among the mothers of first-born androphilic males, whose sexual orientation cannot be due to any FBOE.

Limitations

The present study had two noteworthy limitations. Although significant time and energy was invested in trying to locate sisters of *muxes*, this task proved quite difficult even after several months of fieldwork. Consequently, there were only 27 female participants per sister group which could have led to a Type I error. Moreover, a previous test of the SAGH among the Istmo Zapotec found elevated reproduction among the families of *muxes* with feminine gender presentations (*muxe gunaa*), but not among the families of those with masculine ones (*muxe nguiiu*) (see Chapter 6). Therefore, it is possible that different results would be obtained if *muxe* sisters were subcategorized into sisters of masculine-presenting and feminine-presenting *muxes*. Although data regarding male siblings' gender presentation were collected, there were not sufficient *muxe* sisters to create such subcategories. Future research should assess the extent to which males' sexual orientation and gender presentation is associated with their female relatives' reproduction and facial attractiveness.

Secondly, the inclusion of female participants that were past their peak age of fertility (~22-35 years; see Sugiyama, 2015) could have affected the attractiveness ratings given by gynephilic men. Although statistical measures were taken to control for the influences of women's age, an ideal sample would only include women in their peak reproductive years. On that note, Skorska et al. (2020) only sampled women who were 19- to 29-years old, but the study nonetheless found results that were similar to our own despite the fact that the two studies were conducted in very different cultures that are considered to be independent from one another (Murdock & White, 1969). Therefore, it seems unlikely that the findings from the present study are a result of the variability in women's age.

Conclusions

This study found that Istmo Zapotec gynephilic men rated the faces of women with androphilic male siblings as less attractive than those of women with only gynephilic male siblings. This finding is inconsistent with one of the key premises of Barthes et al.'s (2013) hypergyny hypothesis which holds that the female relatives of androphilic males exhibit elevated attractiveness. This study, coupled with the work of Skorska et al. (2020), downgrades the viability of the hypergyny hypothesis as an explanation for the evolution of male androphilia.

Chapter 8: General Summary and Discussion

Male androphilia is a trait that occurs in most cultures worldwide (Hames et al., 2017; Murray, 2000). In the majority of these cultures, male androphilia generally takes one of two forms: cisgender and transgender (Bailey, 2003; Murray, 2000; Vasey & VanderLaan, 2014; Whitam & Mathy, 1986). Chapter 1 reviews the research on the numerous psychodevelopmental and cognitive correlates that cisgender and transgender androphilic males share across cultures, all of which suggest that androphilic males' behavior and cognitive abilities are shifted toward a female typical pattern. Nevertheless, most of this research is limited by a lack of within-culture comparisons between cisgender and transgender male androphiles. Chapter 1 also discusses the research indicating how male androphilia—a trait that reduces reproduction—can persists across cultures and evolutionary time. In doing so, three potential solutions for this evolutionary paradox are discussed: the kin selection hypothesis, the sexually antagonistic genes hypothesis, and the hypergyny hypothesis. However, support for these hypotheses is either equivocal or mostly found in one segment of the world: Southeast Asia and Polynesia. With these limitations in mind, Chapters 2 through 7 present novel research on the cross-cultural correlates and evolution of male androphilia from a non-Euro-American culture in the southern region of Mexico where both forms of male androphilia are prevalent—the Istmo Zapotec.

Chapter 2 examined the childhood sex-typed behavior (e.g., play behavior) recalled by Istmo Zapotec gynephilic men, androphilic women, cisgender androphilic males (i.e., *muxe nguiiu*), and transgender androphilic males (i.e., *muxe gunaa*). The results indicated that both cisgender and transgender *muxes* recalled engaging in more female-typical and less male-typical behavior than gynephilic men during childhood. These findings provide further evidence to suggest that having elevated sex-atypical behavior during childhood is a cross-culturally invariant correlate of male androphilia. Moreover, while cisgender *muxe nguiiu's* recalled female-typical behavior was in between those of gynephilic men and androphilic women, transgender *muxe gunaa's* recalled behavior was indistinguishable from that of androphilic women. Thus, the research presented in Chapter 2 suggests that cisgender androphilic males demonstrate a pattern of behavior—in this case, childhood interests and behavior—that is shifted in a female-typical direction, whereas transgender androphilic male exbibit one that mirrors those of androphilic females.

Expanding on this research, Chapter 3 tested whether the elevated sex-atypical behavior recalled by cisgender and transgender androphilic *muxes* in childhood was also evident in adulthood. To do so, Chapter 3 examined the occupational preferences of Istmo Zapotec gynephilic men, androphilic women, *muxe nguiiu*, and *muxe gunaa*. In addition, Chapter 3 also assessed whether recalled childhood sex-atypical behavior was correlated with adulthood occupational preferences. This research demonstrated that Istmo Zapotec males and females who recalled greater sex-atypical behavior during childhood also had the most sex-atypical occupational preferences in adulthood. Furthermore, both cisgender and transgender *muxes* had a greater preference for female-typical occupations (e.g., event decorator, clothing designer) and a lower preference for male-typical occupations (e.g., car mechanic, fishing boat crew member) than gynephilic men. Thus, the study provides further evidence to suggest that having sex-atypical occupational preferences is a cross-culturally invariant correlate of male androphilia. That said, a distinction was observed between the two types of *muxes*. While *muxe nguiiu's* preference for female-typical occupations was intermediate between those of gynephilic men and androphilic women, *muxe gunaa's* female-typical occupational preferences was identical to those of women. Thus, similar to Chapter 2, the research presented in Chapter 3 supports the idea that cisgender androphilic males' psychology—in this case, their occupational interests in adulthood—is shifted in a female-typical manner, whereas transgender androphilic males' behavior is similar to that of androphilic females.

Culminating the thesis' focus on the cross-cultural correlates of male androphilia, Chapter 4 looked at the cognitive abilities of Istmo Zapotec gynephilic men, androphilic women, and cisgender and transgender *muxes*. This empirical chapter also included data on the cognitive abilities of Samoan gynephilic men, androphilic women, and non-binary androphilic males known locally as *fa'afafine*. Only one male sexual orientation difference was observed in Samoa. *Fa'afafine's* scores for the test assessing judgement of line orientation—a male-favoring visual-spatial ability (e.g., Archer, 2019; Lippa et al., 2010)—was in between those of gynephilic men and androphilic women. This finding suggests that *fa'afafine*'s visual-spatial cognitive abilities are shifted in a female-typical direction, similar to those of Euro-American gay men (e.g., Xu et al., 2017, 2020). Nevertheless, among the Istmo Zapotec, no male sexual orientation differences were found in mental rotation and judgement of line orientation abilities—that is, male-favoring visual-spatial abilities (e.g., Archer, 2019; Lippa et al., 2010). It is possible that sample size limitations could have been responsible for the lack of significant male sexual orientation differences in the male-favoring visual-spatial abilities among the Istmo Zapotec. However, no male sexual orientation differences were observed in object location memory among Samoans and the Istmo Zapotec, and in verbal fluency among the Istmo Zapotec, both of which are female-favoring cognitive abilities (e.g., Silverman et al., 2007; Xu et al., 2020). Overall, the research presented in Chapter 4 provides some, albeit limited, evidence to suggest that androphilic males' visual-spatial abilities are shifted in a female-typical direction across cultures. In contrast, the present study provides no evidence indicating that having female-shifted spatial memory and verbal abilities are cross-cultural correlates of male androphilia. These results suggest that cultural context plays an important role in the expression of these cognitive abilities.

Chapter 5 attempts to provide a solution to the evolutionary puzzle of male androphilia by testing the kin selection hypothesis among the Istmo Zapotec. The study found that cisgender and transgender *muxes* report being more willing to take care of kin children than gynephilic men and androphilic women, after controlling for general altruism towards children. Furthermore, the sisters of *muxes* reported receiving more childcare support from their androphilic male sibling compared to the amount of childcare support that women without *muxe* siblings reported receiving from their gynephilic brother. This finding suggests that the elevated willingness to engage in kin-directed altruism reported by androphilic males manifests into real-world behavior. Moreover, this is the first study to document elevated kin-directed altruism among a discrete group of cisgender androphilic males (*muxe nguiiu*), among cisgender and transgender androphilic males from the same culture, and among androphilic males outside of Southeast Asia and Polynesia. Theoretically speaking, this elevated kin-directed altruism could facilitate the survival of androphilic males' kin, who could then pass on their genes, some of which are shared with the androphilic males relative. Additionally, the assistance in childcare provided by androphilic males could free up enough of their relatives' (e.g., siblings) time and energy to produce and support additional children. Thus, the research presented in Chapter 5 provides further evidence to support the kin selection hypothesis as a partial solution for the evolutionary paradox of male androphilia.

Chapter 6 follows up the evolutionary research presented in Chapter 5 by determining whether the extended female relatives of Istmo Zapotec *muxes* have elevated reproduction, as predicted by the sexually antagonistic genes hypothesis. The study found that the mothers, paternal aunts, and the maternal aunts and uncles of transgender *muxe gunaa* had more offspring than those of gynephilic men. While the sexually antagonistic genes hypothesis makes no prediction about the reproduction of male androphiles' male relatives, the elevated reproduction found among *muxe gunaa's* female relatives is consistent with the hypothesis. Specifically, the maternal aunt's elevated reproduction provides more definite support for the sexually antagonistic genes hypothesis because their reproduction is not shared, and, thus, confounded, by a male who is genetically related to the androphilic male proband (e.g., fathers and grandfathers). Nevertheless, the reproduction of cisgender *muxe nguiiu's* relatives did not significantly differed from those of gynephilic males. Given qualitative reports indicating that *muxe nguiiu* come from higher socioeconomic classes (e.g., Miano Borruso, 2001; Mirandé, 2017), it is possible that their families practice the same "stopping rules" exhibited by the families of cisgender androphilic males in Euro-America (Blanchard & Lippa, 2007; Xu & Zheng, 2017; Zucker, et al., 2007). This could help explain why the female relatives of cisgender *muxes* did not exhibit the predicted elevated reproduction. Overall, the research presented in Chapter 6 provides partial support for the sexually antagonistic genes hypothesis.

While the additional offspring produced by the mothers of *muxe gunaa* relative to the mothers of gynephilic men would be enough to balance out their androphilic male offspring's lack of reproduction (mean difference = 1.22; see Table 6.2), it is not clear what mechanism are responsible for this elevated reproduction. Chapter 7 attempted to clarify this conundrum by testing one of the premises of the hypergyny hypothesis. Specifically, the study tested whether the sisters of *muxes* are considered to be more attractive than women without androphilic male siblings. Elevated attractiveness would hypothetically allow the female relatives of androphilic males to attract mates of higher socioeconomic classes who could provide them with sufficient resources to produce and sustain multiple offspring. Nevertheless, Istmo Zapotec gynephilic men rated the faces of women without *muxe* siblings as more attractive than the faces of women with *muxe* siblings, which is inconsistent with the hypergyny hypothesis. This finding suggests that facial attractiveness, and consequently, hypergyny, is the not the mechanism that facilities the elevated reproduction observed among *muxe gunaa's* female relatives.

Overarching Significance and Future Directions

The differences in sex-atypical behavior between androphilic and gynephilic males across cultures are perhaps the largest and most consistent male sexual orientation differences ever documented with respect to non-sexual behaviors. In a meta-analytical review of 32 retrospective studies, Bailey and Zucker (1995) found that the mean effect size for the difference between androphilic and gynephilic men in sex-atypical behavior during childhood was $d = 1.31$ ($SD = 0.43$). While no meta-analysis has been conducted on male-sexual orientation differences in adulthood sex-atypical behavior, individual studies have found greater sex-atypical occupational preferences among androphilic males in Australia, Brazil, Canada, China, Guatemala, India, New Zealand, the Philippines, Samoa, UK, USA, and Western Europe (see Chapter 3). The present research expanded this literature by finding male sexual orientation differences among the Istmo Zapotec—a non-Euro-American culture where both cisgender and transgender androphilic males exist. Indeed, the findings demonstrated very large male sexual orientation differences ranging from $d = 2.33$ to 4.99 for childhood sex-atypical behavior and from $d = 2.36$ to 3.44 for sex-atypical occupational preferences in adulthood. Given the cross-cultural consistency of male sexual orientation differences in sex-atypical behavior, it is no surprise that multiple lines of research have found evidence suggesting that androphilic males' elevated femininity is influenced by biological factors. This includes hormonal, immunological, and genetic factors.

With respect to hormonal factors, research on genetic males with complete androgen insensitivity syndrome (CAIS), whose body does not respond to androgens, demonstrates that relative to unaffected males, CAIS males are more likely to be androphilic and have female-typical gender presentation (e.g., Hines, 2003). Furthermore, longitudinal studies demonstrate that the testosterone surge that occurs during the first months of human male infants' lives (referred to as mini-puberty) is positively related to male-typical behavior, and negatively related to female-typical behavior (Lamminmäki et al., 2012; Pasterski et al., 2015). However, studies examining the relationship between *prenatal* sex-steroid hormone exposure and childhood sex-typed behavior in human males have provided inconsistent results, with some showing a positive relationship and others showing none at all (reviewed in Hines et al., 2015). Thus, further research is needed before any firm conclusion can be drawn regarding the amount of variability in childhood sex-typed behavior among androphilic and gynephilic males that is accounted for by sex-steroid hormones during the prenatal period, neonatal period, or both.

With respect to immunological factors, it is possible that androphilic males owe their sexual orientation and elevated feminine gender expression to the same immunological effects predicted by the maternal immune hypothesis (MIH). As discussed in Chapters 6 and 7, the MIH is one of the leading explanations for the fraternal birth order effect (FBOE)—that is, the finding that androphilic males are more likely to be later born among their male siblings than gynephilic males. Specifically, the MIH proposes that with every gestation of a male fetus, mother are exposed to male-specific antigens linked to the fetal brain development (Bogaert & Skorska, 2011; Bogaert et al., 2017). Over a succession of such pregnancies, the mother's immune system becomes increasingly proficient at recognizing these antigens and responding to them with antibodies that compromises male-typical development. Thus, it is possible that a greater number of older brothers increases the probability that a male will be androphilic and develop female-typical gender expressions.

Even though several studies have found no direct association between childhood sex-atypical behavior and the FBOE (Bogaert 2003, 2005; Gómez Jiménez et al., 2020b; Kishida & Rahman, 2015; Semenyna, VanderLaan, & Vasey, 2017; Swift-Gallant et al., 2017), a meta-analysis conducted by Blanchard (2018a) demonstrated that the FBOE was stronger in feminine or transgender androphilic males than in cisgender ones. This suggests that androphilic males' levels of male femininity (at least in adulthood) are positively predicted by the number of older brothers. Thus, future studies and meta-analyses should assess the relationship between androphilic males' number of older brothers and their sex-typed behavior in childhood *and* adulthood (e.g., occupational preferences) to further assess the potential associations between male androphilia, male femininity, and the FBOE.

Finally, with respect to genetic factors, twin studies conducted on three- to ten-year-old children have demonstrated that both sex-typical and sex-atypical behaviors are partly heritable (Iervolino et al., 2005; Knafo et al., 2005; van Beijsterveldt et al., 2006). Twin studies also suggest that common genetic factors underlie the co-variance between childhood sex-atypical behavior and male androphilia (Alanko et al., 2010; Bailey et al., 2000). Furthermore, molecular genetic studies have found evidence suggesting that Caucasian male-to-female transsexuals have longer polymorphism in the androgen receptor gene than non-transsexual males—a pattern associated with lower sensitivity to circulating androgens. This suggests that male gender identity and femininity could be partially mediated by genetic differences in the receptivity of androgen receptors (Hare et al., 2009; Henningsson et al., 2005). Unfortunately, the authors of these studies did not determine the participants' sexual orientation. As such, future research is needed to determine whether these findings are specific to androphilic male-to-female transsexuals, as well as all other forms of male androphilia, regardless of their gender expression, gender identity, or desire for sex reassignment surgery.

Altogether, this research suggests that androphilic males' sexual orientation and gender expression are influenced by hormonal, immunological, and genetic factors. It is unclear however, if these factors have an additive effect on the development of male sexual orientation and gender expression or whether they represent distinct developmental pathways towards androphilia and femininity among males. Addressing this question, Swift-Gallant et al. (2019) assessed whether markers of different biological processes associated with the development of male androphilia cluster within the same individuals or are present in different subgroups of males. The proportion of older brothers was used as biomarkers of immunological factors, the proportion of androphilic male relatives was used as biomarker of genetic factors, and the degree of left-handedness was used as the biomarker of hormonal factors. This is because non-right-handedness has been associated with prenatal testosterone exposure and elevated rates of childhood sex-atypical behavior, androphilia, and transgender identification among males (reviewed in Wong & VanderLaan, 2020). Swift-Gallant's et al. (2019) analysis found that there were three distinct subsets of males, each of which consisted of males who had one of the three biomarkers and were primarily androphilic. Furthermore, these three subsets of males scored significantly higher in measures of childhood femininity compared to a fourth subset of males who did not display any of the biomarkers and were primarily gynephilic. These findings suggests that there exist multiple biodevelopmental pathways towards androphilia and elevated femininity among males. Future research should attempt to replicate this study across cultures to assess the validity of these findings. If replicated, future studies should then assess what additional biological and behavioral traits characterize these distinct subsets of androphilic males.

Moving on to more ultimate explanations, Chapters 5, 6, and 7 looked at potential solutions to the evolutionary paradox of male androphilia. These were the kin selection hypothesis, the sexually antagonistic genes hypothesis, and the hypergyny hypothesis. Since the publication of the empirical research of Chapter 6 in Gómez Jiménez et al. (2020a), one meta-analysis (Blanchard et al., 2020) and one population-level study in the Netherlands with approximately nine million participants (Ablaza et al., 2022) have challenged previous findings in support of the sexually antagonistic genes hypothesis. These studies indicate that the significant difference in the total number of siblings between androphilic and gynephilic males disappear once the number of older brothers (i.e., the fraternal birth order effect) is controlled for. This finding suggests that the association between large family sizes and male androphilia found in previous studies are not due to sexually antagonistic genes, but rather to increasing immunological reactions towards male fetuses among some high fertility females, which increase the likelihood that their later born males will be androphilic. If true, this would help explain why the results from previous tests of the sexually antagonistic genes hypothesis have been so inconsistent across cultures, and why more consistent evidence in support of the hypothesis have been found in high-fertility cultures like Samoa (see Chapter 6). Future research should revisit the elevated reproduction observed among female relatives of androphilic males in Samoa and the Istmo Zapotec to verify where these are true female fecundity effects or spurious associations resulting from the fraternal birth order effect. Such research will be vital in assessing the viability of the sexually antagonistic genes hypothesis as a solution to the evolutionary paradox of male androphilia.

If future research on the sexually antagonistic genes hypothesis determines that there are no female fecundity effects, then further tests of the Barthes' et al. (2013) hypergyny hypothesis will be rendered moot. This is because the hypergyny hypothesis hinges upon the assumption that the female relatives of androphilic males exhibit elevated fecundity. However, until such future research presents the final nail in the coffin for the sexually antagonistic genes hypothesis, there are other facets of the hypergyny hypothesis that could be explored. For example, future studies could test whether the female relatives of androphilic males are more likely than those of gynephilic males to exhibit hypergyny—that is, obtain mates of higher socio-economic status—which remains unexplored to this date. As it stands, however, both existing tests of the hypergyny hypothesis have failed to find any supporting evidence for the hypothesis (see Chapter 7 and Skorksa et al., 2020).

While evidence against the sexually antagonistic genes hypothesis and the hypergyny hypothesis appears to be accumulating, evidence in support of the kin selection hypothesis appears to be stacking up. Indeed, the research presented in Chapter 6 provides evidence for the kin selection hypothesis by indicating that Istmo Zapotec *muxes* exhibit greater kin-direct altruism than gynephilic men. Nevertheless, there are still aspects of the kin selection hypothesis that require further investigation. For example, research conducted in Canada and Samoa suggest that androphilic males' elevated kin-directed altruism emerge in early in life in the form of elevated concern for the well-being of kin during childhood (VanderLaan et al., 2015; VanderLaan, Petterson, & Vasey, 2017). Moreover, evidence from Samoa also indicate that greater concern for kin wellbeing in childhood is correlated with kin-directed altruism in adulthood among androphilic males (VanderLaan, Petterson, & Vasey, 2017)

Research among the Istmo Zapotec have found that cisgender and transgender *muxes* exhibit elevated kin-directed altruism (see Chapter 6) and recall elevated indicators of childhood separation anxiety (Gómez et al., 2017)—which partially consist of elevated concern for kin wellbeing. Thus, future research should assess whether Istmo Zapotec *muxes'* elevated indicators of childhood separation anxiety is associated with their elevated kin-direct altruism in adulthood. Conducting such research would provide an opportunity to triangulate the findings from Canada and Samoa. In doing so, this research will help determine whether the elevated indicators of childhood separation anxiety exhibited by androphilic males across cultures (Gómez et al., 2017; VanderLaan et al., 2011a, 2015; Vasey et al., 2011) is a developmental precursor to elevated kin-directed altruism.

Conclusion

An overwhelmingly majority of psychological research is conducted using samples primarily derived from White, Educated, Industrialized, Rich, and Democratic (i.e., WEIRD) cultures (e.g., Arnett, 2008; Henrich, 2020; Henrich et al., 2010), which is used to make inferences about the nature of human behavior. Because of this, most of what we understand about male androphilia is provided through the lens of WEIRD cultures that do not necessarily represent how this trait is expressed and understood in non-WEIRD cultural contexts. My dissertation attempts to widen the scope of the lens by presenting empirical research on male androphilia from the Polynesian island nation of Samoa and the Istmo region of Oaxaca, Mexico, where androphilic males identify as non-binary genders that are distinct from men and women. This research found that the female-shifted behaviors and, to a lesser extent, cognitive abilities that characterize androphilic males in WEIRD cultures are also evident among androphilic males in non-WEIRD cultures. The thesis also attempted to understand how a seemingly non-adaptive trait such as male androphilia can persist throughout evolutionary time. In doing so, my thesis provides support for the kin selection hypothesis and, to a lesser extent, the sexually antagonistic genes hypothesis. In contrast, no support for the hypergyny hypothesis was found. Thus, the research presented in this thesis brings us one step closer to finding a solution to the evolutionary paradox of male androphilia.

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APPENDIX 1: Avuncular/Materteral Tendencies Subscale

Imagine that the brother or sister you are closest with has children and asks you to help with some childcare activities. How willing would you be to do the following activities?

1. Take care of the nieces/nephews (i.e., babysitting, supervising) for an evening

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

2. Take care of the nieces/nephews (i.e., babysitting, supervising) on a regular basis

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

3. Take care of nieces/nephews (i.e., babysitting, supervising) for a week while their parents are away

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

4. Buying a gift for the nieces/nephews (i.e., candy, toys)

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

5. Tutoring niece/nephews in a subject you know well

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

6. Help expose the nieces/nephews to traditional Zapotec culture (e.g., dances, songs, stories)

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

7. Contributing money for daycare for the nieces/nephews

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

8. Contribute money for the nieces/nephews' medical expenses (i.e., paying doctors, traditional healers, buying medicine)

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

9. Help pay for the nieces/nephews' school fees and other education expenses

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

10. Confront other children that are bothering or bullying the nieces/nephews

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

11. Contribute money for the nieces/nephews' clothes or diapers

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

12. Contribute money for the nieces/nephews' food (including baby milk)

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

APPENDIX 2: Altruistic Tendencies Towards Non-Kin Children Subscale

Please indicate how willing you would be to do the following tasks for a child of the neighborhood who is not a member of your family:

1. Take care of the child (i.e., babysitting, supervising) for an evening

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

2. Take care of the child (i.e., babysitting, supervising) on a regular basis

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

3. Take care of the child (i.e., babysitting, supervising) for a week while their parents are away

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

4. Buying a gift for the child (i.e., candy, toys)

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

5. Tutoring the child in a subject you know well

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

6. Help expose the child to traditional Zapotec culture (e.g., dances, songs, stories)

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

7. Contributing money for daycare for the child

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

8. Contribute money for the child's medical expenses (i.e., paying doctors, traditional healers, buying medicine)

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

9. Help pay for the child's school fees and other education expenses

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

10. Confront other children that are bothering or bullying the child

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

11. Contribute money for the child's clothes or diapers

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

12. Contribute money for the child's food (including baby milk)

Very Willing	Somewhat Willing	Slightly Willing	Not Sure	Slightly Unwilling	Somewhat Unwilling	Very Unwilling

APPENDIX 3: Avuncular Tendencies Questionnaire

Please respond honestly to these questions in relation to your *muxe*/gay sibling. If you do not have one, please think of the brother you are closest with. How often does that sibling do the following activities?

1. Take care of your child/children (i.e., babysitting, supervising) for an evening

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always

2. Take care of your child/children (i.e., babysitting, supervising) on a regular basis

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always

3. Take care of your child/children (i.e., babysitting, supervising) for a week while you are away

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always

4. Buy a gift for your child/children (i.e., candy, toys)

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always

5. Tutor your child/children in a subject they know well

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always

6. Help expose your child/children to traditional Zapotec culture (e.g., dances, songs, stories)

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always

7. Contributing money for daycare for your child/children

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always

8. Contribute money for your child/children's medical expenses (i.e., paying doctors, traditional healers, buying medicine)

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always

9. Help pay for your child/children's school fees and other education expenses

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always

10. Confronted other children (or their parents) that have bothered or bullied your child/children

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always

11. Contribute money for your child/children's clothes or diapers

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always

12. Contribute money for your child/children's food (including baby milk)

1	2	3	4	5
Never	Rarely	Sometimes	Often	Always