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The dark side of the rainbow: Homosexuals and bisexuals have higher Dark Triad traits than heterosexuals [★]

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ABSTRACT

Research on the Dark Triad traits—psychopathy, Machiavellianism, and narcissism—reveals malevolent, transgressive, and self-centered aspects of personality. Little is known about the Dark Triad traits in individuals differing in sexual orientation, with some studies showing that non-heterosexual individuals have Dark Triad profiles resembling those of opposite-sex heterosexual individuals. In a cross-national sample (N=4063; 1507 men, 2556 women; $M_{age}=24.78$, $SD_{age}=7.55$; 90.58% heterosexual, 5.74% bisexual, 2.83% homosexual) collected online via student and snowball sampling, we found in sex-aggregated analyses that bisexuals and homosexuals were more Machiavellian than heterosexuals. Bisexuals were more psychopathic and narcissistic than heterosexuals. The only significant findings in within-sex comparisons showed that self-identified bisexual women scored higher on all Dark Triad traits than heterosexual women. The findings support the gender shift hypothesis of same-sex sexual attraction in bisexual women, but not in lesbians nor in men. The finding that bisexuals are the sexual orientation group with the most pronounced Dark Triad profiles is opposite to what would be predicted by the prosociality hypothesis of same-sex sexual attraction. The life history and minority stress implications of these findings are discussed as alternative hypotheses to the gender shift hypothesis.

1. Introduction

Psychological and behavioral differences between the sexes have been studied scientifically for more than a century (Archer, 2019; Darwin, 1871; Woolley, 1910). As findings on sex differences have accumulated over time, the way in which non-heterosexual individuals may differ from heterosexuals on a range of psychobehavioral traits has received increasing attention (Allen & Robson, 2020; Luoto, 2021a; Zheng et al., 2011), as have the evolutionary–developmental mechanisms that create sex differences (Archer, 2019; Luoto & Varella, 2021) and sexual orientation differences (Luoto, 2020a; Luoto et al., 2019a,b; Rahman & Wilson, 2003) in such psychobehavioral traits.

Sexual differentiation of the mammalian brain constitutes an integral evolutionary—developmental process which causes a cascade of sexually differentiated outcomes in men and women, ranging from physiological, cognitive, and behavioral traits to different life outcomes, for instance,

in health and in educational and professional trajectories (Archer, 2019; Luoto, 2020b; Luoto et al., 2019a,b; Luoto & Varella, 2021; Mauvais-Jarvis et al., 2020; McCarthy, 2020; Luoto et al., 2021). Developmental disturbances in the sexual differentiation of the brain may result in various kinds of non-heterosexual phenotypes, which show sexatypicality across a range of biobehavioral traits (Luoto, 2021a; Luoto et al., 2019a,b; Rahman & Wilson, 2003; Swift-Gallant et al., 2019). One conceptualization of personality traits is that they are behavioral syndromes (e.g., complexes of correlated behaviors creating patterns) as opposed to internal traits, and as such, might also be subject to such differentiation (Woodley of Menie et al., 2021). Given that sexuality and sexual orientation are characterized by specific behaviors, and behaviors are related to personality traits, understanding how personality traits relate to various manifestations of sexuality seems warranted (Lippa, 2020; Luoto et al., 2019a; Luoto, 2021a).

One potential hypothesis for explaining the opposite-sex shift

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observed in non-heterosexual individuals' psychobehavioral and morphological traits is the gender shift hypothesis, which posits that homosexual and bisexual men are partially feminized and homosexual and bisexual women are partially masculinized on several psychobehavioral and morphological traits (Bailey et al., 2016; Luoto et al., 2019a; Luoto, 2021a). The gender shift hypothesis assumes that the effective sexuality phenotype (1) has been ancestrally calibrated to increase inclusive fitness but (2) developmental disturbances may occur in this sexually differentiated process, creating phenotypes that may diverge from sex-specific optima. Natural variation in neurodevelopmental processes may lead to sex-atypical behaviors and attitudes (e.g., sexual desire, sexual orientation, and personality) as in the case of non-heterosexual men and women. This hypothesis has received broad though not fully clear support across several studies (Abé et al., 2021; Lippa, 2020; Luoto, 2020a; Luoto et al., 2019a; Luoto, 2021a; Rahman & Wilson, 2003; Schmitt, 2006). Moreover, bisexual men and women tend to show gender nonconformity and cross-sex neuroanatomical changes which place them between heterosexual and homosexual participants (Abé et al., 2021; Rieger et al., 2020). On other psychobehavioral traits, such as neuroticism, extraversion, and agreeableness, bisexual women tend to be more masculine than heterosexual women; with traits such as sex drive, sociosexuality, conscientiousness, and openness to experience, bisexual women tend to be even more masculine than lesbian women (Luoto & Rantala, in press). Bisexual men had higher sex drive, sociosexuality, openness to experience, and neuroticism and lower conscientiousness than heterosexual men (Lippa, 2020; Schmitt, 2006), only partially supporting the gender shift hypothesis. In this article, we sought to test the gender shift hypothesis using the Dark Triad traits in men and women differing in (self-reported) sexual orientation (i.e., heterosexual, bisexual, homosexual).

The Dark Triad traits (i.e., narcissism, Machiavellianism, and psychopathy) are "darker" sides of personality; yet despite being sometimes viewed as harmful for individuals and groups, they can in fact be adaptive (Furnham et al., 2013; Koehn et al., 2019). Narcissistic people have a sense of grandiosity, egotism, and self-orientation; Machiavellian individuals are often manipulative and exploitative, with a ruthless lack of morality; and psychopathic people engage in antisocial behavior, are impulsive, and lack empathy and remorse. The traits may enable fast life history strategies that allow people to pursue selfish social and sexual agendas that impose costs on those around them (e.g., Jonason et al., 2017). Life history theory suggests that organisms have a finite amount of resources to solve the adaptive problems of mating and surviving, and the way organisms navigate such resource-allocation decisions is by trading off one goal for another. Those who prioritize survival over mating are r-selected or fast life history strategists whereas those who prioritize mating over survival and/or development are K-selected or slow life history strategists. Fast, as opposed to slow, life history strategies at the species level translate to faster maturation, more mortality, and less investment in offspring (e.g., elephants are slow; mice are fast). At the within-species level (cf. Woodley of Menie et al., 2021), fast life history traits can include promiscuity, risk-taking, aggression, and limited empathy, all of which are heightened in those characterized (with some contextual modification at times) by the Dark Triad traits (Jonason et al., 2017; Koehn et al., 2019; Luoto et al., 2019a).

The Dark Triad traits comprise an interesting test case for analyzing psychological differences across the sexual orientation spectrum because of their heritability and the reported sex differences in the traits. The Dark Triad traits reveal small (Cohen's $d \approx 0.20$) to large ($d \approx 0.70$) sex differences cross-nationally (Jonason et al., 2013; Jonason, Zemojtel-Piotrowska, et al., 2020). Social role (e.g., social learning, structural powerlessness) and evolutionary (e.g., sexual selection, parental investment, and life history theory) models provide explanations for these sex differences (e.g., Archer, 2019; Luoto et al., 2019a). For instance, researchers relying on the former model might suggest that women may be punished more for these traits; therefore, women suppress their "bad" behaviors more than men do. Alternatively, ancestral

men may have reaped reproductive fitness benefits for being "bad", leading to differences in the sexes that persist to this day. For instance, men may accrue more sex partners while women may be more likely to suffer from reproductive health problems for having more pronounced Dark Triad traits and associated behaviors (Jonason et al., 2009; Jonason & Lavertu, 2017). While evolutionary models of sex differences writ large (Archer, 2019; Luoto & Varella, 2021) and in the Dark Triad traits (Jonason, Żemojtel-Piotrowska, et al., 2020) might be superior in accounting for these differences than social constructionist accounts (Luoto et al., 2019a), the two should not be seen as completely in conflict given that they are concerned with proximate (e.g., how) and ultimate (e.g., why) questions. For instance, the adaptive utility of pursuing particular life history strategies describes effects originating both in the past and the current environments, whereas sex-specific norms describe how people learn and calibrate their behaviors to fit their current social contexts. That is, instead of a blank slate hypothesis (i.e., environmental determinism), as often relied on by social constructivists, an evolutionary account can merge ancestrally derived predispositions and biases with current conditions and needs. Evolutionary approaches are therefore inherently interactionist, not genetically deterministic, focusing as they do on the proximate (neuro) developmental and other biopsychosocial mechanisms underlying sex differences and sexual orientation differences (Luoto et al., 2019a; Luoto & Varella, 2021).

Despite the popularity of research on the Dark Triad traits in the context of sex differences and sexual behavior, few studies have examined whether there are differences in the Dark Triad traits between people of different sexual orientations. This may be related to limited access to enough non-heterosexual individuals in convenience samples and a lack of hypotheses about why there might be any sexual orientation differences. We acknowledge the third possibility that researchers may have avoided asking this question because of fears of the results being misinterpreted as portraying non-heterosexuals in a negative light. Two studies (we know of) on sexual orientation differences in Dark Triad traits have found that bisexual women scored higher on the Dark Triad traits than heterosexual women or lesbians (Semenyna et al., 2018; Stolarski et al., 2017). These findings conform to a broader pattern of psychological masculinization in non-heterosexual women across a variety of personality measures (Luoto et al., 2019a,b; Luoto, 2021a). Besides these results in women, we are unaware of any studies that have analyzed the Dark Triad traits across the sexual orientation spectrum (i. e., including bisexual men, and ideally also "mostly heterosexual" individuals). In one study, homosexual men scored lower on Machiavellianism (d = 0.11), narcissism (d = 0.17), and psychopathy (d = 0.42) relative to heterosexual men (Barelds et al., 2017). In women, the only difference of note was the slightly higher psychopathy scores in homosexual women (d = 0.15) relative to heterosexual women (Barelds et al., 2017). Overall, these results support the gender shift hypothesis of homosexuality.

In this study, we sought to test the gender shift hypothesis of homosexuality in a cross-national sample which, unlike previous studies, also included bisexual males. Based on prior theoretical and empirical work (Lippa, 2020; Luoto, 2020a; Luoto et al., 2019a), we predicted that non-heterosexual women would score higher (more male-typical) on the Dark Triad traits than heterosexual women. We extended the gender shift hypothesis (Luoto, 2020a; Luoto, 2021a) to men and predicted that non-heterosexual men would score lower (more female-typical) on the Dark Triad traits relative to heterosexual men. In addition, we provide a novel test of a new and potentially problematic (Luoto, 2020a) suggestion—which appears to originate from work on Bonobos (*Pan*

¹ We calculated these effect sizes based on the means, standard deviations, and sample sizes provided in Barelds et al. (2017). We do not provide *p*-values for these effect sizes because of the *post-hoc*, exploratory nature of this analysis. Bisexual individuals were not included in Barelds et al.'s (2017) analyses.

paniscus)—suggesting homosexuality may have evolved as part of increased prosociality (Barron & Hare, 2020).

2. Method

2.1. Participants and procedures

In 2014, an international team of researchers collected self-report data² from 42 countries online in English or a local language (e.g., French) from 4063 people (2556 female, 1507 male) who received course credit or were volunteers, aged 18 to 69 years old (M=24.78, SD=7.55).³ The participants came from W.E.I.R.D. (i.e., Western, educated, industrialized, rich, and democratic; e.g., Canada, USA) (n=2606) and non-W.E.I.R.D. (n=1457; e.g., Brazil, Czechia) nations, and self-identified as heterosexual (n=3675), homosexual (n=115), bisexual (n=233), and "other" (n=34; removed from analyses), with six non-responders (removed from analyses); more details provided in the Online Supplemental Tables S2 and S3. At each site, researchers obtained ethical clearance, informed participants of the nature of the study, administered a larger battery of self-reported variables not reported here, and upon completion, thanked, and debriefed participants.

2.2. Measures

We used the Dark Triad Dirty Dozen, a 12-item measure of the Dark Triad traits with four items per subscale (Jonason & Webster, 2010). Participants were asked how much they agreed (1 = Strongly disagree; $5 = Strongly \ agree$) with statements such as: "I tend to want others to admire me" (i.e., narcissism), "I tend to lack remorse" (i.e., psychopathy), and "I have used deceit or lied to get my way" (i.e., Machiavellianism). Items were averaged together to create indexes of narcissism (Cronbach's $\alpha = 0.80$), Machiavellianism ($\alpha = 0.68$), and psychopathy ($\alpha = 0.75$); Machiavellianism was correlated (p < .001) with psychopathy (p = 0.47) and narcissism (p = 0.49), and psychopathy was correlated with narcissism (p = 0.31). Previous research suggests this scale translates well into other languages and maintains appropriate psychometric properties in cross-cultural research (Jonason et al., 2013; Jonason, Żemojtel-Piotrowska, et al., 2020).

3. Results

We refrained from testing a full ANOVA model because of sample

Table 1Summary of *F*-tests testing the relationship between the Dark Triad traits and sexual orientation overall and by participant's sex and country-type.

	Machiavellianism	Psychopathy	Narcissism
Overall	9.49**	8.63**	4.93**
Men	5.39**	0.37	0.18
Women	4.18**	16.08**	6.75**
W.E.I.R.D.	6.40**	4.21**	0.77
non-W.E.I.R.D.	4.04*	5.09**	7.02**

p < .05.

size concerns and instead relied on planned comparisons with t-tests and one-way ANOVAs with Scheffe's post-hoc tests, which adjust significance levels to account for multiple comparisons. In Table 1 we summarize F-tests to understand the correlations between sexual orientation and the Dark Triad traits overall (Fig. 1). In sex-aggregated analyses, we found that bisexuals (p=.008, d=0.21) and homosexuals (p=.007, d=0.29) were more Machiavellian than heterosexuals. Bisexuals were more psychopathic (p<.001, d=0.25) and narcissistic (p=.011, d=0.21) than heterosexuals.

We next looked at these effects in men and women (Fig. 2). Among men, homosexuals (p=.062, d=0.28) and bisexuals (p=.058, d=0.31) were slightly more Machiavellian than heterosexuals, though the differences were marginally non-significant. No other differences approached significance. In contrast, among women, bisexuals were more Machiavellian (p=.020, d=0.22), psychopathic (p<.001, d=0.41), and narcissistic (p<.001, d=0.29) than heterosexual women. Bisexual women were slightly more psychopathic than homosexual women (p=.055, d=0.40), though the effect was marginally non-significant (owing partially to the small sample size of homosexual women).

Next, we examined these effects by the type of nation people live in (Fig. 3). In W.E.I.R.D. nations, bisexuals were more Machiavellian ($p=.011,\ d=0.26$) and psychopathic ($p=.033,\ d=0.22$) than heterosexuals. In non-W.E.I.R.D. nations, homosexuals were more Machiavellian than heterosexuals ($p=.028,\ d=0.39$), and bisexuals were more psychopathic ($p=.009,\ d=0.32$) and narcissistic ($p=.002,\ d=0.40$) than heterosexuals.

And last, we tested sex and country differences by sexual orientation. Heterosexual men were more Machiavellian ($t[3673]=7.01,\,p<.001,\,d=0.23$), psychopathic ($t[3673]=16.12,\,p<.001,\,d=0.53$), and narcissistic ($t[3673]=6.45,\,p<.001,\,d=0.21$) than heterosexual women. Homosexual men were more Machiavellian ($t[113]=2.17,\,p=.032,\,d=0.40$) and psychopathic ($t[113]=2.63,\,p=.010,\,d=0.49$) than homosexual women. Bisexual men were more Machiavellian ($t[113]=2.47,\,p=.014,\,d=0.48$) than bisexual women. Among heterosexuals, non-W.E.I.R.D. participants were more psychopathic than W.E.I.R.D. ones ($t[3673]=6.60,\,p<.001,\,d=0.22$), with no other sex differences or sexual orientation differences found between the samples.

4. Discussion

Overall, we revealed that rates of the Dark Triad traits differed in people who had different sexual orientations, a topic that has rarely been considered in prior research. Our findings suggest that including non-heterosexual men and women in aggregated sex difference analyses may suppress sex differences in traits because non-heterosexual individuals—women in particular—have gender-atypical scores on several of these measures. Conducting analyses with all sexual orientations included may attenuate sex difference findings in heterosexual men and women not only because mean sex differences decrease in such aggregate analyses, but also because increased variation driven by non-

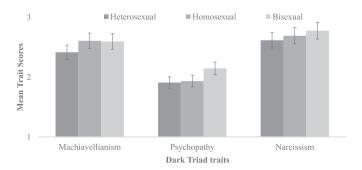
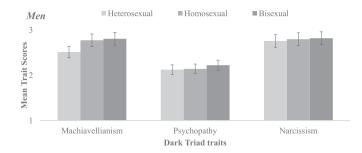


Fig. 1. Differences in the Dark Triad traits across sexual orientation. Note. Error bars are 5%; See S1 on OSF for full details.

^{**} p < .01.

Data and Supplementary (S1–3) files for this study are available on the Open Science Framework: https://osf.io/dzgqp/?view_only=ef15e99613224

³ Participants' age did not differ between sexual orientation groups (F=0.18) and only narcissism was correlated with age (r=-0.14, p<.01) so we did not control for age in the analyses.



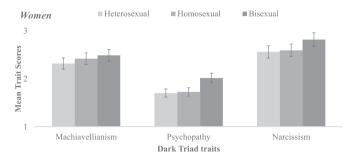
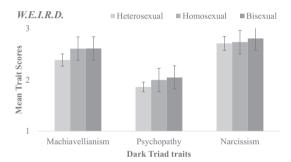


Fig. 2. Differences by sexual orientation in the Dark Triad traits in men and women. Note. Error bars are 5%; See S2 on OSF for full details.



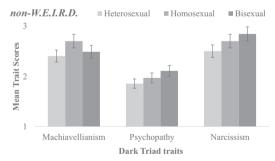


Fig. 3. Differences by sexual orientation in the Dark Triad traits by nation-type. Note. Error bars are 5%; See S3 on OSF for full details.

heterosexual individuals' sex-atypical scores increases standard deviations and thus reduces effect sizes. Thus, studies on psychological sex differences may reveal clearer patterns if sex difference analyses include only heterosexual men and women (e.g., Luoto, 2021a).

The gender shift hypothesis of same-sex sexual attraction received some support. Recall that this hypothesis suggests that non-heterosexual men will resemble or be moderately shifted towards heterosexual women whereas non-heterosexual women will resemble or be moderately shifted towards heterosexual men (Luoto, 2021a). Bisexual women, but not homosexual women, had higher psychopathy, Machiavellianism, and narcissism scores relative to heterosexual women. It may be that the psychobehavioral masculinization from heterosexual through bisexual to homosexual women (Luoto et al., 2019a) is not

linear, at least with the Dark Triad traits. Instead, some psychological traits are in fact more male-typical and more common in bisexual women relative to homosexual women (Luoto & Rantala, in press). A potential explanation for this is that the life history strategies of nonheterosexual women are faster than heterosexual women's, for which there exists abundant evidence (Luoto et al., 2019a,b). One manifestation of this psychobehavioral masculinization in non-heterosexual women is their increased interest in casual sex (i.e., a fast mating strategy) and heightened aggression (Luoto et al., 2019a), both of which have been repeatedly linked to psychopathy and narcissism. This aligns with our (somewhat mixed) finding of higher Dark Triad scores in bisexual women, as Machiavellianism and psychopathy are associated with faster life history strategies (Jonason et al., 2017), while different elements of psychopathy and narcissism are associated with fast and slow life history factors (McDonald et al., 2012). Indeed, the higher rates of psychopathy among bisexual women relative to homosexual women may reflect greater intrasexual competition (e.g., rivalry) and stronger mating motives given the bidirectional breadth of bisexual women's sexual/romantic interests.

The unexpected results in non-heterosexual men also diverged from the predicted pattern of a shift towards more female-typical scores on the Dark Triad traits. Instead, both homosexual and bisexual men scored higher on Machiavellianism than heterosexual men, and thereby showed a slightly "hypermasculine" psychological profile. These results were only approaching statistical significance, however, partially because of the small sample size of non-heterosexual men. Studies on larger samples of non-heterosexual men are required to provide more support for this finding. To our knowledge, this is the first such finding (besides bisexual men's higher sociosexuality and sex drive: Lippa, 2020) reporting a hypermasculine psychological profile in homosexual and bisexual men: most other findings indicate that homosexual men are feminized on most traits while being sex-typical on others (Allen & Robson, 2020; Barelds et al., 2017; Luoto, 2021a; Rahman & Wilson, 2003). It is possible that because bisexual and homosexual men are subject to greater amounts of discrimination and harsher treatment than heterosexual men are (Bailey et al., 2016; Cuerda-Galindo et al., 2017; Symons et al., 2017), this may prompt an adaptive response to be duplicitous, deceptive, and disguise themselves (i.e., Machiavellianism). Under this hypothesis, heightened Machiavellianism in nonheterosexual men would not be a pathology but, instead, a pseudopathology that can help men with atypical sexual orientations navigate the dangerous or hostile social contexts they sometimes face. We emphasize the need to replicate these preliminary findings in larger samples of nonheterosexual men. If we add to this the apparent "dark" shift in women who are also subject to and susceptible to discrimination and socioecological harshness (Lingiardi et al., 2005; Luoto et al., 2019a,b; Symons et al., 2017), a picture starts to emerge that those who-by characterization of their sex (male) and sexual orientation (non-heterosexual)-may respond to local harshness by becoming more selfish, deceptive, and impulsive. On the other hand, this "pseudopathology" view is challenged by findings that have revealed that while delinquent behavior is correlated with the Dark Triad traits (Alsheikh Ali, 2020), bisexual individuals had the highest rates of delinquency of all sexual orientation groups for both sexes (Beaver et al., 2016). This suggests that the pronounced Dark Triad profiles in bisexual individuals could contribute to their delinquent behavior.

The sex-aggregated results of this study indicated that bisexuals and homosexuals had higher Machiavellianism than heterosexuals. Bisexuals, but not homosexuals, had higher psychopathy scores relative to heterosexuals. Bisexuals, but not homosexuals, had higher narcissism scores than heterosexuals. Notably, these results are distinctly opposite from the predictions that arise from a recent hypothesis on the evolution of same-sex sexual attraction. Barron and Hare (2020) hypothesized that same-sex sexual attraction evolved as a suite of traits responding to strong selection for ease of social integration and prosocial behavior. This hypothesis leads to the prediction that non-heterosexual

individuals should have a low prevalence of the Dark Triad traits—a prediction which was not supported by the current findings. The prosociality hypothesis may be lacking in overall evidentiary support (Luoto, 2020a; Luoto, 2021b), and the findings reported in this article further call into question the prosociality hypothesis of same-sex sexual attraction.

5. Limitations and conclusions

The limitations of this study include the relatively small samples of non-heterosexual participants, which attenuated our ability to reliably detect smaller sexual orientation differences. Nevertheless, the proportions of bisexuals and homosexuals in our sample are relatively high given the usually reported prevalence of bisexuality and homosexuality, which indicate that a total of approximately 3.5% of U.S. adults identify as gay, lesbian, or bisexual (Bailey et al., 2016). The relatively small sample of non-heterosexual participants has the unfortunate implication, however, in the interpretation of our effects because smaller samples (1) have more error and (2) may not as accurately reflect the population as larger samples can. Another limitation of this study was the lack of additional granularity in sexual orientation identification, which should be addressed in further research by adding the option for participants to identify as butch/femme and/or mostly heterosexual (cf. Bailey et al., 2016; Luoto et al., 2019a,b).

Furthermore, our study population was limited to university students and snowball samples collected through social media, restricting overall participant diversity despite the inclusion of data from people from over 40 nations. Because sex differences and sexual orientation differences in the Dark Triad traits tend to be relatively minor, well-powered studies are needed to establish the extent to which the differences reported here replicate in other populations, particularly outside university students. Yet, to the best of our knowledge, this is the first study on the Dark Triad traits which includes bisexual men, and the largest study to date on homosexual men in relation to the Dark Triad traits. Only a few studies on the Dark Triad traits have been conducted in non-heterosexual individuals in general (Barelds et al., 2017; Semenyna et al., 2018; Stolarski et al., 2017), which makes the current cross-national findings a valuable addition to the literature, as does our use of samples from non-W.E.I.R.D. nations.

An additional concern might be social desirability. Those who are members of sexual minority groups may under-report information about their health relative to heterosexuals (Savin-Williams & Joyner, 2014). However, the Dark Triad traits are not known to be particularly linked with socially desirable responding, with narcissism having only a weak link (e.g., Raskin et al., 1991). Indeed, the very nature of psychopathy might lead to a greater willingness to endorse and report socially undesirable behaviors given psychopathic individuals' tendency to violate social norms (e.g., Jonason, Koehn, et al., 2020).

In conclusion, our study improves what researchers know about dark personality manifestations as a function of sexual orientation. With data from over 40 countries including three self-reported labels for sexual orientation, we showed in sex-aggregated analyses that bisexuals had higher Dark Triad traits than heterosexuals. Differences between homosexuals and heterosexuals were limited to Machiavellianism, which was more pronounced in homosexuals. These results directly contradict the prosociality hypothesis for the evolution of homosexuality and support the gender shift hypothesis only in women. In contrast, the results may be more consistent with a life history model (Luoto et al., 2019a,b; Xu et al., 2019) and/or with observations about minority stress, suggesting that with greater experienced harshness of sexual minorities (i.e., non-heterosexuals), engaging in Dark Triad trait approaches to life might help non-heterosexual people stay safe, avoid detection, and get what they want from their lives.

CRediT authorship contribution statement

JONASON primarily served as the data manager and analyst, secondarily he authored the Results, and tertiarily served as an author whereas LUOTO was the primary author of the Introduction/Discussion and worked secondarily on analyses.

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