COMMENTARY

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Female Nonheterosexuality Is Associated with Both "Fast" and "Slow" Male-Typical Strategies: Implications for Evolutionary Scenarios

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The Target Article by Luoto, Rantala, and Krams (2018) is an ambitious attempt to review and synthesize the current hypotheses on the evolution of female nonheterosexuality in light of the available data on development, phylogeny, and proximate mechanisms (particularly hormonal factors). The article packs a lot of information, and I commend Luoto et al. for bringing many disparate sources of evidence to bear on this important question. The most original aspect of the article is the hypothesis that female nonheterosexuality results from selection for male-typical "fast" life history strategies (a similar argument regarding male nonheterosexuality was advanced by Xu, Norton, and Rahman, 2018). According to this hypothesis, the behavioral correlates of masculinized life history strategies include unrestricted sociosexuality, impulsivity, sensation seeking, risky sexual behavior, and a preference for physically attractive, but noninvesting partners. While exclusive homosexuality substantially reduces reproductive success, the benefits of faster strategies in male and/or female relatives who express milder variants of the same pattern may be enough to offset the fitness loss (Burri, Spector, & Rahman, 2015; Camperio Ciani, Battaglia, Cesare, Camperio Ciani, & Capiluppi, 2018).

My goal in this Commentary is to critically evaluate Luoto et al.'s (2018) life history hypothesis. While Luoto et al. make a compelling case that female nonheterosexuality is linked to physiological and behavioral masculinization, I argue that the data do not support a unique association with fast life history strategies. Rather, nonheterosexuality in women is associated with male-typical trait profiles at *both* ends of the fast–slow continuum. This empirical pattern has implications for some of the evolutionary scenarios reviewed in the Target Article; more broadly, the case of female sexual orientation illustrates the potential pitfalls of conflating male-typical strategies with fast life histories.

Throughout the Target Article, Luoto et al. (2018) subscribe to the idea that, on average, male strategies are faster than their female counterparts because of men's higher investment in mating at the expense of parenting. (Although at times they describe this trade-off as one between reproductive and parental efforts, reproductive effort is a broader category that subsumes both mating and parenting.) This formulation of sex differences is sometimes found in the human and animal literature (e.g., Hämäläinen, Immonen, Tarka, & Schuett, 2018) and can be useful for some purposes, but is not without limitations. In particular, the allocation problems faced by males and females may be distinct enough that it becomes difficult to compare the sexes on the same axis used to describe individual differences within each sex. Consistent with upregulated mating effort, men score lower than women in agreeableness and higher in risk-taking, sensation seeking, and unrestricted sociosexuality. However, sex differences in other key life history-related traits, such as impulsivity and conscientiousness, are small and unreliable (Cross, Copping, & Campbell, 2011; Del Giudice, 2015, 2018). Also, boys tend to mature later than girls despite their higher mortality—another exception to the idea that males are faster strategists across the board (Bogin & Smith, 1996; Del Giudice, Gangestad, & Kaplan, 2015). Of note, in sexually reproducing species each offspring has one mother and one father, which constrains the scope for *average* sex differences in allocation to offspring quality versus quantity.

When addressing the issue of male- and female-typical strategies in humans, it may be more accurate to state that fast strategies involve somewhat different allocation patterns in the two sexes: while fast strategies in men are primarily characterized by increased mating effort and risky competition, fast strategies in women are more strongly linked to earlier maturation and reproduction, owing to the tighter physiological constraints on female fertility and fecundity

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(see Del Giudice, 2018). This alternative formulation allows for the fact that the male average of some mating-related traits (e.g., sociosexuality, risk-taking) is shifted toward the fast end of the continuum, without equating sex differences with overall differences in life history speed (for more discussion of sex-specific strategies, see Hämäläinen et al., 2018).

An even stronger challenge to the idea that male-typical strategies are necessarily faster comes from research on autistic-like traits, also known as the "broader autism phenotype" (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). These traits include poor mindreading skills ("empathizing"), difficulties in communication (e.g., irony, humor, and other forms of nonliteral speech), restricted imagination, preference for routines, narrowly focused interests, and heightened attention to details and patterns, which in turn correlates with enhanced drive to reason about rule-based systems ("systemizing"; Baron-Cohen, 2003). Autistic-like traits are consistently higher in males, people in technical professions, and relatives of patients with autism spectrum disorder (ASD) (Baron-Cohen et al., 2001; French, Bertone, Hyde, & Fombonne, 2013; Ruzich et al., 2015a, b). The male-typical nature of this phenotype is underscored by the strongly sex-biased distribution of autism, which is about 4:1 overall, but reaches 10:1 for milder cases of ASD with normal intelligence and high familiality (Anney, 2013; Robinson et al., 2014). Unsurprisingly, research has found evidence that prenatal exposure to androgens contributes to the risk of autism (Auyeung & Baron-Cohen, 2013; Kosidou et al., 2016; Teatero & Netley, 2013). As my colleagues and I have shown, autistic-like traits in the nonclinical population bear the hallmarks of a male-typical variant of slow life history strategy: for example, they are associated with restricted sociosexuality, reduced sex drive, high investment in long-term romantic relationships, and low levels of impulsivity and sensation seeking (see Del Giudice, 2014, 2018; Del Giudice, Angeleri, Brizio, & Elena, 2010; Del Giudice, Klimczuk, Traficonte, & Maestripieri, 2014). Baron-Cohen (2003) famously described autism as the manifestation of an "extreme male brain," but this catchphrase disregards the remarkable variability of male strategies. At the fast end of the life history continuum, male-typical strategies include psychopathy and antisocial personality disorder (ASPD), whose behavioral profile is marked by extreme impulsivity, sexual promiscuity, and risky competition—another kind of "extreme male brain." At the slow end of the continuum, the spectrum from autistic-like traits to mild ASD reflects the existence of a male-typical strategy geared toward long-term resource allocation and indirect parental investment. (In contrast, most cases of severe ASD with intellectual disability seem to arise from rare deleterious mutations and are likely unrelated to variation in life history strategy; for extended discussion, see Del Giudice, 2018.)

As is apparent from the previous paragraph, autism is an ideal test case to discriminate between a generic masculinization account of female nonheterosexuality and Luoto et al.'s

(2018) more specific life history hypothesis. If nonheterosexuality were uniquely associated with fast strategies, it should correlate positively with impulsivity, sensation seeking, unrestricted sociosexuality, and psychopathy (as documented in the Target Article; see also Kerridge et al., 2017 for evidence of higher ASPD rates), but not (or negatively) with autistic-like traits and ASD. Conversely, a higher prevalence of autistic phenotypes in lesbian and bisexual women would be more consistent with a nonspecific pattern of masculinization cutting across the fast–slow continuum. As it turns out, the available data consistently support the latter alternative. In the nonclinical population, autistic-like traits predict increased likelihood of same-sex attraction and nonheterosexual orientation in females (Qualls, Hartmann, & Paulson, 2018). As noted in the Target Article, there is also some evidence that butches have higher systemizing scores than femmes (Zheng & Zheng, 2013). Likewise, women with ASD are much more likely to experience same-sex attractions and identify as bisexuals or lesbians compared with typically developing controls (Bejerot & Eriksson, 2014; Dewinter, De Graaf, & Begeer, 2017; George & Stokes, 2017, 2018; Gilmour, Schalomon, & Smith, 2012). Developmental data cast further doubt on the hypothesis of a specific association with fast life histories. As noted in the Target Article, findings on puberty timing in nonheterosexual females are mixed (and largely negative; see Bogaert, Friesen, & Klentrou, 2002; Grossman, Foss, & D'Augelli, 2014; Reese, Trinh, & Halpern, 2017; Savin-Williams & Ream, 2006). Luoto et al. also suggest that prenatal stress (a cue of harsher environmental conditions) should affect masculinization—and hence sexual orientation—in female offspring as a predictive adaptive response; however, the few available studies have failed to find consistent associations between prenatal stress and nonheterosexuality in women (Bailey, Willerman, & Parks, 1991; Ellis & Cole-Harding, 2001; Rahman, 2005).

To sum up, female nonheterosexuality is clearly linked to masculinized phenotypes, with a highly plausible femme–butch gradient of increasing masculinity. Of the hormonal factors reviewed in the Target Article, androgens enjoy the strongest empirical support, while the evidence is considerably more mixed for a role of estrogen and/or progesterone (and thus for the existence of "discrete" hormonal mechanisms in the development of butches vs. femmes). At the same time, the hypothesis of a specific link with fast strategies is challenged by the data on autism and by the lack of reliable associations among nonheterosexuality, puberty timing, and prenatal stress. Instead, the evidence indicates that nonheterosexual women are more likely to show male-typical fast strategies characterized by impulsivity, risk-taking, and unrestricted sociosexuality (including psychopathy and ASPD), but also male-typical slow strategies marked by elevated autistic-like traits.

What is the evolutionary relevance of these findings? As noted above, Luoto et al.'s (2018) life history hypothesis does not seem tenable, at least in its original formulation. The

hypothesis might be revised along these lines: if selection for male-typical fast traits in women (and/or their male relatives) translates into selection for higher masculinization, male-typical slow traits (including autistic-like traits) may also increase in frequency as a nonadaptive or weakly maladaptive side effect of selection for masculinization. The plausibility of this revised hypothesis hinges on the relative impact of masculinization on fast versus slow traits and the corresponding fitness costs and benefits. If, on the other hand, both fast and slow traits can be adaptive in different circumstances and/or different individuals in a population, the data reviewed here may support an extended version of the "balanced polymorphism of masculinity" hypothesis—one in which the potential adaptive benefits of masculinization include those of slow, future-oriented strategies. As discussed in the Target Article, Burri et al. (2015) found evidence of a common latent factor underlying same-sex attraction, gender nonconformity in childhood, and number of sexual partners. However, the latent factor accounted for a relatively small proportion of variance (13–22%) in the manifest behavioral traits. An intriguing possibility is that overall correlations among traits obscure the existence of more complex effects, whereby some nonheterosexual women (those engaging in slow strategies) tend to have *fewer* rather than more sexual partners. Crucially, a small number of sexual partners are disadvantageous in the context of fast, mating-oriented strategies, but can be perfectly adaptive for slow, parenting-oriented strategists (who should also be selected to have fewer, higher quality offspring; see Del Giudice et al., 2015). This complicates the interpretation of existing findings, including those on fertility in nonheterosexual women and their relatives (e.g., Camperio Ciani et al., 2018). As others have noted, contemporary fertility data are especially tricky to interpret because contraception and abortion decouple intercourse from reproduction, and indeed, there is some evidence that modern conditions boost the relative fertility of people with "slower" personality profiles (Woodley of Menie et al., 2017; see also Del Giudice, 2018). Finally, it might be interesting to consider a hypothesis that my colleagues and I advanced in a recent paper, namely, that early androgen exposure may increase susceptibility to environmental conditions in both sexes (Del Giudice et al., 2018). The hypothesis is admittedly speculative, but if it turns out to be correct, it may prove relevant to some of the issues raised in the Target Article and this commentary, from the variability of female strategies to the development of sexual fluidity.

In conclusion, Luoto et al. (2018) have made a valuable contribution to this topic, even if the life history hypothesis they advanced is problematic and should be revised or abandoned. I expect that their call for deeper consideration of proximate mechanisms, development, and phylogeny will have a salutary effect on the scientific debate. There is still much we do not understand about the origin and development of sexual orientation (Bailey et al., 2016), but research is becoming more theoretically sophisticated and empirically grounded, and the solution of this endlessly fascinating puzzle may soon be within our reach.

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