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TARGET ARTICLE

# A Life History Approach to the Female Sexual Orientation Spectrum: Evolution, Development, Causal Mechanisms, and Health

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## Abstract

Women's capacity for sexual fluidity is at least as interesting a phenomenon from the point of view of evolutionary biology and behavioral endocrinology as exclusively homosexual orientation. Evolutionary hypotheses for female nonheterosexuality have failed to fully account for the existence of these different categories of nonheterosexual women, while also overlooking broader data on the causal mechanisms, physiology, ontogeny, and phylogeny of female nonheterosexuality. We review the evolutionary-developmental origins of various phenotypes in the female sexual orientation spectrum using the synergistic approach of Tinbergen's four questions. We also present femme-specific and butch-specific hypotheses at proximate and ultimate levels of analysis. This review article indicates that various nonheterosexual female phenotypes emerge from and contribute to hormonally mediated fast life history strategies. Life history theory provides a biobehavioral explanatory framework for nonheterosexual women's masculinized body morphology, psychological dispositions, and their elevated likelihood of experiencing violence, substance use, obesity, teenage pregnancy, and lower general health. This pattern of life outcomes can create a feedback loop of environmental unpredictability and harshness which destabilizes intrauterine hormonal conditions in mothers, leading to a greater likelihood of fast life history strategies, global health problems, and nonheterosexual preferences in female offspring. We further explore the potential of female nonheterosexuality to function as an alloparental buffer that enables masculinizing alleles to execute their characteristic fast life history strategies as they appear in the female and the male phenotype. Synthesizing life history theory with the female sexual orientation spectrum enriches existing scientific knowledge on the evolutionary-developmental mechanisms of human sex differences.

**Keywords** Female sexual orientation · Homosexuality · Neurodevelopment · Evolutionary-developmental psychology · Behavioral endocrinology · Life history evolution · Women's health

## Introduction

> [E]ven the most flexible models have artificial assumptions. [...] Therefore, we attempt to treat the same problem with several alternative models each with different simplifications but with a common biological assumption. Then, if these models, despite their different assumptions, lead to similar results we have what we can call a robust theorem which is relatively free of the details of the model. Hence our truth is the intersection of independent lies. (Levins, 1966, p. 423)

There has been a considerable disequilibrium in past evolutionary research focusing on male rather than female sexual orientation. Theoretical discussion on the evolution of female nonheterosexuality has, however, substantially increased in recent years (Apostolou, 2016a, b; Apostolou, Shialos, Khalil, & Paschali, 2017; Burri, Spector, & Rahman, 2015; Camperio

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Ciani, Battaglia, Cesare, Camperio Ciani, & Capiluppi, 2018; Kanazawa, 2017; Kuhle & Radtke, 2013). Advances in the study of female sexual orientation have been partially decelerated by a lack of attempts to integrate research from broader areas of inquiry. By neglecting research on the causal mechanisms, physiology, ontogeny, and phylogeny of various manifestations of female sexual orientation, recent evolutionary theorizing has provided an inadequate account of its evolutionary trajectories (see Fleischman, Fessler, & Cholakians, 2015 for an exception), valuable though the hypothesizing and subsequent research has been.

Complete biological explanations of behaviors or traits need to address four different levels of analysis—phylogeny, ontogeny, proximate mechanisms, and ultimate function(s) (Bateson & Laland, 2013; Lewis, Al-Shawaf, Conroy-Beam, Asao, & Buss, 2017). These can be reformulated into four questions concerning any feature of an organism: How did it evolve over the history of a species and what is its relationship to corresponding features in other species (phylogeny)? How does it develop during the lifetime of an individual (ontogeny)? How does it work (proximate mechanisms)? And what is it for (ultimate function)? Answers to these "Tinbergen's four questions" are ideally synthesized into a common explanatory network elucidating the origins and fitness benefits of behaviors or traits (Bateson & Gluckman, 2011; Bateson & Laland, 2013; Tinbergen, 2005).

Recent evolutionary hypotheses about female nonheterosexuality have focused specifically on ultimate fitness value without adequately considering the other three questions. The existence of the various phenotypes in the female sexual orientation spectrum has also mostly been overlooked. By addressing and synthesizing not only one, but all four of Tinbergen's questions, we are better able to review the validity of recent hypotheses on the evolution of female nonheterosexuality and suggest novel hypotheses when the existing ones are inadequate to explain patterns of experimental findings.

The present article reviews comparative, developmental, neurophysiological, psychological, and biobehavioral research on the various manifestations of female nonheterosexuality in humans. Our final aim is to explore the evolutionary origins of variation in female sexual orientation. These different levels of analysis are essential for clarifying what is often a misunderstood or a mischaracterized relationship between sociocultural and evolutionary hypotheses (Lewis et al., 2017).

## Life History Theory

One of the primary suggestions given in this review is that research on female sexual orientation would benefit from integrating life history (LH) theory into its explanatory framework (see especially "Hormonally Mediated Fast Life History Strategy" section). This is because of the central link that sex hormones create between the development of sexual orientation (Balthazart & Court, 2017; Baum & Bakker, 2017; Breedlove, 2017a, b; Fisher, Ristori, Morelli, & Maggi, 2018; Motta-Mena & Puts, 2017) and the calibration of life history evolution (Adkins-Regan, 2005; Bribiescas, Ellison, & Gray, 2012; Ellison, 2017; Gettler et al., 2017; Hau & Wingfield, 2011; Jasienska, Bribiescas, Furberg, Helle, & Núñezde la Mora, 2017; Minkov & Bond, 2015; Muehlenbein & Flinn, 2011; Roney, 2016). Despite this important mechanistic connection between LH evolution and sexual orientation—occurring both in humans and in nonhuman animals—prior research has failed to integrate LH theory into research on female sexual orientation. This has been a crucial omission. Because LH theory makes sense of covariation among different traits, psychological dispositions, behaviors, and their biological substrates (Immonen, Hämäläinen, Schuett, & Tarka, 2018), it makes important contributions to individual differences psychology (Csathó & Birkás, 2018; Del Giudice & Belsky, 2011; Ellis, Skorska, & Bogaert, 2017b; Richardson et al., 2016; Sng, Neuberg, Varnum, & Kenrick, 2017), to motivational psychology (Kenrick, Griskevicius, Neuberg, & Schaller, 2010; Neel, Kenrick, White, & Neuberg, 2016), to biomedical science (Maner, Dittmann, Meltzer, & McNulty, 2017; Wells, Nesse, Sear, Johnstone, & Stearns, 2017), to human development (Kuzawa & Bragg, 2012; Muehlenbein & Flinn, 2011; Said-Mohamed, Pettifor, & Norris, 2018; Stearns, Allal, & Mace, 2008; Worthman & Trang, 2018), and as we argue here, to female sexual orientation.

A mid-level theory derived from general evolutionary theory, LH theory is a powerful tool for describing organismal allocation of bioenergetic resources between somatic effort (the growth and survival of an organism) and reproductive effort (production and support of offspring) (Ebneter, Pick, & Tschirren, 2016; Figueredo, Cabeza de Baca, & Woodley, 2013; Stearns, 1992; Worthman & Trang, 2018). LH theory analyzes how the entire life cycle of an organism is designed by natural selection to optimize reproductive success in the face of environmental challenges (Stearns et al., 2008; Wells et al., 2017). This design—set within a framework of constraints and trade-offs shaped by past evolutionary pressures and current environmental contingencies—works on the materials out of which organisms are built, as well as the developmental, physiological, and psychological mechanisms that they have inherited from their ancestors (Figueredo et al., 2004, 2005, 2006; Flatt & Heyland, 2011; Hämäläinen et al., 2018; Immonen et al., 2018; Krams et al., 2016, 2017a, b, c; Stearns et al., 2008).

LH theory has traditionally been applied to differences between species (characterized as *r*-selected or *K*-selected ones depending on species-typical LH traits), but the theory has since then been fruitfully utilized in analyzing individuals *within* species (Ellis, Bianchi, Griskevicius, & Frankenhuis, 2017a; Frankenhuis, Panchanathan, & Nettle, 2016; Hämäläinen et al., 2018; Maner et al., 2017; Woodley, Cabeza de Baca, Fernandes, Madison, & Figueredo, 2017). A biodemographic approach to LH evolution measures developmental characteristics, while a psychological approach measures a suite of cognitive and behavioral traits (Black, Figueredo, & Jacobs, 2017). Life history strategies are a composite of developmental, somatic, and psychological variables commonly represented on a fast-to-slow continuum: the fast end is occupied by species/individuals that mature quickly, reproduce early, and focus on offspring quantity rather than quality. Species/individuals with the opposite features are said to have slow life histories (Ellis et al., 2017a; Figueredo et al., 2005; Hämäläinen et al., 2018; Wells et al., 2017; Woodley et al., 2017).

Males and females have fundamentally discrepant reproductive optima—males biased toward reproductive effort, females toward parental effort—due to biological differences in parental investment and maximal reproductive rates (Bribiescas et al., 2012; Cabeza de Baca, Figueredo, & Ellis, 2012; Hämäläinen et al., 2018; Sisk, 2016). *Ipso facto*, male LH strategies are typically "faster" than those of females (Arnocky et al., 2018; Asamoah & Agardh, 2018; Del Giudice & Belsky, 2011; Fernandes, Woodley, Hutz, Kruger, & Figueredo, 2016; Hämäläinen et al., 2018; Howard & Perilloux, 2017; Hyde, 2014; Immonen et al., 2018; Jonason, Koenig, & Tost, 2010; Kenrick et al., 2010; Klug, Bonsall, & Alonzo, 2013a, b; Kruger, 2014; Kubinski, Chopik, & Grimm, 2017; Mishra, Templeton, & Meadows, 2017; see also Baranowski & Hecht, 2015; Carroll, Volk, & Hyde, 1985; Hrgović & Hromatko, 2017; Kontula, 2015; Ostovich & Sabini, 2004; Schützwohl, Fuchs, McKibbin, & Shackelford, 2009; Sjoberg & Cole, 2017). This difference is largely mediated by testosterone (T) (Arnocky et al., 2018; Bribiescas et al., 2012; Hau & Wingfield, 2011; Hau, Ricklefs, Wikelski, Lee, & Brawn, 2010; Muller, 2017; Santi et al., 2018; Sisk, 2016). Despite wide variability in male parental investment (e.g., Bribiescas et al., 2012), higher parental care by mothers is well documented in human cross-cultural research (Cabeza de Baca et al., 2012; Konner, 2016) while men, on average, have higher mating effort. Nevertheless, the rate of maturation in human males is slower than in human females because of the need to grow a proportionately larger body, which also has greater nutritional demands (cf. Del Giudice & Belsky, 2011; Gluckman & Hanson, 2006; Kuzawa & Bragg, 2012). Sexual dimorphism in body size results from sexual selection (Polo, Fernandez, Muñoz-Reyes, Dufey, & Buunk, 2018; Stulp & Barrett, 2016) and creates trade-offs between central LH traits such as growth pattern, age- and size-specific reproductive investments, and immune function (Flatt & Heyland, 2011; Foo, Nakagawa, Rhodes, & Simmons, 2017; Georgiev, Kuzawa, & McDade, 2016; Gluckman & Hanson, 2006; Kubinski et al., 2017; Kuzawa & Bragg, 2012; Muehlenbein & Bribiescas, 2005; Murray, Gildersleeve, Fales, & Haselton, 2017; Said-Mohamed et al., 2018).

## Prevalence of Nonheterosexual Behavior and Orientation

When analyzing the prevalence and adaptive value of nonheterosexuality, a distinction should be made between nonheterosexual orientation and nonheterosexual behavior (e.g., Bailey et al., 2016; Baldwin et al., 2017). On the one hand, a person has a nonheterosexual orientation if they experience strong sexual attraction toward same-sex individuals, regardless of their prior engagement in sexual intercourse with same-sex individuals and regardless of the strength of their opposite-sex attractions. This definition therefore includes "mostly heterosexuals" (scored 1 on the Kinsey scale of sexual orientation), bisexuals (Kinsey 2–5), and exclusively homosexual individuals (Kinsey 6).

On the other hand, a heterosexual person may in some situations engage in same-sex sexual behavior in spite of their sexual orientation (e.g., Kuperberg & Walker, 2018). Further, due to factors such as societal pressure, a nonheterosexually oriented person may be in a relationship with an opposite-sex individual, living their entire life devoid of nonheterosexual behavior while still being nonheterosexually oriented. The potential disconnect between sexual orientation and actual expressed behavior can alleviate selection pressures against various manifestations of female nonheterosexuality (cf. "Weak Selection Pressures" section).

Nonheterosexual behaviors and attractions are not uncommon in women. Of the 5940 women interviewed in the famous Kinsey Report in the 1950s (Kinsey & Institute for Sex Research, 1998), 13% reported having had an orgasm from sex with another woman, but the total proportion of self-identified lesbians was only 2%. In New Zealand, 9.7% of women had had same-sex sexual contact, while 24.5% of women reported an experience of same-sex attraction at some point in their lives (Dickson, Paul, & Herbison, 2003). Although 97.7% of U.S. women identified as heterosexual (Ward, Dahlhamer, Galinsky, & Joestl, 2014), other data on U.S., UK, and French women indicate that 9–12% report same-sex attractions, 2–4% engage in some same-sex sexual behavior, while exclusive same-sex behavior occurs in less than 1% of women (Savin-Williams, 2009). Heterosexuality is the most common sexual orientation in women, and graded deviations from it become incrementally rarer toward the other end of the sexual orientation spectrum of exclusive homosexuality (Calzo, Masyn, Austin, Jun, & Corliss, 2017; Greaves et al., 2017; Li, Kung, & Hines, 2017; Savin-Williams & Vrangalova, 2013; Trocki, Drabble, & Midanik, 2009). Female same-sex sexual behavior has also been reported in various non-industrial, non-Western societies, but is less commonly reported than male same-sex sexual behavior (Blackwood, 1986; Dynes & Donaldson, 1992).

## Categories of Nonheterosexual Women

Biological explanations for female nonheterosexual behavior are complicated because of the existence of a feminine and a masculine type of nonheterosexual women (Bassett, Pearcey, & Dabbs, 2001; Blackwood, 2010; Faderman, 1992; Singh, Vidaurri, Zambarano, & Dabbs, 1999; Zheng & Zheng, 2013) as well as a spectrum of female nonheterosexualities,

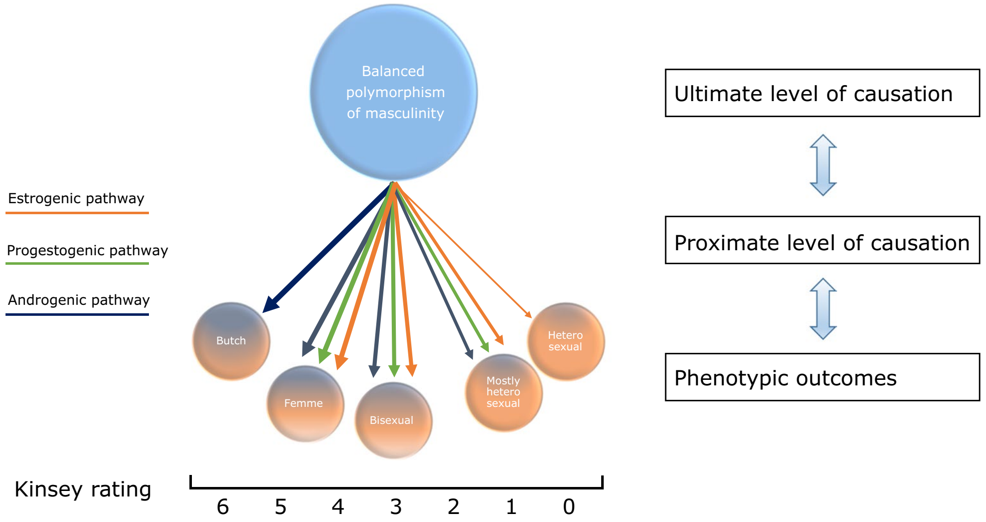

**Fig. 1** Balanced polymorphism of masculinity in women: a pendulum model. *Y*-axis (descending) indicates evolutionary trajectory from ultimate level of causation through proximate developmental mechanisms to phenotypic outcomes. *X*-axis indicates masculinity and sexual orientation, with values increasing as the pendulum "swings" left so that individuals are incrementally more masculine and homosexual in the left-hand side of the model. At the *proximate* level of causation, an orange arrow indicates an estrogenic pathway in neurodevelopment; a green one, a progestogenic pathway; a dark blue one, an androgenic pathway. The breadth of the arrow indicates relative level of exposure to corresponding sex hormone in neurodevelopment. An estrogenic pathway is required for the development of heterosexual orientation in women (Baum & Bakker, 2017; Koebele & Bimonte-Nelson, 2015). Estrogenic (notably xenoestrogens), progestogenic (notably progestins), and androgenic (either endogenous or exogenous) pathways can all lead to different degrees of nonheterosexuality in women (cf. Meyer-Bahlburg, Dolezal, Baker, & New, 2008; Rahman & Wilson, 2003; Reinisch, Ziemba-Davis, & Sanders, 1991, 2017). It seems most likely that butch type nonheterosexuality is only caused by an androgenic neurodevelopmental pathway and/or genetic or epigenetic factors (untested hypothesis). Note that besides balanced polymorphism of masculinity, other possible *ultimate*-level explanations underlying this incremental masculinization model include at least the by-product hypothesis and the hormonally mediated fast LH strategy hypothesis, as discussed in "What is the ultimate fitness value of female nonheterosexuality?" section and illustrated in Fig. 2. The bidirectional arrows (in the right-hand side of the model) between ultimate level of causation, proximate level of causation, and phenotypic outcomes indicate the notion of *reciprocal causation*, i.e., the idea that developmental processes can influence evolutionary change (Bateson & Gluckman, 2011; Dickins & Barton, 2013; Laland, Sterelny, Odling-Smee, Hoppitt, & Uller, 2011) (Color figure online)

including a "mostly heterosexual" category (Fig. 1) (Savin-Williams & Vrangalova, 2013; Vrangalova & Savin-Williams, 2014). Individuals in these categories tend to differ from one another both physically and psychologically. Research on nonheterosexual women should therefore verify which category subjects naturally identify with. Conflating results on different types of nonheterosexual women risks distorting research results, which is a weakness in some of the research data that we review. Whether these categories are allomorphic (meaning that they vary on a continuum with a great deal of overlap between the categories) or polymorphic (i.e., discontinuous categories with no overlap between them) is an open question, one that depends on which variable is being assessed and whether it is done longitudinally or cross-sectionally (cf. Adkins-Regan, 2017; Baldwin et al., 2017).

The term *femme* is used for nonheterosexual women who behave in a feminine way and whose appearance is feminine, while masculine lesbians are referred to with the term *butch*. It is possible that butch/femme represents a cultural dichotomization of a masculinity–femininity continuum which exists both in men and women. On the other hand, given that butch/femme roles or equivalents exist cross-culturally (Allen, 2012, 2016; Asencio, 2009; Blackwood, 2010; Dynes & Donaldson, 1992; Sinnott, 2004; Whitam, Daskalos, Sobolewski, & Padilla, 1998; Zheng & Zheng, 2011, 2016) and that they persist despite feminists' attempts to homogenize lesbians (reviewed in Faderman, 1992; Singh et al., 1999), it seems more plausible that either (1) discrete developmental and evolutionary etiologies underlie these categories or (2) that they lie on a continuum of incremental masculinization caused by genetic and epigenetic factors as well as high intrauterine sex hormone exposure. In "What Are the Proximate Mechanisms Behind Female Nonheterosexuality?" section, we hypothesize that discrete proximate mechanisms lead to the development of butches and femmes.

It should be emphasized that the butch/femme division is not merely a scientific way for researchers to try to categorize nonheterosexual women—the majority in fact feel that they clearly match either of these types (Bassett et al., 2001; Brown, Finn, & Breedlove, 2002b; Loulan & Thomas, 1990; Zheng, Wen, & Zheng, 2018; Zheng & Zheng, 2013). Percentages vary as to the proportion of nonheterosexual women identifying themselves within the butch/femme categories as opposed to an "androgynous" or "independent" one (Rosario, Schrimshaw, Hunter, & Levy-Warren, 2009). For instance, when asked to rate the degree to which women identify as butch/femme, 26% of women rated themselves as equally butch and femme and 73%

rated themselves as at least somewhat butch or femme (Loulan & Thomas, 1990). Despite differences in the proportion of nonheterosexual women (33–85%; see Rosario et al., 2009) identifying themselves within the butch/femme dichotomy, consistent findings in Western samples indicate that more individuals identify themselves as femmes than as butches (Bailey, Kim, Hills, & Linsenmeier, 1997; Bassett et al., 2001; Henrichs-Beck & Szymanski, 2017; Levitt & Horne, 2002; Rosario, Schrimshaw, & Hunter, 2008, 2009; Smith & Stillman, 2002; Weber, 1996).[1] It is also noteworthy that other lesbians may be more likely to perceive individuals as butch or femme than individuals actually self-identifying as such (Rosario et al., 2009).

## Psychological Characteristics of Nonheterosexual Women

The majority of masculine lesbians experience stronger attraction to femmes than to one another (Caramagno, 2002). Almost all butch lesbians see themselves as exclusively homosexual, whereas about half of femmes categorize themselves as bisexual (Rosario et al., 2008, 2009; cf. Blackwood, 2010). Femmes and bisexuals are therefore partially overlapping categories. Butches typically report significantly more lifetime female partners and encounters than femmes, whereas femmes report more lifetime male partners and encounters than butches (Rosario et al., 2009). Butches have more masculine patterns of jealousy and mate preferences than heterosexual women and femmes (Bassett et al., 2001). Correspondingly, VanderLaan and Vasey (2008) found that lesbians (not controlling for butch/femme identity) had sex-atypical mate retention tactics in respect to all six tactics that were characterized by a heterosexual sex difference.

Butches often express more assertiveness and dominance (reviewed in Rosario et al., 2009) and they have more masculine personality traits (Zheng & Zheng, 2011) and cognitive styles than femmes (Zheng & Zheng, 2013). In a Chinese sample, butches scored significantly higher than femmes on the systemizing quotient, a cognitive trait typically associated with high values in men (Zheng & Zheng, 2013). Notably, in another study with a Chinese sample, Zheng and Zheng (2015) found no differences in empathizing–systemizing between heterosexual and nonheterosexual women. This result could, however, have been confounded by the researchers' failure to distinguish between femmes and butches (Zheng & Zheng, 2015), despite an earlier exhortation to do so (Zheng & Zheng, 2013). A more recent study that analyzed butches and femmes separately found that butches outperformed femmes and heterosexual women on a mental rotation task, thus showing cognitive masculinization (Zheng et al., 2018).

More generally, lesbians have masculinized self-identity (Rieger, Savin-Williams, Chivers, & Bailey, 2016, not controlling for butch/femme differences) and personality traits, while bisexual women's personality traits are intermediate between heterosexual and homosexual women (Lippa, 2005). A similar finding has been reported for nonheterosexual women's gender-typed behavior in childhood. It significantly and consistently predicted adolescents' sexual orientation at age 15 years, both when sexual orientation was conceptualized as a binary (heterosexual/lesbian) or as a spectrum (divided into three or five groups based on Kinsey scores) (Li, Kung, & Hines, 2017). In another study, nonheterosexual women in general scored significantly lower on the gender role scale (i.e., they had higher masculinity) than heterosexual women (Schmitt, 2007). A similar finding was reported in a Chinese sample, while lesbians also showed increased masculinity in occupational and hobby preferences (Zheng, Lippa, & Zheng, 2011). These findings indicate higher masculinity in the psychological self-identity and behavioral outcomes of nonheterosexual women (conceptualized here as a heterogeneous group of individuals) when compared with their heterosexual peers.

Another personality trait, sensation-seeking, indexes the need for varied and novel sensations and the willingness to take risks for the sake of such experiences (Zuckerman, 1979). Men score consistently higher on sensation-seeking than women both in questionnaire measures and in behavioral risk-taking tasks (Cross, Copping, & Campbell, 2011; cf. Apicella, Crittenden, & Tobolsky, 2017). When women of different sexual orientations were analyzed, only 10% of exclusively heterosexual women were in the highest quartile on the personality dimension of sensation-seeking, compared with 23% of mostly heterosexual women, 30% of bisexual women, and 34% of lesbians (Trocki et al., 2009).[2] These results show how incrementally more homosexually oriented women became increasingly masculine on this psychological dimension.

Slightly different results have been reported on the Dark Triad traits, comprising of psychopathy, narcissism, and Machiavellianism. This cluster of traits is positively correlated with masculinity, sociosexuality,[3] and a present-hedonistic time orientation. Bisexual women had significantly higher Dark Triad scores than heterosexual women or lesbians (Semenyna, Belu, Vasey, & Honey, 2018; Stolarski, Czarna, Malesza, &

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[1] Brown et al. (2002b) recorded almost equal numbers of butches ($n=87$) and femmes ($n=89$) in a U.S. sample of predominantly or exclusively homosexual women. In Chinese lesbian samples, butches consistently and significantly outnumber femmes (Zheng et al., 2018, and references therein). Perhaps surprisingly, a sample of Chinese bisexuals consisted of equal numbers of femmes, butches, and androgynous women (Zheng et al., 2018).

[2] In a Spanish sample, however, sexual sensation seeking (as opposed to general sensation seeking) was lower in self-identified lesbians ($n=90$) than in heterosexual women ($n=92$) (Gil-Llario, Morell-Mengual, Ballester-Arnal, Giménez-García, & Castro-Calvo, 2015). Notably, bisexual women were excluded from the study due to a low sample size ($n=4$) (Gil-Llario et al., 2015). Another study found that bisexual women had higher sexual sensation-seeking scores than either lesbian or heterosexual women (Stief, Rieger, & Savin-Williams, 2014).

[3] That is, willingness, attitudes, and desires associated with uncommitted sexual behavior.

Szymańska, 2017). In the aggregate, these findings illustrate the psychological masculinization of nonheterosexual women across a variety of personality measures. The Dark Triad findings complicate the picture because they suggest that lesbians are not as masculinized as bisexual women are. Nevertheless, bisexual women (0.35–0.48) and lesbians (0.26) have substantially higher psychopathy scores than heterosexual women (−0.07) (Semenyna et al., 2018). This finding is consistent with the psychobehavioral masculinization hypothesis: psychopathy is the only Dark Triad trait that has shown robust sex differences, being more pronounced in men than in women (Muris, Merckelbach, Otgaar, & Meijer, 2017). We frame the totality of these findings in an LH perspective in "Hormonally Mediated Fast Life History Strategy" section, which is also informed by the following sections on the proximate mechanisms, ontogeny, and phylogeny of female nonheterosexuality.

## What Are the Proximate Mechanisms Behind Female Nonheterosexuality?

### Genetic Influences

Several twin studies have explored the heritability of nonheterosexual behavior and orientation in women, finding different degrees of heritability for both (Alanko et al., 2010; Bailey, Pillard, Neale, & Agyei, 1993; Bailey, Dunne, & Martin, 2000; Langstrom, Rahman, Carlstrom, & Lichtenstein, 2010, Santtila et al., 2008). Since heritability studies only provide estimates of population-level variance (Visscher, Hill, & Vray, 2008), their applicability in assessing the development of individual phenotypes is non-existent (Crusio, 2012; Johnson, Penke, & Spinath, 2011). Only one study has attempted to locate candidate genes for homosexual behavior in women, without finding any (Hu et al., 1995). Empirical findings indicate that the prevalence of female nonheterosexuality is significantly higher in families of nonheterosexual women than in the families of heterosexual women (Camperio Ciani et al., 2018).

### Socialization Influences

Besides genetic influences, it has been suggested that girls who are molested develop a sexual aversion toward the sex of the person who molested them and consequently become lesbian. The molestation is a devastating experience and may cause women to develop an aversion for heterosexual intercourse (Harrison, Hughes, Burch, & Gallup, 2008; see Xu & Zheng, 2017 for criticism of this argument). This hypothesis is supported by multiple studies which indicate a much higher probability of lesbians and bisexual women reporting prepubertal sexual abuse than heterosexuals (Balsam, Rothblum, & Beauchaine, 2005; Gundlach, 1977; Hall, 1996; Harrison et al., 2008; Hughes, Johnson, & Wilsnack, 2001; Weingourt, 1998; Xu & Zheng, 2017). A meta-analysis of 75 studies reported lifetime sexual assault prevalence estimates of 15.6–85% for nonheterosexual women as opposed to 11–17% for women overall (Rothman, Exner, & Baughman, 2011). Importantly, however, same-sex molestation seems to have a greater effect on the development of sexual orientation than opposite-sex molestation: 66.7% of lesbians who report having been molested by a woman maintained that it impacted their sexual orientation, whereas 41.5% of lesbians who report having been molested by a man reported an impact on their sexual orientation (Steed & Templer, 2010). This finding challenges the hypothesis that girls who are sexually molested develop an aversion toward the sex of the person who molested them. If that was the case, then the women molested by other women would either not become lesbian, or they would be unlikely to report that the molestation had an impact on their sexual orientation.

We note that psychoanalytical and social constructionist theories of sexual orientation—despite being accepted and taught in some disciplines—have garnered limited empirical support, if any. We have found it particularly challenging to explain the wealth of data we review below using those theories. That is why we refrain from a more thorough discussion of those approaches and instead refer interested readers to sources in which such theories have already been challenged or dismantled (Balthazart, 2011; Balthazart & Court, 2017; Balthazart & Young, 2015; Bao & Swaab, 2011; Breedlove, 2017a; Lippa, 2008; Motta-Mena & Puts, 2017; Poiani, 2010). Given that being raised by nonheterosexual parents does not seem to affect a child's sexual orientation or gender identity (Anderssen, Amlie, & Ytteroy, 2002; Green, 1978; Richards, Rothblum, Beauchaine, & Balsam, 2016; cf. Bao & Swaab, 2011) and, further, that genetic influences obviously do not account for the sexual orientation phenotype(s) *in toto*, what are the environmental factors that predispose women to be sexually attracted to other women?

### Prenatal Estrogen Exposure and the Development of Femme Nonheterosexuality

While mammalian sexual differentiation in general is a complex process which involves chromosome-specific developmental pathways (Arnold, 2017; Immonen et al., 2018) and sex-specific epigenetic mechanisms (Lenz, Nugent, & McCarthy, 2012; Rice, Friberg, & Gavrilets, 2016), it is the prenatal hormonal environment that is generally thought to be the central determinant of whether a human fetus develops a masculine or a feminine brain (Bao & Swaab, 2011; Breedlove, 2017a, b; Fisher et al., 2018). A masculine brain develops if the fetus undergoes prenatal exposure to T. A feminine brain develops in the absence of T exposure regardless of whether the fetus has male or female sex chromosomes, or male or female genitalia (Bao & Swaab, 2011; Koebele & Bimonte-Nelson, 2015; Lenz et al., 2012; Sisk, 2016; Swaab, Chung, Kruijver, Hofman, & Hestiantoro, 2003). Prenatal brain masculinization is irreversible, and cannot be influenced with sex hormone treatment later in life (Bao & Swaab, 2011).

### Evidence from Nonhuman Animal Research

Research in rodents has shown that it is not T that masculinizes the area in the brain that influences sexual behavior and orientation. Instead, aromatase converts T to estrogen (Cooke, Nanjappa, Ko, Prins, & Hess, 2017; Fisher et al., 2018; Koebele & Bimonte-Nelson, 2015), which then interacts with estrogen receptors to masculinize the hypothalamic preoptic area SDN-POA. This area influences sexual behavior in adults and is larger in males than in females (Breedlove, 2017a; Morris, Jordan, & Breedlove, 2004; see Luoto & Rantala, 2018; Puts & Motta-Mena, 2018, for a discussion of these mechanisms in humans). Epigenetic mechanisms (acting through sex hormones) have a further role in masculinizing the SDN-POA (Lenz et al., 2012; Nugent et al., 2015). Treating developing female rats with estrogens, including the xenoestrogens genistein, zearalenone, and diethylstilbestrol (DES), reduces female-typical sexual behavior and increases same-sex preferences, male-typical sexual behavior, and the volume of the SDN-POA (de Jonge, Muntjewerff, Louwerse, & Van de Poll, 1988; Döhler et al., 1984; Faber & Hughes, 1991; Maclusky & Naftolin, 1981). Treating female rats prenatally with androgen induces female-directed sexual preferences, decreases female-typical sexual behavior (lordosis), increases male-typical sexual behavior (mounting), and increases the size of SDN-POA (de Jonge et al., 1988; Gorski, Gordon, Shryne, & Southam, 1978, 1980). Blocking the conversion of androgen to estrogen, or blocking estrogen receptors in utero, decreases female rats' behavioral masculinization as adults, even in the presence of high levels of T (Clemens & Gladue, 1978; Doughty, Booth, McDonald, & Parrott, 1975; McCarthy, 2008; McEwen, Lieberburg, Chaptal, & Krey, 1977). Current evidence therefore suggests that moderate prenatal exposure to estrogen may cause same-sex preferences in female rats without inducing a significant divergence from sex-typical juvenile behavior or sex-typical adult body morphology, while high exposure to estrogen may also masculinize play behaviors (Auger & Olesen, 2009; Bakker et al., 2006).

### Hypothesized Proximate Mechanism for the Femme Phenotype

Based on the different effects that prenatal T and prenatal estrogen have on sexual differentiation of brain and behavior, we suggest that there may be a neurodevelopmental mechanism which explains why female nonheterosexuality exists in (at least) two different forms: the masculine butch and the feminine femme types. According to this model (Fig. 1), if a female human fetus is exposed to high prenatal T at a critical point during neurodevelopment, it develops a male-type (large) INAH3 (which is considered the human homologue of the SDN-POA: Byne et al., 2001). This process is caused by the conversion of T to estrogen (cf. Koebele & Bimonte-Nelson, 2015; Wood, 2014).[4] Because of more global masculinizing effects of T, the fetus also develops a more masculine brain in general than heterosexual women, more masculine body morphology, and exclusive or near-exclusive homosexual orientation. Alternatively, if a female human fetus is exposed to high prenatal estrogen levels at a critical point during neurodevelopment, a male-type (large) INAH3 develops, leading to femme phenotypes of various degrees of same-sex attractions but with a more feminine body morphology than in butch lesbians because of lower androgenic action. Notably, heightened maternal stress may lead to increased estrogen in fetal blood because its production occurs via adrenocorticotropin (ACTH) secretion by the fetal pituitary (reviewed in Wood, 2014). Heightened bioavailability of estrogen may constitute a mechanism that links maternal stress to the development of same-sex sexual preferences in offspring (cf. Bailey, Willerman, & Parks, 1991).

### Evidence from Human Research

Evidence for this hypothesis comes from both nonhuman animal and human research. The research summarized in "Evidence from Nonhuman Animal Research" section corresponds with findings that have emerged from studies in humans: butch females behave in a gender-atypical way in childhood and adulthood while femmes generally behave in a gender-typical way in childhood (Hiestand & Levitt, 2005; Levitt, Gerrish, & Hiestand, 2003; Zheng et al., 2018). Likewise, butch lesbians have a more masculine body morphology than femmes (Singh et al., 1999), including more masculine digit ratios (Brown et al., 2002b). More support for our hypothesis that prenatal exposure to elevated levels of estrogen causes *femme* type nonheterosexuality comes from cases where pregnant women have been exposed to synthetic estrogen, diethylstilbestrol (DES). Approximately 5–10 million people (mothers and their children) in the U.S. alone were exposed to diethylstilbestrol (DES) during pregnancy for the prevention of miscarriage (Giusti, Iwamoto, & Hatch, 1995). DES did not prevent miscarriages, but turned out to be a synthetic estrogen which increased not only DES-exposed daughters' risk of getting cancer, but also their probability to develop bisexual or homosexual preferences if prenatally exposed to DES (Ehrhardt et al., 1985; Meyer-Bahlburg et al., 1995). Despite increased homoerotic preference, DES did not increase masculinization

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[4] See Swaab and Hofman (1988) for another interpretation of the developmental mechanism underlying SDN dimorphism, namely that the size of the SDN decreases due to postnatal cell death. Note that the authors used the term "SDN" rather than "INAH3." It was only in future research that the term "INAH3" became established (Byne et al., 2001).

of gender-related behavior (Lish, Meyer-Bahlburg, Ehrhardt, Travis, & Veridiano, 1992). Instead, DES-exposed women tend to have higher femininity scores than controls (Bekker et al., 1996). In addition, DES-exposed women reported a stronger wish for having children and expressed more concern about it than non-DES-exposed controls (Bekker et al., 1996; cf. similar findings in Singh et al., 1999: femmes reported a significantly higher desire to give birth than butches). Thus, it seems likely that DES—a synthetic estrogen—gave rise to *femme* rather than butch phenotypes. This provides a plausible explanation for Ehrhardt et al.'s (1985) finding that 24% of the DES-exposed women were bisexual or homosexual (while approximately 75% were exclusively or nearly exclusively heterosexual)—phenotypic outcomes more aligned with femme rather than butch manifestations of female sexuality. Whether DES exposure causes an increased size of the INAH3 in women is unknown, but female rats exposed to DES develop a male-sized SDN-POA (Döhler et al., 1984; Tarttelin & Gorski, 1988). This illustrates the masculinizing effect of estrogen not only on sexual behavior and sexual partner preference (as described above) but also on neurophysiology.

Evidence against the hypothesis of estrogen's effect on human female sexual orientation comes from a large-scale study on DES-exposed women. Prenatally DES-exposed women ($n=3946$) were no more likely than control women ($n=1740$) to report same-sex sexual behavior (Titus-Ernstoff et al., 2003). As opposed to the studies discussed above (Ehrhardt et al., 1985; Meyer-Bahlburg et al., 1995), however, Titus-Ernstoff et al. (2003) studied same-sex sexual behaviors, not orientation. From Titus-Ernstoff et al.'s data, it is not possible to rule out heightened same-sex sexual orientation in DES-exposed women. What is more, the level of DES exposure varies greatly in these studies (e.g., Meyer-Bahlburg et al., 1995) and so clear-cut conclusions on the effect of DES exposure on sexual orientation are impossible to make based on existing data (Luoto & Rantala, 2018; Puts & Motta-Mena, 2018).

It is theoretically noteworthy, however, that environmental chemicals and endogenous hormones *can* have sex-specific effects on the developing neuroendocrine system (Cowell & Wright, 2017; Immonen et al., 2018; Kundakovic, 2017). Despite the skepticism shown by Puts and Motta-Mena (2018, citing a rodent study: De Vries et al., 2002), estrogen's prenatal effects on neurodevelopment in one sex cannot be directly extrapolated to the other sex (Luoto & Rantala, 2018; cf. Rice et al., 2016).

Due to the mixed results from humans, comparative evidence may help shed further light on the effect of prenatal estrogen exposure on behavior. In rhesus macaque females, long-term prenatal DES exposure had moderate masculinizing effects both on mounting behavior and on play behavior (Goy & Deputte, 1996). This suggests that synthetic estrogen can masculinize not only sexual behavior but also other behaviors in primates more generally.

## Prenatal Androgen Exposure, Masculinization, and Sexually Dimorphic Biomarkers

### Atypical Prenatal Hormone Environments: CAIS and CAH

There are several kinds of indirect evidence in humans about the effect of prenatal androgen exposure on sexual orientation and gender identity (Bao & Swaab, 2011; Breedlove, 2017a, b; Fisher et al., 2018; Poeppl, Langguth, Rupprecht, Laird, & Eickhoff, 2016). Genetic (XY) males who are affected with complete androgen insensitivity syndrome (CAIS) are similar to unaffected (control) females in their body morphology and sexual orientation. This indicates a central role for androgen in the masculinization of body and sexual orientation (Arnold, 2017; Hines, Ahmed & Hughes, 2003; Money, Schwartz, & Lewis, 1984; Wisniewski et al., 2000). Genetically male (XY) CAIS individuals almost always develop a female gender identity, an outcome that is consistent with the lack of effective androgen exposure (Hines et al., 2003; Mazur, 2005; Wisniewski et al., 2000). That individuals with CAIS have reduced male-typical and increased female-typical play behavior (Hines et al., 2015) further indicates the masculinizing role that prenatal androgen exposure has on human behavior.

Another line of evidence for the prenatal androgen theory comes from girls with congenital adrenal hyperplasia (CAH), in which girls are exposed to high levels of androgens in utero. CAH girls tend to choose boys as playmates, prefer masculine play styles, boys' toys, masculine hobbies, and exhibit some male-typical personality features (e.g., Hines et al., 2004; Hines, 2011a; Pasterski et al., 2011, 2015). CAH women and girls show increased physical aggression (Berenbaum & Resnick, 1997; Mathews, Fane, Conway, Brook, & Hines, 2009; Pasterski et al., 2007; Spencer et al., 2017), a trait associated with high prenatal and/or postnatal testosterone exposure (e.g., Fragkaki, Cima, & Granic, 2018; Mailhos, Buunk, Del Arca, & Tutte, 2016; Mascaro et al., 2018; Nguyen et al., 2016; Turanovic, Pratt, & Piquero, 2017) and fast LH strategies (Figueredo et al., 2018; Hurst & Kavanagh, 2017).[5] Women with CAH are approximately six times more likely to have nonheterosexual orientation as adults compared to unaffected women (a finding that has been replicated cross-nationally). The severity of the androgen exposure elevates the degree of nonheterosexual orientation in a dose-dependent manner (cf. Fig. 1) (Dittmann, Kappes, & Kappes, 1992; Frisen et al., 2009; Hines, 2011b; Hines et al., 2004, 2015; Meyer-Bahlburg et al., 2008). CAH women also showed a diminished desire to

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[5] See Spencer et al. (2017) who, despite reporting higher aggression in CAH girls than in unaffected girls, found that amniotic fluid testosterone was not a significant predictor of aggression. Spencer et al. suggest that amniotic fluid testosterone may not be a sensitive measure of prenatal androgen exposure.

have children, less interest in children, and a higher preference for having a career versus staying at home (Dittmann et al., 1990; Mathews et al., 2009).[6]

CAH girls and women show similar behavioral characteristics as typical butch women, which lends support to the hypothesis that high prenatal testosterone exposure is the proximate neurodevelopmental mechanism which predisposes women to develop a butch phenotype. However, not all CAH women develop same-sex preferences (Fisher et al., 2018; Pasterski, 2017), which indicates the involvement of other mechanisms rather than simply high prenatal T exposure. It is likely that polymorphisms in the androgen receptor gene (Fisher et al., 2018; Gettler et al., 2017; Minkov & Bond, 2015; Santi et al., 2018) and/or sexually antagonistic epigenetic mechanisms (Rice, Friberg, & Gavrilets, 2012, 2016) constitute some of the main proximate mechanisms which cause differences in the sexual orientation of CAH women.

### Click-Evoked Otoacoustic Emissions

Click-evoked otoacoustic emissions (CEOAEs)—echo-like waveforms emitted by cochleas in response to a transient sound—are a putative biomarker of prenatal androgen exposure (McFadden, 2009). A sexually dimorphic trait, females emit stronger and more frequent CEOAEs than males do (McFadden & Pasanen, 1998). The CEOAEs of bisexual and homosexual women, in contrast, are intermediate to those of heterosexual men and women (butch/femme differences have not been analyzed) (McFadden & Pasanen, 1998). A similar pattern of findings has been reported with auditory evoked potentials, i.e., gross neural potentials evoked by brief acoustic stimuli and measured using scalp electrodes (McFadden & Champlin, 2000). Control men, and women with CAH, produced fewer spontaneous OAEs in the right ear (i.e., the expected masculine pattern) than control females and women with CAIS (who exhibited the expected feminine pattern) (Wisniewski et al., 2014).

These findings extend also to nonhuman animals. In rhesus macaques (*Macaca mulatta*), females had stronger CEOAEs than males. Substantial seasonal fluctuations in CEOAEs were reported in accordance with the changing levels of hormones that increase in breeding season and decrease after it (McFadden, Pasanen, Raper, Lange, & Wallen, 2006). Female sheep (*Ovis aries*) whose mothers were treated with T prenatally had substantially masculinized CEOAEs in relation to control females (McFadden, Pasanen, Valero, Roberts, & Lee, 2009). These findings are consistent with another sexually dimorphic measure which indexes eyeblink startle responses to acoustic stimuli and prepulse inhibition (PPI) to those responses. In humans and in rats, PPI occurs less frequently in females than in males. However, homosexual women's PPI frequencies were masculinized, similar to those of heterosexual men (Rahman, Kumari, & Wilson, 2003, not controlling for butch/femme differences).

### Digit Ratio

Digit ratio studies provide another line of evidence for prenatal androgen exposure on sexual orientation (Breedlove, 2017b). The 2D:4D ratio is supposedly a universal feature of sexual dimorphism in humans (Manning et al., 2000; Manning, Churchill, & Peters, 2007), mice (Brown et al., 2002a; Zheng & Cohn, 2011), and rats (Auger et al., 2013; Talarovicova, Krskova, & Blazekova, 2009). Men have a lower digit ratio than women, a difference that develops by the end of the first trimester of gestation (Galis, Ten Broek, Van Dongen, & Wijnaendts, 2010). Since the sex difference occurs during the time of sexual differentiation of the brain, digit ratio might be an indicator of prenatal androgen exposure (Manning, Scutt, Wilson, & Lewis-Jones, 1998). Current findings support this hypothesis (Breedlove, 2010, 2017b; Malas, Dogan, Evcil, & Desdicioglu, 2006; Manning, 2010, 2011; Zheng & Cohn, 2011). Further corroboration for the hypothesis has been provided by the finding that men with CAH and women with CAH have lower (more masculine) 2D:4D ratios than unaffected individuals (Brown et al., 2002c). In contrast, genetic (XY) males with androgen insensitivity syndrome have more feminine digit ratios than control men, but similar to those of control women (Berenbaum, Bryk, Nowak, Quigley, & Moffat, 2009; van Hemmen, Cohen-Kettenis, Steensma, Veltman, & Bakker, 2017). Women (not controlled for sexual orientation) who were labeled as "tomboys" in childhood had lower (more masculine) digit ratios as adults when compared with women not labeled as tomboys in childhood (Atkinson, Smulders, & Wallenberg, 2017).

A meta-analysis of 21 studies found no significant differences between the digit ratios of heterosexual and homosexual men; however, lesbians had a lower (more masculine) digit ratio than heterosexual women (Grimbos, Dawood, Burriss, Zucker, & Puts, 2010). Due to the existence of inconsistent findings in nonheterosexual women (Kangassalo, Pölkki, & Rantala, 2011), however, the association between digit ratio and sexual orientation may not be straightforward. This may partially be because of population-level variation in 2D:4D (Manning et al., 2007), or the fact that some studies have failed to analyze femmes and butches separately. A study that *did* distinguish between femmes and butches found that butch lesbians had a more masculine digit ratio than femmes, an effect almost

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[6] This is aligned with the finding of a recent meta-analysis that lesbians have 9% higher wages than heterosexual women (Klawitter, 2015). This difference appears to be driven by higher work intensity, i.e., more working hours for lesbians than heterosexuals, which may, in part, be explained by more frequent childbearing (and child rearing) in heterosexual women (Sabia, Wooden, & Nguyen, 2017).

entirely driven by greater 4D (ring finger) length in butch lesbians (Brown et al., 2002b).[7]

Crucially, experimental research on mice has shown that different levels of prenatal sex steroids lead to differential skeletogenic gene expression profiles in 4D. This is because androgen receptors and estrogen receptors are higher in the digit condensations of 4D than 2D. Inactivation of androgen receptors decreases the growth of 4D while inactivation of estrogen receptors increases 4D growth (Zheng & Cohn, 2011). Higher prenatal T exposure therefore directly explains the 4D elongation observed in butches by Brown et al. (2002b). Furthermore, the lower the testosterone levels in amniotic fluid, the higher (more feminine) are newborn girls' 2D:4D ratios (Ventura, Gomes, Pita, Neto, & Taylor, 2013). Thus, converging evidence from correlational and experimental studies both in humans and in nonhumans indicates that 2D:4D ratio is a biomarker that predicts prenatal androgen exposure (Breedlove, 2017b) and may indicate the different prenatal hormonal environments that butches and femmes are exposed to.

## Facial Morphometrics

Another research paradigm has explored relationships between facial masculinity, sexual orientation, and prenatal T exposure. A 20-year follow-up study found that T concentrations measured from umbilical cord blood from subjects in 1989–1991 correlated with their facial masculinity both within and between sexes in 2012–2014. 2D:4D, however, did not show a strong correlation with facial masculinity within sexes (Whitehouse et al., 2015). While the 2D:4D ratio likely reflects androgen exposure during the first and second trimester of pregnancy, the traces of T found in umbilical cord blood are an indication of androgen levels late in gestation. These measures provide different temporal windows onto androgen exposure, which partially explains the divergent findings. Another study analyzed 63 facial metrics in homosexual and heterosexual women and found significant differences in 17 metrics: 10 of them were masculinized in homosexual women while only two were more feminine (Skorska, Geniole, Vrysen, McCormick, & Bogaert, 2015).[8] In a study where subjects were asked to rate the facial femininity and masculinity of heterosexual and homosexual women, homosexual women (not controlling for butch/femme differences) were rated as more masculine than heterosexual women. Heterosexual women, in turn, were rated more feminine than homosexual women (Lyons, Lynch, Brewer, & Bruno, 2014). Participants also identified the sexual orientation of heterosexual and homosexual men and women more accurately than chance levels (Lyons et al., 2014).

Strikingly, a recent large-scale study found that a computer algorithm can distinguish between homosexual (not controlling for butch/femme differences) and heterosexual women with 71% accuracy when provided one image of both a heterosexual and a homosexual subject. The accuracy increased to 83% with five images of both subjects (Wang & Kosinski, 2018). The computer algorithm had substantially higher performance than chance (50%) and human raters (54%, when presented with one image per rated subject) (Wang & Kosinski, 2018). The method relying on a computer algorithm also found a significant negative correlation between facial femininity and women's probability of being homosexual ($r = -.21$, $p < .001$; 95% CI [$-0.21$, $-0.20$]) (Wang & Kosinski, 2018). Wang and Kosinski noted that lesbians used less eye makeup, had darker hair, and wore less revealing clothes, which indicated less gender-typical grooming and style. Besides this cultural gender-atypical grooming style, lesbians' sex-atypical facial morphology (larger jaws, smaller foreheads) led Wang and Kosinski to conclude that their findings provide strong support for the prenatal androgen exposure theory of sexual orientation. The other studies on facial morphometrics reviewed above further support this conclusion.

## Anthropometrics, Body Composition, and Immune Function

Yet another putative biomarker of how sex hormone exposure organizes sexual preference is given by anthropometric measures which show sexual dimorphism before puberty. The long bone growth of exclusively homosexual women is masculinized, and their arm/stature ratio is 33% closer to men than that of heterosexual women (Martin & Nguyen, 2004). It is unfortunate that this study discarded bisexual women from the analysis: it would have been instructive to know how the anthropometric measures differed in bisexual as opposed to exclusively homosexual and heterosexual women. Butch/

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[7] See Rahman and Wilson (2003) for null findings between digit ratios of butches and femmes in a sample that was substantially smaller than that of Brown et al. (2002b). Rahman and Wilson (2003), however, reported a general replication of the finding that homosexual women had more masculine 2D:4D than heterosexual women. See also Vásquez-Amézquita et al. (2018) for a failure to replicate the finding between digit ratio and sexual orientation in a sample of 16 nonheterosexual women from Colombia (who scored 5 or 6 on the Kinsey scale, i.e., mainly or exclusively homosexual). This may have been caused by the researchers' failure to distinguish between butches and femmes, or the small sample sizes of heterosexual ($n = 21$) and nonheterosexual women ($n = 16$).

[8] Skorska et al. (2015) compared 52 exclusively or near-exclusively homosexual women with 134 heterosexual women. Skorska et al. did not distinguish between butch and femme women, which may have confounded the results.

femme differences were also not controlled for. Nevertheless, Martin and Nguyen's (2004) findings are in line with comparative studies which have found that neonatal androgen treatment of female rats leads to increased adult body weight, tibial length (Dubuc, 1976; Jansson, Eden, & Isaksson, 1985a; Jansson, Ekberg, Isaksson, Mode, & Gustafsson, 1985b), and a shift to same-sex sexual preference (de Jonge et al., 1988). Besides having increased long bone growth (Martin & Nguyen, 2004), nonheterosexual women have been frequently reported to be both taller and heavier than heterosexual women (Boehmer, Bowen, & Bauer, 2007; Bogaert, 1998; Bogaert & Friesen, 2002; Kenyon, 1968; Martin & Nguyen, 2004). Non-right-handedness also correlates with nonheterosexual orientation both in women and in men (reviewed in Xu & Zheng, 2017; see also Ellis et al., 2017b).

The existing literature is relatively clear about the finding that nonheterosexual women have greater relative body weight than heterosexual women (Boehmer et al., 2007; Sabia et al., 2017; Singh et al., 1999; see Bowen, Balsam, & Ender, 2008 for mixed results). Research indicates that the greater body mass of nonheterosexual women is driven primarily by adiposity instead of lean muscle mass (Boehmer et al., 2007; Boehmer & Bowen, 2009; Yancey, Cochran, Corliss, & Mays, 2003). What could cause the greater adiposity of nonheterosexual women in relation to heterosexual women? Nonheterosexual women are likely exposed to higher psychosocial stressors (Juster et al., 2016; Lewis et al., 2016; Rosario & Schrimshaw, 2013), which is known to cause abdominal visceral obesity (Björntorp, 1991a; Isasi et al., 2015; Sinha & Jastreboff, 2013). High circulating testosterone (T) promotes the same outcome (Björntorp, 1991a, b; see also Krams, Rantala, Luoto, & Krama, 2018). Estrogen, on the other hand, inhibits fat deposition in the abdominal region and facilitates fat deposition in the gluteofemoral region (Björntorp, 1991b; Lovejoy, Sainsbury, & Stock Conference 2008 Working Group, 2009). Therefore, high circulating estrogen would result in a primarily gynoid fat distribution around the thighs and buttocks (feminine WHR) whereas high circulating T—together with psychosocial stressors (Lehavot & Simoni, 2011)—results in a masculine WHR and an android fat distribution primarily around the abdomen (Singh, 1993). Butch lesbians have higher circulating T levels but lower or equal levels of psychosocial stress than femmes, *and* their waist-to-hip ratios are more masculine (Blair & Hoskin, 2015, 2016; Lehavot, Molina, & Simoni, 2012; Singh et al., 1999). This suggests that the fat deposits of butch lesbians consist predominantly of android fat and are driven by circulating T. The evidence therefore points to a greater effect of circulating T rather than psychosocial stressors on butch lesbians' higher body weight.

A similar etiological conclusion was reached in a study on inflammation and immune function, which reported lower (male-typical) C-reactive protein (CRP) in lesbians than in heterosexual women (Everett, Rosario, McLaughlin, & Austin, 2014, not controlling for butch/femme differences). A marker of systemic inflammation, CRP can become elevated in response to psychosocial stress. The minority stress hypothesis therefore predicts higher CRP in lesbians compared with heterosexual women; however, the opposite finding was reported by Everett et al. (2014). Corresponding evidence comes from a study on personality traits, which found that nonheterosexual women in fact have *lower* neuroticism than heterosexual women (Lippa, 2005; see also Sabia et al., 2017; Zheng, Lippa, & Zheng, 2011). Since men score typically lower than women on neuroticism, these findings are in line with the theory that nonheterosexual women are biobehaviorally and psychologically masculinized (Costa, Terracciano, & McCrae, 2001; Lippa, 2005). If psychosocial stressors were a major factor causing the psychophysiological differences between nonheterosexual and heterosexual women (cf. Eliason & Fogel, 2015; Rosario, Schrimshaw, & Hunter, 2008), we would expect nonheterosexual women to score *higher* on neuroticism and have higher CRP values than heterosexual women—which they do not.

### Sexually Antagonistic Epimarks and Androgen Sensitivity

Recent theoretical discussions have focused on potential epigenetic mechanisms underlying the development of sexual orientation. These mechanisms include reduced androgen sensitivity in normally developing XX fetuses and enhanced sensitivity in XY fetuses. The rationale behind these hypothesized mechanisms is that sex-specific epigenetic modifications control sexually dimorphic development prior to the secretion of T by the testes (Rice et al., 2016). These *epimarks* have the potential to become sexually antagonistic, however, if they fail to erase across generations and become inherited by opposite-sex offspring, influencing their ontogeny. Thus, sexually antagonistic epimarks are adaptive for the parent but potentially maladaptive for opposite-sex offspring by contributing to discordance between gonadal sex and a sexually dimorphic trait (Rice et al., 2016), including sexual orientation (Rice et al., 2012). Since this work still requires empirical validation, we refrain from a more expansive review and direct interested readers instead to the original articles that discuss these epigenetic mechanisms in greater detail (Ngun & Vilain, 2014; Rice et al., 2012; Rice, Friberg, & Gavrilets, 2013, 2016).

## Progesterone: Organizational and Activational Effects on Sexual Orientation

It has been suggested that besides estrogen and testosterone, another sex hormone, progesterone (P), mediates same-sex preferences in women (Fleischman et al., 2015). P evolved some 450 million years ago (Thornton, 2001) and is involved in the regulation of female reproduction across nearly all vertebrate groups (Nelson, 2011). Produced mainly in the ovaries of women (and the adrenal glands of men), P prepares the uterine lining for implantation of a fertilized egg, sustains the uterus as a hospitable growth environment for the fetus, modulates immune function (Gangestad & Grebe, 2017), increases pathogen disgust (Fleischman & Fessler, 2011), relationship commitment (Jones et al., 2005), and decreases sexual desire (Roney, 2016; Roney & Simmons, 2013). Notably, P only seems to decrease *general* sexual desire while increasing in-pair sexual desire (Grebe, Thompson, & Gangestad, 2016), lending some support to the hypothesis that circulating progesterone mediates affiliative behaviors in humans (Fleischman et al., 2015).

The overall evidence for the affiliation hypothesis of P in the evolution of female nonheterosexuality is still inconclusive (see Gangestad & Grebe, 2017 for a review). There have been two recently published reports gathering some evidence that, on the one hand, female sexual fluidity may have evolved to facilitate affiliation in polygynous marriages (Kanazawa, 2017) and, on the other, that circulating P increases both affiliative behavior and homoerotic motivation in men and women (Fleischman et al., 2015). Integrating the latter proposition with existing evidence is somewhat problematic. Since P increases relationship commitment (Jones et al., 2005) and sexual interest toward one's partner (but not toward extra-pair individuals) (Grebe et al., 2016), one would expect P to also lower sociosexuality in nonheterosexual individuals, especially if it mediated nonheterosexual preferences activationally. Yet existing evidence is diametrically opposite to this prediction: nonheterosexual women have elevated sociosexuality (Burri et al., 2015; Hartnett, Lindley, & Walsemann, 2017; Howard & Perilloux, 2017; Kanazawa, 2017; Lippa, 2006; Schmitt, 2007) but they also have higher P levels than heterosexual women (Juster et al., 2016). Future research on the role of P in affiliation and nonheterosexual motivation should seek to consolidate this inconsistency. Its role in the nonheterosexual behavior of other primates should be analyzed to further explore the phylogeny of affiliation and P in female nonheterosexuality.

Besides these activational effects, progesterone can also have organizational effects on sexual development, especially when administered exogenously. Notably, prenatal administration of progestins (synthetic progestogens) to pregnant mothers in order to treat miscarriage resulted in genital masculinization of seventy female infants in the 1950s (Wilkins, 1960; see Jacobson, 1962 and Voorhess, 1967 for similar results). Prenatal exposure to another progestin, medroxyprogesterone acetate (MPA), did not masculinize girls' genitals but in fact feminized some of their behavior (Ehrhardt, Grisanti, & Meyer-Bahlburg, 1977). A meta-analysis found no association between prenatal sex hormone exposure (synthetic estrogens, progestins, and combination agents) to external genital malformations, while also noting the lack of research on infant girls exposed to exogenous sex hormones in utero (Raman-Wilms, Tseng, Wighardt, Einarson, & Koren, 1995). These inconsistent findings may be somewhat consolidated by the observation that progestogens have both antiestrogenic and antiandrogenic effects, which vary both in terms of dosage and the type of progestogen administered (reviewed in Reinisch et al., 1991; Sanders & Reinisch, 1985).

In this context, we draw attention to an important recent finding. Women and men who were prenatally exposed to a synthetic progestogen had a significantly higher likelihood than control individuals of (1) identifying as nonheterosexual, (2) reporting same-sex attractions, and (c) engaging in same-sex behavior in adulthood (Reinisch, Mortensen, & Sanders, 2017). The progestin in question, lutocyclin, is a brand name of ethisterone, a synthetic progestogen which has androgenic activity. It can masculinize female sexual orientation (and feminize that of men). Ethisterone has previously been reported to cause urogenital anomalies and a lower likelihood of exposed men to be married in adulthood (Beral & Colwell, 1981). However, subjects in that study were also exposed to stilboestrol (also known as DES) (Beral & Colwell, 1981), and so disentangling the effects of synthetic estrogens and progestogens based on that study is not possible (cf. Raman-Wilms et al., 1995, who used DES exposure as an exclusion criterion in their meta-analysis).

In the aggregate, current evidence points to prenatal administration of synthetic progestogens as a potential factor that masculinizes women both physiologically and psychobehaviorally, resulting in a higher likelihood for nonheterosexual attractions and behavior in women and men. Besides the organizational role of synthetic progestogens, endogenous P may have an activational role in mediating same-sex motivation and affiliation in men and women.

## Neurophysiological Differences Between Heterosexual and Homosexual Women

Changes in sexual orientation caused by brain lesions in the temporal lobe and hypothalamus have been reported both in humans and in nonhuman animals, highlighting the importance of neurophysiology in the determination of sexual orientation (Poeppl et al., 2016; Swaab, 2003; Swaab & Garcia-Falgueras, 2009). To our knowledge, there is no single autopsy study done in nonheterosexual women (most are done in men), but brain scanning studies have found either anatomical differences or differences in brain functions between nonheterosexual and heterosexual women. Ponseti et al. (2007) found that homosexual women have less gray matter in the temporo-basal cortex, ventral cerebellum, and left ventral premotor cortex compared to heterosexual women. The most marked difference was found in the left perirhinal cortex in which there was less gray matter in homosexual women than heterosexual women (Ponseti et al., 2007). This area is sexually dimorphic, containing more gray matter on average in women than in men, and is known to be involved in a variety of sexually dimorphic functions (Ponseti et al., 2007). Savic and Lindström (2008) found that heterosexual men and homosexual women showed right cerebral asymmetry, whereas volumes of the cerebral hemispheres were more symmetrical in homosexual men and heterosexual women. Sex-atypical amygdala connections were also reported in homosexual women (Savic & Lindström, 2008). In addition, a sex-atypical pattern of activation of the anterior hypothalamus occurs in homosexual women when smelling putative pheromones (Berglund, Lindstrom, & Savic, 2006). A recent analysis reported a difference between homosexual women and heterosexual women in resting-state functional connectivity, with no differences in cortical thickness, subcortical structural volumes, nor fractional anisotropy (Manzouri & Savic, 2018). Collectively these studies suggest that homosexual women's brain morphology has at least partially shifted in the masculine direction—a shift probably associated with sex-atypical brain function in nonheterosexual women.

## Ontogeny: How Does Female Nonheterosexuality Emerge in Individual Development?

To better understand the evolution of the female sexual orientation spectrum, we propose that it is necessary to analyze individuals in each category of nonheterosexual women separately. Butch lesbians typically behave in a gender-atypical way since childhood both in Chinese (Zheng et al., 2018) and in Western samples, and are often perceived as tomboys in childhood (Hiestand & Levitt, 2005). Femmes, on the other hand, regularly behave in a gender-typical way in childhood and early adolescence and are perceived as heterosexual girls (Levitt, Gerrish, & Hiestand, 2003). Another butch/femme difference is the timing of becoming aware of one's own sexual orientation. Although the average age of becoming aware of one's sexuality for lesbians is 18 years, butch lesbians do so only a few years later than heterosexual girls, at an average age of 14.6. Femmes, however, become aware of their nonheterosexual orientation at the age of 22 on average (Levitt & Horne, 2002).

The most prominent difference between women's and men's nonheterosexuality is that female nonheterosexual behavior appears to be more malleable in general and liable to change with age in particular (Diamond, 2008a, b; Kanazawa, 2017). Current data suggest that women who have lived their entire lives as nonheterosexuals are a rarity. According to an Australian study, only 7% of women who classify themselves as homosexual had not engaged in intercourse with men (Fethers, Marks, Mindel, & Estcourt, 2000), effectively entitling them "gold star" lesbians (Richter, 2011). Two studies in the UK and the U.S. found that between 77.3 and 82% of self-identified lesbians had had one or more male sexual partner (Bailey, Farquhar, Owen, & Whittaker, 2003; Diamant et al., 1999; neither study controlled for butch/femme differences).

It seems that many women have the *capacity* to adopt a bisexual reproductive strategy: their sexual attraction patterns are less affected by a partner's sex per se than in men, and more by specific contextual and interpersonal factors (Chivers, 2017a; Diamond, 2007; Kuhle & Radtke, 2013). Diamond (2008a) used the term "sexual fluidity" to describe women's love and desire, specifying that "all women are sensitive to interpersonal and situational influences on their sexuality, albeit to differing degrees" (cf. a more precise operationalization of the term in Kanazawa, 2017). This view is supported by research which has demonstrated that the majority of women who classify themselves as heterosexual experience genital arousal when being shown erotic films or photos of women (reviewed in Chivers, 2017a) regardless of their menstrual cycle phase (Bossio, Suschinsky, Puts, & Chivers, 2014). That the majority of self-identified heterosexual women also experience pupil dilation when viewing erotic photos of the same sex implies that they have a capacity for nonheterosexual arousal (Rieger & Savin-Williams, 2012). In a Finnish study on a population sample of twins, 65.4% of the 6001 participating women admitted having potential for nonheterosexual behavior while about 35% thought it quite impossible (Santtila et al., 2008).

Empirical evidence, however, indicates that Diamond's (2008a) conclusion (about all women being sensitive to interpersonal and situational influences on their sexuality) is too broad and that exclusively homosexual women should be excluded from it. Women who classify themselves as exclusively homosexual do not respond to the sexual pheromones of the opposite sex (Berglund et al., 2006). Likewise, they do not have dilated pupils nor experience arousal when viewing erotic material of men (Chivers, Seto, & Blanchard, 2007; Rieger & Savin-Williams, 2012; see Chivers, 2017a for a review).[9] A functional magnetic resonance imaging (fMRI) study reported similar results: in contrast to bisexual and heterosexual women, homosexual women showed uniquely gynephilic (female-preferring) neural activation patterns when exposed to visual erotic stimuli (Safron et al., 2018). It seems that Diamond's conclusion is valid for *most* women, since they have the potential for same-sex arousal which can be activated by various environmental or interpersonal stimuli (Chivers, Bouchard, & Timmers, 2015; Diamond, 2008a), but that exclusively homosexual women should be excluded from that generalization since they show male-typical sex-specific arousal patterns and seem to lack the psychophysiological capacity for sexual malleability. For a more detailed discussion on the proximate mechanisms and ultimate functions of the specificity of women's sexual response, we refer interested readers to Luoto and Rantala (2017) and Chivers (2017a,b).

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[9] Though see Rieger et al. (2016, not controlling for butch/femme differences) for findings that suggest that even exclusively homosexual (Kinsey 6) women experience some genital arousal when shown erotic material of men.

## Phylogeny: What Is the Evolutionary History of Female Nonheterosexuality?

To understand the evolution of nonheterosexual preferences in women, it is necessary to consider not only the evolutionary history of humans, but also the antecedents of human nonheterosexual behavior in nonhuman animals (Poiani, 2010). For example, arguments that explain women's sexual fluidity by the sexualization of female bodies in media (e.g., Diamond, 2017) become less plausible when analyzed on a broader evolutionary scale. The lack of such cultural mechanisms in nonhuman animals highlights the value of using comparative research both at the proximate and at the ultimate levels of analysis.

Although same-sex sexual behavior in females is much less often reported and probably less widespread than in males, it still occurs naturally in multiple species in many different forms (Bagemihl, 1999; Jankowiak, Tryjanowski, Hetmański, & Skórka, 2018; Poiani, 2010; Young, Zaun, & VanderWerf, 2008). Interestingly, same-sex sexual behavior is more common in the sex that invests less in parental care, at least among a wide range of bird species (MacFarlane, Blomberg & Vasey, 2010) and humans (Savin-Williams, 2009). Exclusive same-sex behavior has been reported for example in silver gull females (*Chroicocephalus novaehollandiae*), black stilt females (*Himantopus novaezelandiae*), and red fox females (*Vulpes vulpes*) (Bagemihl, 1999, pp. 438, 538, 554).

Female same-sex sexual behavior is prevalent in many primate species. In Japanese macaques, the proportion of females engaging in same-sex sexual behavior varies between populations from 0% up to 78% (Vasey, 2007). In bonobos, 55% of sexual activity occurs between same-sex individuals; only 4.2% of it is between males, meaning that more than half of all sexual behavior in bonobos occurs between females (Fruth & Hohmann, 2006). Exclusive same-sex sexual behavior is extremely rare or non-existent in nonhuman primates, however, which suggests that exclusive homosexuality in humans may be an evolutionary novelty in primates (Dixson, 2012) despite evolving convergently in non-primate taxa (e.g., Bagemihl, 1999, pp. 438, 538, 554; Perkins & Fitzgerald, 1997).

One possible phylogenetic explanation for bisexuality in human females is that it has been inherited from an ancestor shared with bonobos (or a more distant anthropoid ancestor: see Dixson, 2012) and has been retained in humans even though it may no longer serve its original functions of maintaining the social hierarchy of the group or reconciling arguments as in bonobos (Kanazawa, 2017; Kuhle & Radtke, 2013). The behavior could have been retained if it does not impose a specific fitness cost to human females (Apostolou, 2016a; Camperio Ciani et al., 2018) or, in case it does impose a cost, if inadequate evolutionary time has elapsed for it to be eliminated.

It should, however, be kept in mind that the proximate mechanisms and ultimate functions of same-sex sexual behavior may vary between species depending on a range of factors. Therefore, while instructive, between-species comparisons should only be used as an informative source of comparative data, not as a Procrustean bed into which human behavior has to fit. Nevertheless, the overlap of *proximate* mechanisms underlying female same-sex behavior between species is substantial (e.g., Baum & Bakker, 2017; Poiani, 2010). Future research should leverage that level of analysis to inform comparative research also at the *ultimate* level of analysis. One open question concerns the relationship between female–female sexual behavior in bonobos and female nonheterosexuality in humans. Another open question is the degree to which butch/femme phenotypes have analogs in nonhuman animals. de Waal (1998, pp. 53–56), for example, notes the existence of two atypical, masculine-looking female chimpanzees. One of them refused to mate with males, instead mounting females and thrusting them in a male-typical way. The other atypical female chimpanzee mated with males but was sterile.

Likewise, Gilfillan, McNutt, Vitale, de Iongh, and Golabek (2017) reported the rare existence of a maned lioness which displayed sexual mounting behavior with other females. Despite mating with males, this female was never observed to be pregnant over an 8-year period. Strikingly, the lioness displayed a sexually dimorphic feature typically associated with male lions: a conspicuous coat of long hair on chest, neck, and back (Gilfillan et al., 2017). Mane growth covaries with age-related rises in serum T in male lions (West & Packer, 2002), while male castration results in the loss of the mane (Hartman et al., 2013). Therefore, high T exposure seems to have induced both a male-typical morphological feature and same-sex sexual behavior in the lioness.

## What is the Ultimate Fitness Value of Female Nonheterosexuality?

The ultimate level of explanation seeks answers to the question of why did a trait or a behavior evolve—what fitness benefits, if any, does it provide for the alleles underlying that trait (Bateson & Laland, 2013; Luoto & Rantala, 2017; Rantala, Luoto, Krams, & Karlsson, 2018)? Several explanations have been provided for female nonheterosexual behavior and orientation at this level of analysis. In this section, we briefly review the existing hypotheses and spell out new ones ("Hormonally Mediated Fast Life History Strategy" and "Infanticide Avoidance" sections) when the existing hypotheses do not fully account for the complex data.

### Heterosexual Deprivation

The heterosexual deprivation hypothesis posits that nonheterosexual behavior is evoked by a scarcity of opposite-sex mates (cf. Bagemihl, 1999; Vasey & Gauthier, 2000). Evidence for this hypothesis exists for some animals (e.g., Jankowiak et al., 2018; Roselli, Reddy, & Kaufman, 2011). We conceive a more refined version of this hypothesis in humans, according to which women's malleable sexuality may have evolved as an adaptation[10] when women have been unable to secure a preferred man, or a man of an adequately high quality, in a long-term relationship. In these types of situations, it may be more beneficial for two women to form a relationship for rearing offspring rather than stay alone (Kuhle & Radtke, 2013; cf. Jankowiak et al., 2018).

## Alloparenting

The heterosexual deprivation hypothesis is partially connected (Jankowiak et al., 2018) with the alloparenting hypothesis of female nonheterosexuality (Kuhle & Radtke, 2013). In the evolutionary history of the human species, a woman may have been left to raise her offspring alone if the father of her children died or deserted her in search of new mating opportunities. Left alone to take care of offspring in a harsh environment, it would have been more beneficial for a woman to form a relationship with another woman than raise her children entirely alone (Kuhle & Radtke, 2013). In a situation such as this, women with a more malleable sexual orientation may have had an advantage over women with fixed, exclusively heterosexual behavior. Alloparenting is functionally related to affiliation since same-sex social bonds form the bedrock of alloparenting. The affiliation hypothesis posits that natural selection co-opted the reward system underlying sexual behavior to also promote social bonds—thus, homoerotic motivation may have the adaptive function of promoting alliances (Fleischman et al., 2015).

Indirect support for the alloparenting hypothesis is provided by a study that found that mothers who are most in need of alloparental care endorse more positive attitudes toward homosexuality (Playà, Vinicius, & Vasey, 2017). Playà et al. (2017), however, did not analyze the extent to which these positive attitudes were mediated by *actual* same-sex attractions rather than merely a positive attitude toward them. Comparative evidence for the alloparental hypothesis is given by the finding that female pigeons paired with other female pigeons had more offspring than unpartnered female pigeons. The offspring of unpartnered female pigeons were also substantially lighter (less viable) than the offspring of f–f pairs (Jankowiak et al., 2018). Similarly, Laysan albatross (*Phoebastria immutabilis*) females may form a partnership if the number of males inadequately matches the number of females. In a Laysan albatross colony in Hawaii, 31% of breeding pairs consisted of two unrelated females that cooperated to raise a chick (Young et al., 2008). However, female–female pairs had lower fitness than male–female pairs (Young & VanderWerf, 2014).

## Balanced Polymorphism of Masculinity

Despite the explanatory potential of the alloparenting hypothesis, the evolutionary reason for the existence of exclusively homosexual women remains elusive. Miller (2000) theorized that a balanced polymorphism of masculinity is the underlying cause of female homosexuality, though he did not differentiate between femmes and butches. Since masculinity is deemed to be a polygenic trait, higher masculinity is caused by a greater number of masculinity-inducing alleles and masculinizing environmental factors. If sufficiently masculinized, women's psychological mechanisms that deal with mate choice also become masculine, leading to the development of exclusively homosexual orientation in adulthood. However, Miller argues that possessing only *some* of the masculinizing alleles would in fact be beneficial for the female both in intersexual selection and in intrasexual competition (cf. Veiga & Polo, 2008) if possessing them does not entail exclusive homosexuality. According to this hypothesis, greater masculinity could lead to enhanced mate acquisition for the "tomboy" due to a reduced psychological gap between the sexes and the consequently enlarged pool of shared interests that a masculine woman would, in theory, have with men (Miller, 2000).

Empirical studies have set out to test Miller's (2000) balanced polymorphism hypothesis. Zietsch et al. (2008) reported three main findings in a study on Australian twins: (1) that masculine women had a higher probability to be nonheterosexual than feminine women, (2) that masculine women (as opposed to feminine women) had a higher number of sex partners when they are heterosexual, and (3) that pleiotropic genetic effects explained the relationship between female sexual orientation, sex typicality, and number of opposite-sex partners. The study was replicated by Burri et al. (2015) with monozygotic and dizygotic female twins in the UK, with similar findings. The findings reviewed in "Prevalence of Nonheterosexual Behavior and Orientation" section and "Categories of Nonheterosexual Women" section on the prevalence of various phenotypes in the female sexual orientation spectrum lend additional support to the hypothetical balanced polymorphism of masculinity in women. Despite these data that support Miller's hypothesis, we believe that he failed to capture the range of physiological, psychological, and behavioral outcomes associated with this hypothesis. An elaboration of complementary hypotheses is therefore necessary.

## Hormonally Mediated Fast Life History Strategy

As predicted by parental investment theory (Trivers, 1972), men have a significantly higher sociosexuality than women do (Baranowski & Hecht, 2015; Fernandes et al., 2016; Howard & Perilloux, 2017; Schmitt, 2007). High sociosexuality

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[10] An *adaptation* can be defined as an inherited and reliably developing characteristic that came into existence as a feature of a species through natural selection because it facilitated reproductive fitness during the period of its evolution (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Tooby & Cosmides, 1992). See Lewis et al. (2017) for a broad, more recent discussion.

being a masculine trait, it should be no great surprise that psychologically masculinized women have higher sociosexuality than feminine women (Burri et al., 2015; Howard and Perilloux (2017); Ostovich & Sabini, 2004; Zietsch et al., 2008). Instead of more masculine interests enhancing the mate acquisition of more masculine women as Miller (2000) hypothesized, we argue—together with Mikach and Bailey (1999), Lippa (2006, 2007), Burri et al. (2015), and Kanazawa (2017)—that sociosexuality is the mediating factor between women's greater psychological masculinity and number of sexual partners.

It is thus possible that sexual fluidity facilitates alternative reproductive strategies in women. Women who are sociosexually restricted prefer men who show willingness to provide parental care and prefer to commit to long-term relationships. Conversely, women who are sociosexually unrestricted generally seek men who are sexually attractive, masculine, and/or have high social status (Muggleton & Fincher, 2017; Rodrigues & Lopes, 2017; Simpson & Gangestad, 1992). Physically attractive, masculine men may provide "good genes" for their offspring (Rantala et al., 2012, 2013; Sell, Lukazsweski, & Townsley, 2017). These men are, however, less likely to provide extensive parental care (Boothroyd, Jones, Burt, DeBruine, & Perrett, 2008; Gettler et al., 2017)—enabling them to expend effort to acquiring new mates. Women may therefore be faced with a reproductive trade-off between parental investment and genetic benefits to their offspring (e.g., Muggleton & Fincher, 2017). Since bisexual women are significantly more unrestricted in their sexual behavior than heterosexual women (Lippa, 2007; Schmitt, 2007), it is possible that bisexual women have an alternative mating strategy in which they gain genetic quality for their offspring by mating with attractive men who do not provide parental care, while securing the necessary parental care for the resulting offspring from other females (Kuhle & Radtke, 2013).

As indicated by the list of findings summarized in Table 1, there is considerable support for the hypothesis that the greater psychological masculinization of nonheterosexual women leads to their developing male-typical fast LH strategies. The findings listed in Table 1 are characteristic of fast LH strategies, i.e., a preferential allocation of bioenergetic resources into early reproduction over somatic maintenance and survival.[11] The findings in Table 1 also indicate a preference in nonheterosexual women toward immediate over postponed rewards (cf. Frankenhuis et al., 2016; Maner et al., 2017; Mishra et al., 2017; Pine et al., 2010).

More specifically, the higher substance use of nonheterosexual women could be a corollary of evolutionary selection for fast LH strategies. These meaningful functional composites represent coadapted reproductive strategies (Figueredo et al., 2005; Hämäläinen et al., 2018), which lead to risky sexual behavior (Fethers et al., 2000; Zietsch et al., 2010), increased impulsivity, and present-orientedness (Frankenhuis et al., 2016; Minkov & Bond, 2015; Mishra et al., 2017). Nonheterosexual women have higher sociosexuality than heterosexual women (Table 1, Finding 2), a trait that notably correlates with alcohol use (Clark, 2004; Vincke, 2017). Energetic investment in mating rather than growth, maintenance, or parenting is a core feature of fast LH strategies, while alcohol use is a typical corollary of fast LH strategies in humans (Hill & Chow, 2002; Richardson et al., 2016; Vincke, 2017). High alcohol use and alcohol-related problems are also more common in men than in women (Erol & Karpyak, 2015; Nolen-Hoeksema, 2004). The fast LH strategies and associated poorer health outcomes documented here in nonheterosexual women are consistent with the idea that acceleration of reproductive development constitutes an important component in the developmental origins of health and disease in women (Belsky, Ruttle, Boyce, Armstrong, & Essex, 2015).

Taken together, the findings listed in Table 1 support the hypothesis that the range of phenotypes and behavioral patterns associated with female nonheterosexuality is a possible outcome arising from selection on fast LH strategies. In seeking to refine this hypothesis, it could be further predicted that the butch phenotype is associated with faster LH strategies than femme phenotype(s) since butches are biobehaviorally and psychologically more masculine than femmes. We explored this prediction in light of existing studies, presenting evidence in Table 2. As can be seen, most of the evidence (except for BMI) supports the prediction of faster LH indicators in butches than in femmes.

Reverse engineering (see Lewis et al., 2017 for a discussion on reverse task analysis) the aggregate of the findings reviewed in Tables 1 and 2 suggests that there is reason to expect fast LH strategies also in the fathers of nonheterosexual women. This prediction arises because of a substantial heritable component (Cherkas et al., 2004; Figueredo et al., 2004; Gavrus-Ion et al., 2017) and parent–child similarities in LH strategies (Richardson et al., 2016). Fathers who seek novel mating opportunities instead of providing parental investment to offspring are likely to be more masculine and sociosexually unrestricted (Boothroyd et al., 2008; Gettler et al., 2017). What is more, T concentrations have a substantial heritable component in men (Travison et al., 2014), women (Harris, Vernon, & Boomsma, 1998; Coviello et al., 2011), and in nonhuman animals (King, Cline, & Hubbard, 2004). These heritability factors could partially account for the fast LH strategies observed in nonheterosexual women (and predicted in their fathers).

Given that masculinity predicts nonheterosexuality in women and is heritable (Burri et al., 2015; Zietsch et al., 2008), a more masculine father would be likely to produce more masculine (Cornwell & Perrett, 2008) and sociosexually

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[11] This interpretation of the data is further supported by the finding that androgenization in women (Abel, Kruger, & Pandya, 2012) and in pigeons (Matson, Riedstra, & Tieleman, 2016) correlates with a shorter lifespan (sexual orientation was not measured in those studies).

**Table 1** Evidence supporting the hormonally mediated fast LH strategy hypothesis

| Findings | References |
|---|---|
| **Finding 1:** *nonheterosexual women have masculinized biomarkers, indicating high prenatal T exposure* | References compiled in "Prenatal Androgen Exposure, Masculinization, and Sexually Dimorphic Biomarkers" section |
| **Finding 2:** *bisexual women have higher sociosexuality and a significantly higher number of male sex partners than heterosexual women* | Burri et al. (2015), Hartnett et al. (2017), Howard and Perilloux (2017), Kanazawa (2017), Lippa (2006), Mikach and Bailey (1999), Mor and Davidovich (2016), Schmitt (2007), and Singh et al. (1999) |
| **Finding 3:** *bisexual women have greater responsiveness to female and male visual sexual stimuli than heterosexual women, suggesting greater degrees of sexual motivation* | Safron et al. (2018); see also Lippa (2006) and Stief et al. (2014) |
| **Finding 4:** *bisexual women report an earlier sexual debut and have more children by the age of 25 than heterosexuals* | Baker and Bellis (1995) and Mor et al. (2015) |
| **Finding 5:** *women who have children before the age of 22 have increased levels of sexual fluidity between ages 22–29* | Kanazawa (2017); cf. Dunkel and Lukaszewski (2015) |
| **Finding 6:** *the prevalence of risky sexual behavior and teenage pregnancy is higher among nonheterosexual than heterosexual women* | Mor et al. (2015), Mor and Davidovich (2016), Nield, Magnusson, Brooks, Chapman, and Lapane (2015), and Saewyc, Bearinger, Blum, and Resnick (1999) |
| **Finding 7:** *nonheterosexual women have a significantly higher likelihood of unintended pregnancy than heterosexual women* | Hartnett et al. (2017) |
| **Finding 8:** *nonheterosexual women report less frequent contact with their adult children than heterosexual parents (which is an indirect measure of lower investment in existing offspring)* | Richards et al. (2016) |
| **Finding 9:** *young nonheterosexual women report significantly more emergency room visits but are less likely than heterosexual women to take vaccinations or visit their general practitioner and gynecologist, despite being a health risk group* | Boehmer et al. (2012), Jones et al. (2016), McRee et al. (2014), Mor et al. (2015); see Polek and Hardie (2017) for contradictory results |
| **Finding 10:** *nonheterosexual women have greater odds of hazardous drinking and smoking, with bisexual women reporting a significantly greater number of heavy episodic drinking than lesbians* | Boehmer et al. (2012), Hequembourg, Livingston, and Parks, (2013), Hughes et al. (2010), Lee, Griffin, and Melvin (2009), Lindley, Walsemann, and Carter (2012), and Matthews et al. (2011) |
| **Finding 11:** *nonheterosexual women have an elevated likelihood of being obese, which indicates higher motivational salience of present rather than postponed rewards and is correlated with fast LH strategy* | Boehmer et al. (2007), Bowen et al. (2008), Maner et al. (2017), Međedović and Bulut (2018), Shields, Moons, and Slavich (2017), and Yancey et al. (2003) |
| **Finding 12:** *incrementally more homosexually oriented women became increasingly masculine on the central, male-typical personality dimension of sensation seeking* | Trocki et al. (2009); yet see Gil-Llario et al. (2015) and Stief et al. (2014) for somewhat contradictory results |
| **Finding 13:** *nonheterosexual women score higher than heterosexual women on psychopathy, a trait in which men have higher scores than women and which is also associated with fast LH strategies and substance use* | Jonason et al. (2010, 2017), Međedović (2018), Muris et al. (2017), and Semenyna et al. (2018) |
| **Finding 14:** *nonheterosexual women (in this context defined as women who have engaged in nonheterosexual sexual behavior prior to incarceration) are overrepresented as inmates in prison populations (3–44% of the total prison population versus 2–13% in the general population)* | Hensley and Tewksbury (2002) |
| **Finding 15:** *girls who report same-sex attractions have earlier menstrual onset and are more developed for their age, with the exception of breast development* | Savin-Williams and Ream (2006); cf. mixed results by Bogaert, Friesen, and Klentrou (2002) |

unrestricted offspring. He would also be likely to provide limited paternal care himself (Boothroyd et al., 2008). These predictions gain some empirical support from statistical tests that we performed on data extracted from Sabia et al. (2017). The parents of bisexual women ($M=0.67$, $SD=0.47$, $n=107$) were significantly less likely $t(5253)=4.14$, $d=0.36$, $p<0.0001$ to be married when the child was aged 14 than the parents of heterosexual women ($M=0.82$, $SD=0.37$, $n=5148$). The difference in parental marriage status between lesbians ($M=0.76$, $SD=0.42$, $n=81$) and heterosexual women at age 14 was not statistically significant $t(5227)=1.50$, $d=0.16$, $p=0.13$. It is a well-established finding that father absence is associated with early reproduction and the development of fast LH strategies in female offspring (Anderson, 2015; Draper & Harpending, 1982; Ellis et al., 2003, 2012; Guardia et al., 2014; James, Ellis, Schlomer, & Garber, 2012; Salmon, Townsend,

**Table 2** Differences in behavioral, physiological, and psychological life history variables between butches, femmes, and heterosexual women. Heterosexual women were not analyzed in studies conducted by Rosario et al. (2008, 2009)

| Life history indicator | Rank order | Reference and sample description |
|---|---|---|
| Lifetime # of sexual partners (females + males = total partners) | 1. Butch (12.8 + 4.7 = 17.5)<br>2. Femme (3.8 + 6.8 = 10.6) | Rosario et al. (2009). A U.S. sample of 76 young women, mean age 18.4 years |
| Lifetime # of sexual encounters (females + males = total encounters) | 1. Butch (709.3 + 43.6 = 752.9)<br>2. Femme (210.9 + 153.5 = 364.4) | Rosario et al. (2009). A U.S. sample of 76 young women, mean age 18.4 years |
| # of sexual relationships (past 2 years) | 1. Butch (4.5)<br>2. Femme and heterosexual (3.8) | Singh et al. (1999). A sample of 100 lesbian (47 butch and 53 femme) and 58 heterosexual women |
| Cigarette use (quantity) | 1. Butch (1.8–2.0)<br>2. Femme (0.9–1.0) | Rosario et al. (2008). A U.S. sample of 33 butch and 39 femme women, mean age 18.4 years |
| Alcohol use (frequency); (quantity) | 1. Butch (1.4–1.8); (1.9–2.0)<br>2. Femme (0.8–1.6); (1.3–1.6) | Rosario et al. (2008). As above |
| Marijuana use (frequency); (quantity) | 1. Butch (0.8–1.1); (0.8–1.5)<br>2. Femme (0.4–0.6); (0.5–0.7) | Rosario et al. (2008) |
| Substance abuse symptoms | 1. Butch (1.5–1.7)<br>2. Femme (1.4–1.5) | Rosario et al. (2008) |
| Circulating testosterone | 1. Butch (4.1 ng/dl)<br>2. Femme (2.5 ng/dl)<br>3. Heterosexual (2.3 ng/dl) | Singh et al. (1999). A sample of 33 lesbian (17 butch and 16 femme) and 11 heterosexual women |
| BMI | 1. Femme (25.3)<br>2. Butch (24.7)<br>3. Heterosexual (22.2) | Singh et al. (1999). A sample of 100 lesbian (47 butch and 53 femme) and 58 heterosexual women |
| Enjoys erotica | 1. Butch (5.9)<br>2. Femme (4.7)<br>3. Heterosexual (4.3) | Singh et al. (1999). A sample of 33 lesbian (17 butch and 16 femme) and 11 heterosexual women |
| Use of sex toys | 1. Butch (4.6)<br>2. Femme (3.7)<br>3. Heterosexual (2.6) | Singh et al. (1999). A sample of 33 lesbian (17 butch and 16 femme) and 11 heterosexual women |
| Belief in monogamy | 1. Femme (8.7)<br>2. Butch and heterosexual (7.9) | Singh et al. (1999). A sample of 100 lesbian (47 butch and 53 femme) and 58 heterosexual women |
| Belief in casual sex | 1. Butch (2.9)<br>2. Heterosexual (2.8)<br>3. Femme (2.4) | Singh et al. (1999). A sample of 100 lesbian (47 butch and 53 femme) and 58 heterosexual women |

& Hehman, 2016; Schlomer & Cho, 2017). However, genetic factors likely play an important role in shaping father-absent daughters' fast LH strategies rather than the father-absent environment per se driving the effect (Barbaro et al., 2017; Mendle et al., 2009; Schlomer & Cho, 2017). Correspondingly, genetic factors may underlie the composite traits of masculinity, sociosexuality, and nonheterosexual behavior in women, potentially contributing to the existence of a single heritable psychometric factor (cf. Burri et al., 2015; Fethers et al., 2000; Figueredo et al., 2004, 2006; Gruijters & Fleuren, 2018). It has also been suggested that polymorphisms of the X-linked androgen receptor gene may account for a variety of fast LH strategies in women and men (Comings, Muhleman, Johnson, & MacMurray, 2002; Gettler et al., 2017; Mascaro et al., 2018), a hypothesis tested in a vast range of populations by Minkov and Bond (2015).

Crucially, the hormonal environment of the fetus changes when a pregnant woman is exposed to stressors (potentially accompanied with epigenetic changes) (Ellis & Cole-Harding, 2001; Rice et al., 2012, 2016). Indeed, stress-driven maternal depressive symptomology is one factor underlying the development of fast LH strategies in girls and poorer health in newborns in general (Cabeza de Baca, Wojcicki, Epel, & Adler, 2018; James et al., 2012; see also Worthman & Trang, 2018). It therefore seems plausible that the mother detects environmental unpredictability through father absence (or other stressors) and manipulates the intrauterine conditions of the fetus. Such a process can be seen as a predictive adaptive response comprising greater masculinity, higher sociosexuality, earlier reproduction, and a heightened predisposition for nonheterosexual behavior in female offspring (cf. Del Giudice, 2012; Rice et al., 2012, 2016; Schlomer & Cho, 2017).

The law of supply and demand that arises from differential parental investment (Hämäläinen et al., 2018) predicts that women's sexual unrestrictedness will be readily met with men tuned to follow fast LH strategies, i.e., men who make the minimal behavioral investment(s) needed to fertilize the egg but are likely to avoid making further emotional, material, or parental investments (Boothroyd et al., 2008; Schmitt, 2007). The altricial nature of human infants means that they do not become net calories producers until approximately 18 years of age, and so the caloric costs of child development lie primarily with the parents (Kaplan, Hill, Lancaster, & Hurtado, 2000; Wells, 2007), but also with the alloparenting network provided by kin (Hrdy, 2009) or the community (Codding, Bird & Bird, 2011). The survival of the child is compromised if the father is absent—therefore, the viability of fast LH strategies is largely incumbent on the availability of an alloparental buffer that aids with the necessary parental duties of raising human infants. Various manifestations of female nonheterosexuality can constitute an alloparental buffer that enables the fast LH strategies of masculinizing alleles as they appear in the female *and* the male phenotype. In contrast, the alleles that result in a masculinized phenotype when they appear in a female body may produce more masculine physiological and behavioral traits in the male phenotype (Hämäläinen et al., 2018; Immonen et al., 2018). The advantage gained by the male phenotype from this increased masculinity in intrasexual competition and/or intersexual selection may be sufficiently large to offset the potential cost of the alleles when they occur in the exclusively homosexual female phenotype (cf. Camperio Ciani et al., 2018).

## Sexually Antagonistic Selection

The existence of masculine lesbians may thus be a consequence of a similar mechanism of genetically determined sexually antagonistic selection which partially explains homosexual preference in men (Camperio Ciani, Corna, & Capiluppi, 2004; Rahman et al., 2008). Males selectively favored for fast LH strategies may father less fit ("fast") daughters (Hämäläinen et al., 2018). Sexually antagonistic adaptation arises from the fact that the attributes favored in one sex are sometimes diametrically opposed to those favored in the other sex (Hämäläinen et al., 2018; Immonen et al., 2018; Rice et al., 2016). Comparative research on birds and fish, for example, indicates that high T levels in females are an indirect consequence of positive selection for high T levels in males (Mank, 2007; Moller, Garamszegi, Gil, Hurtrez-Bousses, & Eens, 2005; cf. Ketterson, Nolan, & Sandell, 2005). Evidence from an Italian (Camperio Ciani et al., 2018) and an Australian sample (Sabia et al., 2017) suggests that the reproductive success of nonheterosexual women is lower than that of heterosexual women. However, this fitness impairment may be offset by a higher number of offspring in nonheterosexual women's kin compared with the kin of heterosexual women, as found in the Italian sample (Camperio Ciani et al., 2018). Taken together, the findings reported in the three previous subsections indicate that sexually antagonistic selection, hormonally mediated fast LH strategies, balanced polymorphism of masculinity, and alloparenting may all be functionally related phenomena underlying the evolution of female nonheterosexuality (cf. Fig. 2).

## Infanticide Avoidance

We propose another, hitherto untested hypothesis to explain the fluidity of female sexual orientation. This hypothesis can be seen as a possible extension of the scenario described in "Hormonally Mediated Fast Life History Strategy" section. When a male copulates with a fertile female who has existing dependent offspring fathered by another male, it is in some contexts adaptive for the male to kill the existing offspring in order to provide the best chances of survival for his own offspring. This phenomenon (infanticide) is also common in nonhuman animals (Hausfater & Hrdy, 1984; Leclerc, Frank, Zedrosser, Swenson, & Pelletier, 2017; Lukas & Huchard, 2014). In humans, stepfathers are 120 times more likely to commit infanticide than biological fathers, and a child under 3 years of age living in a family with one step-parent is seven times more likely to be abused than one living in a family with two biological parents (Daly & Wilson, 1999). An adaptive response from a female with existing offspring would be to avoid contact with other males and instead seek partnerships with females, who may be psychologically more disposed to providing parental care rather than harming children. In relative absence of reproductive stakes of their own, infanticide is less adaptive for a female entering such a partnership than it would be for a male, and in fact the presence of a child is likely to trigger a nurture response in the woman (Hrdy, 2009, pp. 213–231). Sexual fluidity may, in other words, be a female reaction to the possibility of male infanticide in the intersexual coevolutionary arms race (cf. Hämäläinen et al., 2018).

## By-product

It is also possible that female nonheterosexuality in humans is not an adaption: it could merely be a functionless by-product of an adaptation.[12] Luoto and Rantala (2017) proposed the nutritional rewards hypothesis to explain the finding that both nonheterosexual and heterosexual women become physiologically aroused by visual same-sex stimuli. The rationale of this hypothesis is that neonates may become classically conditioned to women's bodies because breasts are repeatedly associated with nutritional rewards in ontogeny. Selection pressures for nutritional rewards have therefore not equipped women with a similar sexual aversion to same-sex body stimuli as found in most heterosexual men. This hypothesis remains to be empirically tested.

A further noteworthy consideration is that nonheterosexuality in females could be a by-product of high sex hormone

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[12] Byproducts are phenomena that exist because they are intrinsically coupled with an adaptation, despite having no function in and of themselves (see Lewis et al., 2017 for a more detailed discussion).

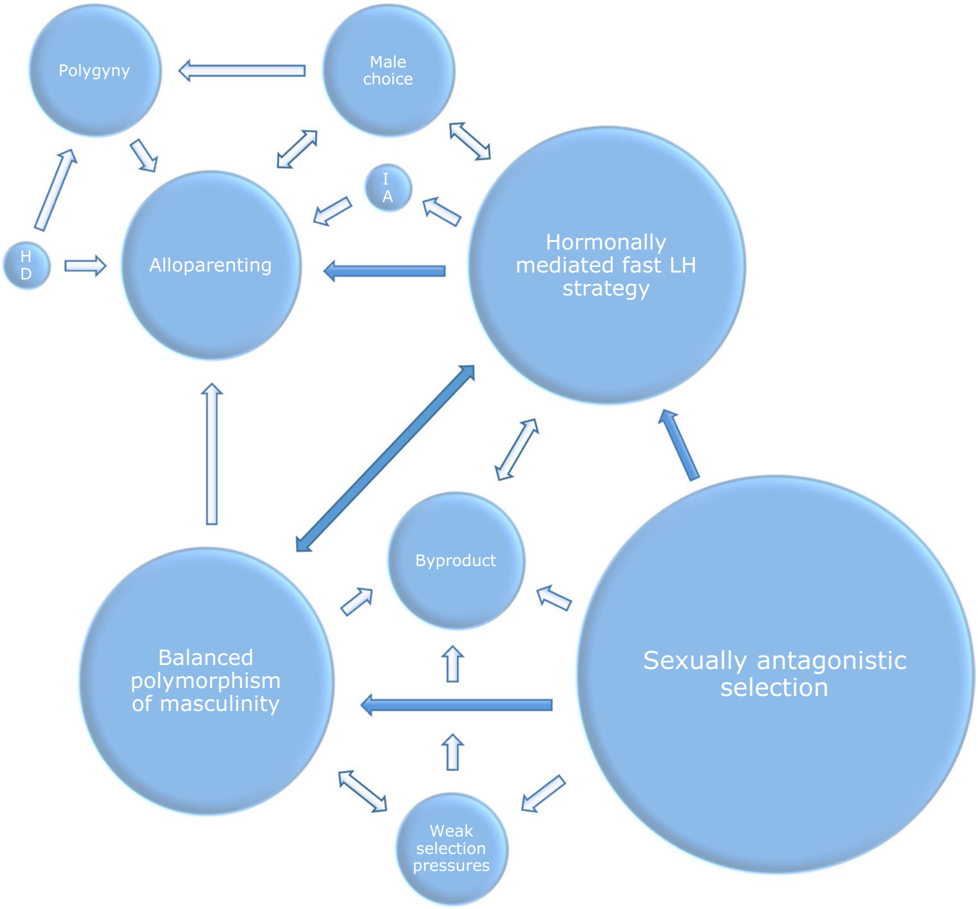

**Fig. 2** Hypotheses on the evolution of female nonheterosexuality. The relative size of each hypothesis in this figure reflects the amount of existing evidence in support of that hypothesis: the smaller the circle, the more limited is the evidence for that hypothesis. Arrows indicate potential causal relationships between the hypotheses, reflecting our view that none of them is likely to appear in isolation but may be interrelated in various ways. The direction of the arrow indicates the direction of causality between the hypotheses. Bolded arrows reflect relationships with strongest existing evidence, while transparent arrows indicate more hypothetical causality. *HD* heterosexual deprivation, *IA* infanticide avoidance

exposure in utero. This view contrasts the one presented earlier in this article—that such a shift in sexual orientation is adaptive at the genotypic level. Same-sex sexual behavior may also be a by-product of mistaken sex recognition (Engel, Männer, Ayasse, & Steiger, 2015), heterosexual deprivation, and/or a skewed sex ratio (Jankowiak et al., 2018, and references therein).

## Weak Selection Pressures

Extending the by-product hypothesis, it has been suggested that female nonheterosexuality may be caused by genetic mutations that are under weak selection pressures (Apostolou, 2016a). The rationale behind this hypothesis is that phenotypic variation is reduced when selection pressures are strong but increased when they are weak (Apostolou, 2016a; Fisher, 1930). Empirical evidence suggests that some men find the same-sex attractions of their partners sexually exciting (Apostolou, 2016b). To further bolster the weak selection hypothesis, Apostolou (2016a) reviews four lines of anthropological and historical evidence: regulation of mating, male–male competition, low emphasis placed on intimacy, and male tolerance toward same-sex attractions.

Importantly, all four lines of evidence for the weak selection hypothesis given by Apostolou (2016a) also support the main hypotheses of this review: balanced polymorphism of masculinity, sexually antagonistic selection, hormonally mediated fast LH strategy, and alloparenting. The findings reported in "Hormonally Mediated Fast Life History Strategy" section on the reproductive behaviors of nonheterosexual women broaden Apostolou's empirical evidence for the lack of substantial selection pressures against female nonheterosexuality.

## Male Choice

Apostolou et al. (2017) have recently proposed a conceptual extension to the weak selection pressures hypothesis. Placing males in the center of attention, the male choice hypothesis posits that if ancestral men have found nonheterosexuality a desirable feature in women, mate choice would have favored women with same-sex attractions (Apostolou et al., 2017). Experimental evidence suggests that at least some modern men prefer women with various degrees of same-sex attractions (Apostolou et al., 2017). Nevertheless, it is important to note that the strength of male choice on female same-sex attractions does not seem high, as it is not a trait that men consciously list as important in mate choice (e.g., Conroy-Beam, Buss, Pham, & Shackelford, 2015; Schmitt, 2014). Therefore, although Apostolou et al. found evidence for a certain degree of male choice for this trait when they specifically asked contemporary subjects about it, it would be important to measure it in relation to other mate preferences (possibly using hunter-gatherer populations). Apostolou et al. also failed to consider other features in nonheterosexual women that could drive male choice for alleles that predispose women to same-sex attractions. As reviewed in "Hormonally Mediated Fast Life History Strategy" section, nonheterosexual women, on average, are sociosexually less restricted than heterosexual women. This is likely a stronger factor in favoring (indirect) male choice for nonheterosexuality in women, rather than *direct* male selection for same-sex attractions in women.

### Polygyny

The male choice hypothesis is linked (Fig. 2) with the polygyny hypothesis, which posits that female sexual fluidity and nonheterosexual behavior may have been evolutionarily selected because they strengthened social bonds and reduced conflicts between women in polygynous marriages (Kanazawa, 2017). Kanazawa makes three predictions in an attempt to test the polygyny hypothesis: (1) bisexually behaving women have more offspring, (2) women who reproduce early in life have an increased tendency for nonheterosexual behavior, and (3) sexual fluidity correlates with unrestricted sociosexuality.[13] Although Kanazawa (2017) provides empirical evidence to support all these predictions, the polygyny hypothesis seems inadequate in light of the present review for several reasons. It cannot explain the existence of exclusively homosexual butch women, nor is it able to plausibly integrate the wealth of neurodevelopmental and psychobehavioral data on the relationship between masculinity, sociosexuality, and female nonheterosexuality into its explanatory framework. The polygyny hypothesis also inflates the importance of polygyny in human evolution (Apostolou, 2017): other work shows that the prevalence of polygyny has been low (Walker, Hill, Flinn, & Ellsworth, 2011) and, when present, relatively unimportant (Fletcher, Simpson, Campbell, & Overall, 2015). We emphasize that the totality of Kanazawa's (2017) evidence also supports the main hypotheses of this review: balanced polymorphism of masculinity, sexually antagonistic selection, hormonally mediated fast LH strategy, and alloparenting.

We have so far described multiple possible hypotheses for the evolution of various manifestations of female nonheterosexuality. These hypotheses are not mutually exclusive and may all be valid in varying degrees (see Fig. 2 for a visualization of their possible interconnectedness). We recognize the relative lack of selection pressures against female nonheterosexuality (but see King et al., 2008; Lewis et al., 2016 for counterexamples), as well as possible male choice for nonheterosexuality in women acting especially via heightened sociosexuality. However, it should be noted that all the evidence used to support these hypotheses (Apostolou, 2016a; Apostolou et al., 2017), as well as the polygyny hypothesis, is explained by the interlinked hypotheses of balanced polymorphism of masculinity, sexually antagonistic selection, hormonally mediated fast life history strategy, and alloparenting (Fig. 2).

## Future Research

Since butches and femmes appear to form phenotypically discrete categories, studies on female nonheterosexuality should always seek to ascertain the proportion of subjects identifying as butch/femme so that the results are not confounded by conflating very different types of nonheterosexual subjects (cf. Zheng & Zheng, 2013, 2015; see also Baldwin et al., 2017). In addition, it should be established whether subjects behave bisexually, in an exclusively homosexual way, or whether they are "mostly heterosexuals". These supporting data are crucial when analyzing the possible effects of sexual orientation on evolutionary fitness. They can also be illustrative when evaluating the interaction between biomarkers of fetal androgen exposure, sexual orientation, and sexual behavior.

Current evidence is not able to establish a causal link between negative sexual experiences with men and the development of nonheterosexual orientation in women ("Socialization Influences" section). In fact, the direction of causality is likely to be the opposite (Alanko et al., 2011; Lehavot et al., 2012). To our knowledge, none of the existing studies on abuse and sexual orientation have discriminated between violence inflicted by a biological father and a stepfather. This would be an essential avenue for further research for two main reasons. Firstly, our review suggests that fathers of nonheterosexual women are likely to be more masculine than those of heterosexual women

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[13] Kanazawa (2017) only analyzed women up to 29 years of age. Our review indicates that the lifetime fitness of nonheterosexual women is no higher than that of heterosexual women (recent findings in an Italian population indicate that nonheterosexual women in fact have lower reproductive fitness than heterosexual women: Camperio Ciani et al., 2018). Early reproduction is characteristic for fast LH strategies, and so Kanazawa's data lends support to our hypothesis about female homosexuality being an outcome of selection for fast LH strategies.

(Prediction 1). The role of T in masculinization and aggressive behavior is relatively well understood (Carre & Olmstead, 2015; Denson, O'Dean, Blake, & Beames, 2018), constituting one proximate-level explanation for the finding that nonheterosexual women experience more violence than heterosexual women (reviewed in Johnson & Grove, 2017). There could be comorbidity patterns with masculinizing alleles, female nonheterosexual orientation, and aggressive behavior inflicted by masculine fathers (Prediction 2). The extent to which these patterns are mediated by substance use of the focal female (as opposed to that of the male: cf. Soler, Vinayak, & Quadagno, 2000) has been found to be significant: higher alcohol use is associated with greater adult sexual victimization in nonheterosexual women (Hequembourg et al., 2013). A prediction that arises from the fast LH strategy hypothesis is that butches, femmes, and bisexual women experience more father absence than heterosexual women (Prediction 3). This is based on the rationale that their fathers likely have high sociosexuality, passed on to their offspring genetically (Mendle et al., 2009), via intrauterine hormone exposure, and/or epigenetic factors mediated by maternal stress (Rice et al., 2016; Wood, 2014), leading to the fast LH strategies and nonheterosexual orientation of their daughters (cf. Bailey et al., 1991). If nonheterosexual women are more likely than heterosexual women to be exposed to father absence (cf. "Hormonally Mediated Fast Life History Strategy" section and Sabia et al., 2017), they might also be more liable than father-present women to experience violence inflicted by stepfathers (Prediction 4). This is because stepfathers are much more likely than biological fathers to abuse their stepchildren (Daly & Wilson, 1999).

Finally, the ultimate fitness value of alleles predisposing to highly masculinized, exclusively homosexual butch phenotypes is more elusive than the fitness value of alleles predisposing to psychologically masculinized (bisexual) female phenotypes. Therefore, research on the reproductive success, masculinity, and sociosexuality of the fathers and brothers of butch lesbians—comparing with corresponding data on the male kin of femme, bisexual, and heterosexual women—would serve to disprove or support the hypothesis of sexually antagonistic selection (cf. Camperio Ciani et al., 2018; Hämäläinen et al., 2018; Manning et al., 2000).

## Conclusions

Despite the recent upsurge of interest in the evolutionary origins of female nonheterosexuality (Apostolou, 2016a, b; Apostolou et al., 2017; Burri et al., 2015; Camperio Ciani et al., 2018; Fleischman et al., 2015; Jankowiak et al., 2018; Kanazawa, 2017; Kuhle & Radtke, 2013), progress in the field has been hampered by broader attempts to synthesize the existing data. We have reviewed physiological, developmental, comparative, psychological, and evolutionary research to explain why and how the capacity for female nonheterosexual behavior presents itself much more commonly in humans than uninformed fitness considerations would lead one to expect.

A suitable starting point for analyzing the ultimate fitness value of female nonheterosexuality is to incorporate the prenatal androgen exposure theory with research on testosterone as the primary hormone that shifts life history loci from organismal development and maintenance to reproduction (Foo et al., 2017; Gettler et al., 2017; Hau & Wingfield, 2011; Muehlenbein & Bribiescas, 2005; Muller, 2017; Santi et al., 2018). Since sex hormones play a crucial role both in the development of female sexual orientation (Balthazart & Court, 2017; Breedlove, 2017a, b; Fisher et al., 2018) and in shaping life history evolution (Adkins-Regan, 2005; Ellison, 2017; Hau & Wingfield 2011; Jasienska et al., 2017; Muehlenbein & Bribiescas, 2005; Muehlenbein & Flinn, 2011), it is reasonable to predict that the biobehavioral and psychological masculinization that occurs in nonheterosexual women influences not only their sexual orientation but also their LH strategies in the expected direction: faster, more masculine.

This is indeed what our review indicates. Fast LH strategies comprise meaningful functional composites which represent coadapted reproductive strategies (Figueredo et al., 2005; Hämäläinen et al., 2018). They lead to risky, unrestricted sexual behavior, increased impulsivity, and present-orientation (Fethers et al., 2000; Figueredo et al., 2018; Frankenhuis et al., 2016; Maner et al., 2017; Minkov & Bond, 2015; Mishra et al., 2017; Stolarski et al., 2017; Zietsch, Verweij, Bailey, Wright, & Martin, 2010). It is a central finding that incrementally more homosexually oriented women became increasingly masculine on the personality dimension of sensation-seeking so that exclusively homosexual women are closest to the male-typical high sensation seeker personality type (Cross et al., 2011; Trocki et al., 2009) while bisexual women appear to be higher than heterosexual and homosexual women on *sexual* sensation-seeking (Stief et al., 2014; see also Safron et al., 2018). High sensation-seeking is the underlying psychological trait driving a range of behaviors associated with fast LH strategies (Burri et al., 2015; Cross et al., 2011; Figueredo et al., 2004, 2005; Mishra et al., 2017; Stolarski et al., 2017; Trocki et al., 2009), explaining the covariation between psychological predispositions and de facto life outcomes in nonheterosexual women (Tables 1, 2).

Connecting these findings with bisexual women's increased masculinization, heightened sociosexuality, early reproduction, and greater number of male sexual partners than in heterosexual women (Table 1, Findings 1–6), we proposed the hypothesis of female nonheterosexuality as a hormonally mediated fast LH strategy, which can provide an alloparental buffer for masculinizing alleles as they appear in the female *and* the male phenotype. Crucially, LH theory is able to offer an explanatory framework (Belsky et al., 2015; Figueredo et al., 2018; Hämäläinen et al., 2018; Hurst & Kavanagh, 2017; Maner et al., 2017; Mishra et al., 2017; Richardson et al., 2016; Shalev &

Belsky, 2016) for the masculinized biomarkers and masculinized psychobehavioral, cognitive, and personality features of nonheterosexual women, as well as their greater likelihood of experiencing violence, substance use, incarceration, obesity, depression, teenage pregnancy, and lower general health. One of the potential effects of this network of adverse life outcomes is a feedback loop of environmental unpredictability and harshness (Ellis et al., 2017a; Sarma et al., 2018) which can destabilize maternal intrauterine hormonal conditions (Wood, 2014), leading to a greater predisposition to suffer from mental disorders (Kundakovic & Jaric, 2017), global physical health problems (Belsky et al., 2015; Cabeza de Baca et al., 2018; Case et al., 2004; Lin et al., 2017; Međedović & Bulut, 2018), and an elevated likelihood of nonheterosexual preferences in female offspring (Bailey et al., 1991; Bao & Swaab, 2011).

This target article suggests that balanced polymorphism of masculinity, sexually antagonistic selection, hormonally mediated fast LH strategies, and the alloparenting hypothesis can all constitute a related functional network underlying the ultimate etiology of female nonheterosexuality (Fig. 2) (Hämäläinen et al., 2018; Kuhle & Radtke, 2013; Miller, 2000). This argument is consistent with the idea that natural selection combines biobehavioral and psychosocial traits into meaningful functional composites (Cain & Ketterson, 2012; Figueredo et al., 2005; Hämäläinen et al., 2018), which create natural variation both in sexual orientation and in LH strategies—both in humans and in nonhuman animals. Taken together, biodemographic, endocrinological, neurophysiological, and psychological evidence suggests that the biobehavioral signatures concomitant with female nonheterosexuality are one such functional composite, which is more generally related to fast LH strategies and a preferential allocation of bioenergetic resources to reproductive rather than somatic effort—to present rather than postponed rewards (cf. Figueredo et al., 2004; Frankenhuis et al., 2016; Hämäläinen et al., 2018; Minkov & Bond, 2015).

Selection for fast LH strategies in males could well be a factor underlying the evolution of female nonheterosexuality (cf. Hämäläinen et al., 2018; Immonen et al., 2018; Ketterson et al., 2005). This means that female nonheterosexuality could either be an adaptive outcome or a by-product of that selection pressure. Rather than being a priori thought of as "suboptimal" female reproductive strategies, however, the predictive adaptive response hypothesis (Gluckman, Hanson, & Beedle, 2007, 2008) posits that these faster LH strategies may in fact be adaptive under certain ecological conditions (e.g., Belsky, 2012; Belsky, Schlomer, & Ellis, 2012; Csathó & Birkás, 2018; Ellis et al., 2017a; Murray et al., 2017; Pepper & Nettle, 2017; Wells et al., 2017). Since the conclusions of this article are by necessity proposed in absence of complete information, we delineated some of the numerous testable predictions that flow from this theoretical synthesis of existing empirical work. We hope that the synthetic approach provided here informs future research which will further refine our understanding of the proximate mechanisms and ultimate fitness repercussions of the various phenotypes in the female nonheterosexuality spectrum.

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## Compliance with Ethical Standards

**Conflict of interest** The authors declare no conflict of interest.

**Ethical Approval** The material contained in this article is a review of previously published or presented data. This article does not contain any studies with human participants or animals performed by the authors.

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