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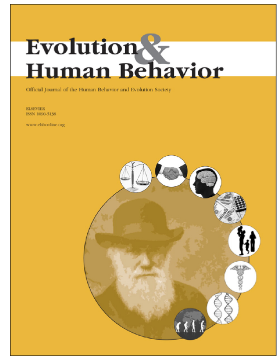

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PII: S1090-5138(16)30244-6
DOI: doi: 10.1016/j.evolhumbehav.2017.08.002
Reference: ENS 6144

To appear in:

Received date: 24 September 2016
Revised date: 8 August 2017
Accepted date: 15 August 2017

Please cite this article as: Tobias L. Kordsmeyer, Lars Penke , The association of three indicators of developmental instability with mating success in humans, (2017), doi: 10.1016/j.evolhumbehav.2017.08.002

The association of three indicators of developmental instability with mating success in humans

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Word count: 9*349

Abstract

Developmental instability (DI) has been proposed to relate negatively to aspects of evolutionary fitness, like mating success. One suggested indicator is fluctuating asymmetry (FA), random deviations from perfect symmetry in bilateral bodily traits. A meta-analytically robust negative association between FA and number of lifetime sexual partners has been previously shown in men and women. We examined the relationship between bodily FA across twelve traits and indicators of quantitative mating success in 284 individuals (141 males, age 19-30 years). Two further indicators of DI, minor physical anomalies (MPAs) and asymmetry in palmar atd angles, were also assessed. For men, no significant associations were detected, whereas for women, unexpected positive relationships of FA with the number of lifetime sexual partners and one-night stands emerged. Thus, in a large sample and using a more highly aggregated FA index, our study fails to replicate previous findings, though equivalence testing also did not support deviation from previous meta-analytic estimates, especially for men. No associations were found for MPAs and FA in atd angles in either sex.

Keywords developmental instability, fluctuating asymmetry, sexual selection, mating success, minor physical anomalies

1. Introduction

1.1 Fluctuating asymmetry and developmental instability

Since the development of bilateral traits is controlled by the same genomic regions, under ideal conditions these traits are assumed to grow identically on both sides of the body (Palmer & Strobeck, 2003). However, external perturbations such as illnesses, toxins, malnutrition, detrimental mutations or oxidative stress undermine ideal developmental conditions to some extent (Palmer & Strobeck, 2003; Van Dongen & Gangestad, 2011; Kowner, 2001; Gangestad, Merriman & Thompson, 2010). How poorly an organism can buffer against such malicious developmental influences is reflected by an individual's developmental instability (DI), which is thought to be an indirect indicator of low genetic quality (e.g., Van Dongen & Gangestad, 2011). The most common indicator of DI is fluctuating asymmetry (FA; e.g., Palmer & Strobeck, 2003), deviations from perfect symmetry in bilateral traits. Here, the term 'fluctuating' entails the notion that the direction of deviations from perfect symmetry, whether trait size being higher on the left or right, is assumed to be random and not under genetic control (Palmer & Strobeck, 2003; Kowner, 2001). FA, as an indicator of DI, is assumed to be related to various outcomes in nonhuman and human animals. For example, an extensive meta-analysis investigated the association between FA and health and quality measures in humans across six domains, one of which was reproductive outcomes (Van Dongen & Gangestad, 2011). Average effect sizes of FA negatively predicting the number of sexual partners of .17 for males (k=8 samples, total N=1071) and .13 for females (k=4 samples, total N=526) were found. Thus, a robust association of small-to-moderate size seems to be present between mating success and FA in humans. However, which anthropometric or behavioral factors mediate this association has received little attention (Haufe, 2008). The current study aims to replicate the association between FA and mating success and explore mediating factors. Replicating previous results is especially crucial for studies on FA, since it is a highly contested topic and has been debated for decades already amongst evolutionary biologists and psychologists alike (Swaddle, 2003; Van Dongen, 2011).

Several fitness-relevant variables and outcomes have been related to FA already in both nonhuman and human animals. In the former, examples are probability of survival in the striped dolphin (Pertoldi et al., 2000) and ejaculate quality in gazelles (Roldan, Cassinello, Abaigar, & Gomendio, 1998). In humans, beyond FA's links with reproductive success, Van Dongen and Gangestad's meta-analysis (2011) showed small-to-medium-sized associations of bodily FA (i.e., aggregate FA across more than one bodily trait including facial FA; henceforth FA_{body}) with maternal risk factors for malicious fetal outcomes and the development of schizophrenia and associated personality variations (e.g., schizotypy). A further meta-analysis by Banks, Batchelor and McDaniel (2010) suggested a negative correlation between FA_{body} and general intelligence (k=14 samples, total N=1871), for which Van Dongen and Gangestad only found a small effect, however (0.11, k=10 samples, total N=1071).

1.2 Fluctuating asymmetry in palmar atd angles

While the literature on DI and sexual selection has focused almost exclusively on FA, DI can be inferred from other indicators as well. Hence, an additional focus are exploratory analyses of two further indicators, minor physical anomalies (MPAs; Ismael, Cantor-Graae, & McNeil, 1998) and fluctuating asymmetry in palmar atd angles (FA_{atd}; Kowner, 2001), which have not been studied in association with mating success to our knowledge. Compared to FA_{body}, FA_{atd} is a dermatoglyphic trait which forms early in prenatal development, and is henceforth affected by environmental influences during the first trimester of pregnancy, after which it shows high temporal stability (Chintamani et al., 2007). Dermatoglyphic traits include asymmetries in finger-ridge counts, fingertip patterns and palmar atd angles, amongst others. Palmar atd angles are measured between three points on the palms where three ridge patterns (a, t and d triradii) converge; the angle is measured between the left and right sides of the triangle (Yeo, Gangestad & Daniel, 1993). Markow and Wandler (1986) detected significantly higher FA in two dermatoglyphic traits (a-b ridge count and fingertip pattern) in schizophrenic in-patients (*n*=81) than in controls (*n*=118). Mellor (1992) extended the assessment of dermatoglyphic FA to four traits (finger-ridge counts, fingerprint patterns, the palmer atd angles and palmer a-b ridge counts) and found similar results in schizophrenic in-patients (*n*=482) versus controls (*n*=1650). Moreover, an association between FA in atd angle (FA_{atd}) and cleft-palate syndrome, a developmental disorder, was detected. This renders FA_{atd} a potential indicator for developmental instability (Woolf & Gianas, 1976; Yeo, Gangestad & Daniel, 1993).

1.3 Minor physical anomalies

Another manifestation of DI that has also been implicated in relation to mental disorders, such as schizophrenia and autism, are minor physical anomalies (MPAs). MPAs are subtle morphological deviations, which are normally found in the face, eye and hand regions and are easily detectable visually (Ismael, Cantor-Graae, & McNeil, 1998). They purportedly arise in the first or early second trimester of gestation, are usually attributed to inherited genetic defects, chromosomal abnormalities and malicious environmental influences and appear to persist throughout the individual's life cycle (Ismail, Cantor-Graae, & McNeil, 2000; Kowner, 2001; Weinberg, Jenkins, Marazita & Maher, 2007). Especially when multiple MPAs are apparent, they can be considered indicating disturbances in early neurodevelopment and thus an increased risk for disease susceptibility (Weinberg, Jenkins, Marazita & Maher, 2007). A meta-analysis on the frequency of MPAs in schizophrenic patients compared to controls, which found both increased overall and regional (e.g., head or ears only) MPA scores (*k*=11 studies, overall *N*=1183; Weinberg, Jenkins, Marazita & Maher, 2007). Also, amongst a sample of undergraduate students (*N*=121), aggregate MPA scores correlated positively and moderately with FA_{body} (r=.18; Yeo, Gangestad & Daniel, 1993), suggesting that they partly tap into the same aspects of DI. Studies on nonhuman animals opened up the possibility of a link between MPAs and behavior and cognition in humans (Kowner, 2001). In the wild type of the fruit fly (*Drosophila*), for example, males with a higher prevalence of morphological abnormalities, mainly concerning sensory channels, showed disruptions in courtship behavior (Markow, 1987). Moreover, a study on children (*N*=62) found that those with a higher prevalence of MPAs also tended to show signs of behavioral abnormalities (Waldrop & Halverson, 1971).

Thus, it appears that besides FA_{body}, two other indicators of developmental instability, MPAs and FA_{atd}, are related to important fitness-relevant variables, such as mental health. Previously, it has been argued that MPAs and FA constitute slightly different manifestations of DI. The former are mainly the result of developmental deviations during the first trimester of pregnancy (Waldrop & Halverson, 1971). FA, in contrast, is related to variability in growth rates across the whole period of pregnancy, to perinatal complications such as prematurity or low birth weight (Livshits, Davidi, Kobyliansky, Ben-Amitai, Levi, & Merlob, 1988) and, after birth, is more prone to environmental influences such as illnesses or oxidative stress (Van Dongen & Gangestad, 2011; Kowner, 2001; Gangestad, Merriman & Thompson, 2010). Thus, this study aims at investigating the differential relationship between FA (both FA_{body} and FA_{atd}) and MPAs on the one hand, and a range of mating success-related variables on the other hand.

1.4 Bodily fluctuating asymmetry and sexual selection

Contrary to FA_{atd} and MPAs, links between FA_{body} and aspects of human sexual selection have been extensively reported in the literature. For example, it has been suggested that women favor men with low DI as sexual partners, purportedly due to their higher genetic quality (e.g. Gangestad & Thornhill, 1997a, b). These preferences, in turn, have been shown to actually map onto greater success in the mating domain. For example, Thornhill and Gangestad (1994) assessed FA_{body} in seven traits. Composite FA_{body} scores correlated inversely with the number of lifetime sexual partners in both men and women (*N*=122) and positively with age at first sex in men. Similarly, FA_{body} across eight traits from the face and hands was found to negatively relate to the number of lifetime sexual partners and the likelihood of sexual contacts outside an existing romantic relationship, as well as positively to age at first sexual intercourse in both sexes (*N*=100; Van Dongen, Cornille & Lens, 2009). Waynforth (1998) conducted an examination of FA_{body} and sexual life history traits in males in rural Belize. For an FA_{body} composite of eight traits, it was found that more symmetric men (*N*=56) fathered more children and reproduced earlier for the first time. However, this study can be criticized for its rather low level of precision: trait sizes were measured only once and to the nearest millimeter, hence some variation in FA_{body} might have been missed and measurement error might have been higher than elsewhere. Other studies, in contrast, usually measure twice and average the values and have relied on digital calipers that can measure up to the nearest 0.01 millimeter (e.g., Furlow, Armijo-Prewitt, Gangestad & Thornhill, 1997b). Also, Gangestad and Thornhill (1997b) examined extra-pair copulations (EPCs), which are sexual intercourses outside an existing romantic relationship. For men, negative associations between aggregate FA_{body} (seven bilateral traits) and both the number of EPCs and the number of times having been an EPC of a woman were found. Thus, a range of studies have so far found associations between FA_{body} and mating success in both men and women (Van Dongen & Gangestad, 2011).

1.5 Are the effects of fluctuating asymmetry related to developmental instability?

However, an important question is whether FA and mating success actually are associated via DI as a common cause, or due to more direct effects of FA on mating success. For example, in the above mentioned study by Van Dongen, Cornille and Lens (2009), a negative association between FA_{body} and both lifetime sexual partners and the likelihood of sexual contacts outside an existing romantic relationship were found, plus a positive effect of FA_{body} on age at first sexual intercourse. However, after performing further Bayesian analyses, treating individual DI as a latent variable, the authors conclude that DI does not underlie the shown relationships between FA and sexual outcomes. According to their statistical models, the strengths of the associations between DI and the sexual outcomes are close to or equal zero. They conclude that effects of FA, for example on human sexual behavior, can be ascribed to bilateral asymmetry per se, rather than being based on DI.

Furthermore, Van Dongen and Gangestad (2011) state that facial attractiveness may be directly affected by facial asymmetry, independent of or beyond effects of underlying DI. This may be since facial asymmetry can be perceived rather well, in contrast to more subtle asymmetries in traits such as the wrist or knee, and influences perceived attractiveness directly via people's preference for symmetry (Haufe, 2008; Perrett et al., 1999). Indeed, in their meta-analysis Van Dongen and Gangestad (2011) find a direct and robust effect of facial FA, but not FA_{body}, on facial attractiveness (mean effect size = .19 for facial FA, compared to a mean effect size = .03 for FA_{body}).

Thus, one needs to be aware that there is no perfect relationship between FA and DI. Instead, the former constitutes an approximation of the latter (e.g., for a composite FA_{body} of eight traits, the validity of measuring shared DI would be between 0.4 and 0.5; Van Dongen & Gangestad, 2011). Also, correlations between FA in different traits vary and rarely (closely) approach one (the mean correlation between independently developing traits has been estimated to be between 0.025 and 0.045; Van Dongen & Gangestad, 2011). Rather, these different measures of FA most likely touch upon slightly different manifestations of underlying DI. Still, when aggregating single traits' FA into a composite measure while being aware of the imperfect mapping of FA on DI, fluctuating asymmetry can be seen as a useful and valid measure for assessing the impact of developmental stability on a range of psychological and related outcomes (Gangestad, Bennett & Thornhill, 2001; Kowner, 2001).

1.6 Confounding and mediating variables

Haufe (2008) criticizes that in previous studies no satisfying explanation has been given for why the relationship between FA and mating success should exist. Haufe discusses Gangestad and Thornhill's finding (1997b) of more symmetric men being preferred by women as EPC partners and indicating higher numbers of EPCs as well. According to Haufe, it remains unclear why exactly women prefer more symmetric men, even if FA would be sufficiently linked to DI. However, a range of candidate mediator variables have been considered in previous studies of FA and may partly account for a potential relationship between FA and mating success. Firstly, personality characteristics such as self-reported social dominance have been related to both FA and mating success (Gangestad & Thornhill, 1997a). Secondly, bodily features such as facial (Gangestad, Thornhill, & Yeo, 1994; Rhodes, Simmons & Peters, 2005; but see Van Dongen & Gangestad, 2011), vocal (Hughes, Dispenza & Gallup Jr., 2004), or overall bodily attractiveness (e.g., Gangestad, Merriman, & Thompson, 2010), and body measures like male shoulder-to-hip ratio (SHR), female waist-to-hip ratio (WHR; Hughes, Dispenza, & Gallup Jr., 2004; Hughes & Gallup Jr., 2003), and height (e.g., Nettle, 2002; see Stulp & Barrett, 2016, for a review) were shown to be associated with either FA or mating success, or both, in previous research. Thirdly, as a potential behavioral mediator, Gangestad and Thornhill (1997b) found men with lower FA_{body} to flirt more with women outside their relationships. A further study by Simpson, Gangestad, Christensen and Leck (1999) coded men's intrasexual competitiveness and social presence from video recordings, which turned out to be associated with their FA_{body} (Simpson et al., 1999). Similar behavioral facets predicted women's attractiveness ratings of the men across different stages of their ovulatory cycles (Gangestad et al., 2004, 2007). Thus, some of these variables may partly explain a potential association between FA_{body} and mating success.

Regarding the mating success outcome measures, we focused on a broad range of variables, some of which had already been employed in previous studies (e.g., number of lifetime sexual partners; Thornhill & Gangestad, 1994; Van Dongen, Cornille & Lens, 2009; EPCs and number of times having been an EPC; Gangestad & Thornhill, 1997b), whereas an additional outcome variable has not been considered in previous studies, at least to our knowledge (i.e., the number of one-night stands). Here, the number of lifetime sexual partners can be seen as a measure of overall mating success, whereas the number of one-night stands is an indicator of general promiscuity, the number of EPCs is a measure of infidelity, and how often one has been an EPC partner corresponds to being preferred by the opposite sex in mate choice (Schmitt, 2004).

1.7 Hypotheses

To summarize, we aimed to test the following hypotheses in a large sample and employing a high number of traits (for FA_{body} and MPAs): Based on meta-analytic results (Van Dongen & Gangestad, 2011), we hypothesized a positive association between our composite FA_{body} measure and number of sex partners, which is stronger in men than in women. Furthermore, we also predicted a positive relationship between FA_{body} and our outcome measures related to the overall number of sex partners in men and, to a lesser degree, also in women. These are number of one-night stands, number of EPCs and number of times having been an EPC partner for someone else. Regarding MPAs and FA_{atd}, our analyses were largely exploratory, due to the lack of relevant previous research and clear theoretical expectations.

2. Methods

2.1 Subjects

A total of 284 young adults were recruited in a major German city (141 males, mean age = 23.7 years (*SD*=2.7, range 19-30). Half of the sample (*n*=142) were currently in a romantic relationship (average length *M*=2.73 years, *SD*=1.63, range 0.67-7.96). Only 59.5% were students, whereas 15.7% had left school with 10 years of formal education or less (i.e., no German Abitur or Fachabitur). All participants reported heterosexual orientation and prior sexual and romantic relationship experience, were unmarried, without children, and German native speakers. This sample has already been described as Study 2 in Penke and Asendorpf (2008).

2.2 Procedure

Participants that were currently in a romantic relationship came to the lab together with their partner and both participated in the study, since in the original study (Penke & Asendorpf, 2008), dyadic effects of sociosexuality and relationship outcomes within romantic couples were investigated.

However, all participants were tested individually. They completed a computerized battery of questionnaires on their own, including detailed self-reports of past sexual behavior and various assessments unrelated to the current analyses. Furthermore, we took high-resolution scans from participants' left and right hands (fingers closed) using a flatbed scanner. Scans were stored as uncompressed greyscale bitmaps. After engaging in an interaction with an opposite-sex confederates not relevant to this study, anthropometric measurements were obtained by a trained same-sex experimenter. Participants were compensated with 16€ (about $19).

2.3 Measures

2.3.1 Bodily fluctuating asymmetry (FA_{body})

Fluctuating asymmetry was measured using a digital caliper accurate to 0.1 mm in the following twelve bilateral traits: foot width, ankle width, knee width, elbow width, wrist width, hand width, 2nd digit (D2) length, D3 length, D4 length, D5 length, ear length and ear width. All bilateral traits were measured on one side, then on the other. Afterwards anthropometric traits unrelated to this study were measured (i.e., sitting height, breast and underbust circumference, body fat percentage). Next, a second measurement of all bilateral traits was conducted. Hence, each measure was taken twice, the values averaged and then combined into an aggregate FA_{body} index, since this has been shown to be a better indicator of DI than FA calculated from single traits or single measurements (Leung, Forbes & Houle, 2000; Palmer, 1994). Participants were asked for bone fractures and sprains for all relevant body parts, and affected measures were removed.

Pre-analyses for the fluctuating asymmetry data (for single traits) were performed based on the walk-through example by Palmer and Strobeck (2003) and on personal communication with S. W. Gangestad (June 18th, 2014). In a first step, scatterplots of pairs of trait averages were inspected for bad raw measurements. No clear outliers were detected. As a second step, we examined whether apparent outliers in measurement error were more deviant than expected due to chance, for which Grubb's statistic with a critical value of 3.70 was used (Grubbs, 1969). Nine values (averages between first and second measurement for single traits) were detected as outliers and hence removed from the data set. In the following, aberrant individuals in terms of trait size and fluctuating asymmetry (to investigate whether FA is artificially inflated due to injury, wear and tear) were investigated by checking scatterplots between each trait's left and right averages (first and second measurement). No additional outliers were detected here. Next, more subtle outliers regarding trait asymmetry were checked for by means of scatterplots between two different traits' FA values. Three fluctuating asymmetry values (for single traits) were deemed outliers based on Grubb's statistic and removed. Furthermore, two-way ANOVAs with side (of the bilateral trait) and individuals as predictors, and fluctuating asymmetry as the outcome, were employed. For all traits, the interaction between sides and individuals turned out to be significant (all Fs > 2.33, all ps < .001), confirming that the subtle asymmetries were greater than measurement error.

As a next step in our pre-analyses, Spearman's ρ correlation between FA and average trait size were examined in order to see any dependence of FA on trait size. Significant negative correlations were detected for finger lengths of the fifth digit and hand width (ρ=-.16, p<.01 and ρ=-.40, p<.001, respectively). These two relationships can be explained by FA decreasing with increasing body size, since larger individuals might inherently have a higher quality and hence reflect real differences in DI (Palmer & Strobeck, 2003). Still, taking these significant relationships between single traits' FA and size into account, we decided to control for trait size in FA_{body}, as described below. Finally, the distributions of the FA for each trait were examined, testing for antisymmetry and directional asymmetry. First, visual inspection of the histograms of the FA values for each traits revealed no clear departures from normality. Kolmogorov-Smirnov tests turned out to be non-significant for all twelve traits (D<.49, ps=.20). Regarding directional asymmetry (DA), we followed the procedure outlined by Palmer and Strobeck (2003) and conducted one-sample t tests comparing the mean difference between left and right trait sizes against zero revealed significant DA (after Bonferroni correction) for foot width, ankle width, knee width, length of the 2nd digit (d2), hand width, and ear length (for the first five right > left, for the last one left > right; unsigned *t*s > 2.94, *p*s < .004). For hand width, the mean was 0.65 SD away from zero, for foot width 0.50 SD, for ankle width 0.44 SD, for knee width 0.36 SD, for d2 length 0.18 SD, for ear length 0.18 SD. Since significant DA invalidates FA measures, we corrected for DA in two separate ways. Firstly, we subtracted the means from all traits' FA values, thus centering all means at zero. However, this method has been criticized since it would wipe out potentially real inter-individual variation in levels of DA (Van Dongen, 2006), which may have a genetic basis (Palmer & Strobeck, 1992) and may be associated with handedness (which would be in line with our DA, since for all, except for ear length, measures were larger for the right laterality; Van Dongen & Gangestad, 2011). Secondly, we calculated a further FA_{body} composite, employing a principal component analysis (PCA) method proposed by Graham, Emlen, Freeman, Leamy and Kieser (1998). When entering the left and right measures (here: means of the first and second measurements) for each trait and sex separately into a PCA (based on a covariance matrix), the first extracted principal component (PC) represents DA, and the second FA independent from DA. The unsigned values for all twelve traits were then combined into an FA_{body} composite score (see also Penke et al., 2009; Simmons, Rhodes, Peters, & Koehler, 2004). These two corrected FA_{body} composites correlated r=.84 in men and r=.80 in women. We report results for both composites.

The composite FA score (FA_{body}) was calculated as follows: First, the averages of the two measures (first and second) for each trait and side were taken, and the unsigned difference between the left and right average measures for each trait calculated. This difference was divided by average trait size of the full sample (i.e., left average plus right average divided by two across all 284 participants for each trait) in order to control for trait size. Then, mean-centered aggregate FA_{body} was calculated by summing up the individual traits' mean-centered FA scores and dividing them by twelve (to get the mean value). For the PCA-based aggregate FA_{body}, the means of the twelve traits' loadings on the second PC (which represents FA independent from DA, see above) were calculated. To render the regression coefficients of regression models (see below) better interpretable, we multiplied the mean-centered FA_{body} values, but not the ones extracted using the PCA method, by 100. Overall intraclass correlation (two-way random, single measures) between FA_{body} of the first and second measures was .58 for both mean-centered FA_{body} and PCA-based FA_{body}. Intraclass correlations for FA of individual traits were also satisfactory, ranging from .30 to .73 for mean-centered FA_{body}, and .32 to .72 for PCA-based FA_{body}. These values are comparable to statistics obtained in earlier studies (e.g., Thoma, Yeo, Gangestad, Halgren, Sanchez, & Lewine, 2005; Gangestad & Thornhill, 1997b). The mean correlation of FA between independently developing traits indicates the proportion of variance in FA due to DI shared across traits (Van Dongen & Gangestad, 2011). In our sample this mean correlation was .014 for mean-centered FA_{body}, and .013 for PCA-based FA_{body}, which is slightly below values in previous studies (Van Dongen & Gangestad, 2011), presumably due to correction for DA.

2.3.2 Minor physical abnormalities (MPAs)

MPAs were assessed based on items from the Waldrop scale (Waldrop, Pedersen, & Bell, 1968), extended by additional items from Ismail, Cantor-Graae and McNeil (1998, 2000). Waldrop and colleagues' manual has been used widely in previous research and provides MPA scores with stability from birth (e.g., over a 5-year period; Firestone & Peters, 1983). One same-sex experimenter observed and coded the following 26 different MPAs: Global head: fused eyebrows, frontal bossings, micrognathia; eyes: telecanthus, epicanthus, heterochromia, ptosis, colobomata; ears: adherent ear lobes, malformed ears, low-seated ears; mouth: thin upper lip; hands: curved fifth finger, single palmar crease, hyperconvex fingernails, small fingernails, marked tapered fingers, retarded fingers, 1 or 3 creases on 5th finger, overlapping 5th finger; feet: big gap between first and second toe, partial syndactyly, retarded 4th or 5th toe, hyperconvex toe nails, overlapping toes, 3rd toe longer than 2nd toe.

Following the original manuals, items were scored as present (0) or absent (1), except for the following, scored gradually as 0 to 2: Epicanthus, telecanthus, low-seated ears, adherent ear lobes, malformed ears, partial syndactyly, 3rd toe longer than 2nd toe, and curved 5th finger. We employed one experimenter per sex, who received several hours of extensive training (including detailed picture material for the different coding levels of each MPA and checks of interrater agreement on training subjects), since the MPAs we assessed are easily detectable visually and high inter-rater reliabilities have been shown before (Waldrop, Pedersen & Bell, 1968).

2.3.3 Fluctuating asymmetry in atd angles (FA_{atd})

From hand-scans (see above), the three dermatoglyphic triradii a, t and d were determined in the palms, and the atd angles were measured using Scion Image. FA in the atd angle (FA_{atd}) was calculated as the difference in atd angle between the left and right hand following Woolf and Gianas (1976; see Yeo, Gangestad & Daniel, 1993, for more details). FA_{atd} could not be determined in some participants due to poor scan quality, leaving a final sample for analyses including FA_{atd} of 213 (111 males; see Table 1).

2.3.4 Self-report questionnaires

Participants filled in questionnaires assessing the following mating success variables: number of lifetime sexual partners (“With how many persons have you had sexual intercourse overall so far in your life?”), number of one-night-stands (“With how many persons have you had sexual intercourse only one time so far in your life?”), number of extra-pair copulations (EPCs; i.e. number of incidences of cheating on one’s partner; “With how many persons have you had sexual intercourse, while being in a relationship with another person?”), and number of times one has been an EPC partner for another person (“With how many persons have you had sexual intercourse, while this person was in a relationship with someone else?”). All items had an open response format.

2.3.5 Control variables

Participants' age and relationship status can naturally confound variables such as the overall number of sexual partners (Thornhill & Gangestad, 1994). Moreover, FA has been shown to increase with age (reviewed in Penke et al., 2009). Finally, increased body fat makes it more difficult to accurately identify the relevant measurement points for traits included in FA_{body}. Thus, the influence of BMI, which was related to FA_{body} in previous studies (e.g., Manning, 1995), was checked.

2.4 Statistical analyses

Power analyses (G*Power v3.1; Faul, Erdfelder, Buchner, & Lang, 2009) revealed a power of 53% for men (*N*=141) and 34% for women (*N*=143; assuming effect sizes of 0.17 for men and 0.13 for women; Van Dongen & Gangestad 2011). Even though this study can still be considered underpowered (assuming a desirable power level of 80 %), it employs a larger sample compared to previous studies on FA_{body} (Van Dongen & Gangestad, 2011 report average sample sizes of *N*=133 across *k*=12 studies on FA_{body} and reproductive success).

Since the outcome variables in our study were count data and strongly positively skewed, and linear regression models are not suitable for these purposes, we employed both Poisson and negative binomial regression models, which are preferred over square root transformation of the count variable (Cohen, Cohen, West & Aiken, 2003). We ran both models and chose the one providing the best fit for our data (see below). In addition, we calculated Spearman correlations between the three indicators of DI and the four mating success variables. Since males and females pursue somewhat different strategies in the mating domain (Buss & Schmitt, 1993), differential relations between DI indicators and mating success can be expected (Van Dongen & Gangestad, 2011). Hence, we performed analyses separately for our male and female participants.

We ran Poisson regression models with the mating success variables as the dependent variable in two versions: (1) predicted by the DI proxy and age, and (2) predicted by the DI proxy and the potential confounds relationship status, age and BMI. Scaled Pearson chi-square parameters greater 1 for the Poisson regression models indicated overdispersion for all models, violating the Poisson variance assumption. Overdispersed Poisson models were employed instead. Here, the dispersion parameter Φ is calculated directly from the data (Cohen, Cohen, West & Aiken, 2003). Additionally, negative binomial models were run. Scaled Pearson chi-square parameters appeared to be close to 1 and even closer to 1 after employing a maximum-likelihood estimation indicating a good model fit (Cohen, Cohen, West & Aiken, 2003). To assess whether overdispersed Poisson or negative binomial models would better fit our data, plots of estimated variance-to-mean relationships for both models were analyzed (Ver Hoef & Boveng, 2007). Negative binomial models fit our data slightly better (see Figure 1 for the number of lifetime sexual partners predicted by FA_{body}).

2.4.1 Data availability

The data associated with this research are available at [link].

3. Results

3.1 Descriptive statistics

Descriptive statistics for all predictor (indicators of developmental instability, DI) and outcome (mating success) variables are shown in Tables 1 and 2, respectively. For descriptive purposes, a correlation matrix showing zero-order Spearman correlations between the three main predictor and the outcome variables is provided in Table 3 (Spearman correlations were chosen since all mating success variables were clearly non-normally distributed; see Table 2 and above)

Table 1. Descriptive statistics and mean sex differences for all predictor variables.

	Males		Females		Sex difference	
	M	*SD*	*M*	*SD*	*t*	Cohen's *d*
FA_{body} (mean-centered)	1.89	0.50	2.02	0.49	-2.24*	0.27
FA_{body} (extracted from PCA)	0.78	0.20	0.78	0.20	-0.06	0.01
MPAs	2.86	1.97	2.44	1.92	1.82	0.22
FA_{atd}	6.12	6.08	5.70	4.72	0.56	0.08
Age	24.4	2.6	23.1	2.8	3.90***	0.48
BMI	23.69	3.22	23.29	4.62	0.84	0.10

Note: FA_{body} = fluctuating asymmetry in body traits; MPAs = minor physical anomalies; FA_{atd} = fluctuating asymmetry in palmar atd angles; BMI = body-mass index; N=140-141 males (for FA_{atd} n=111), N=142-143 females (for FA_{atd} n=102). *p<.05.

Table 2. Descriptive statistics and mean sex differences for outcome variables

	M	*Median*	*SD*	*Min*	*Max*	*t*	Cohen's *d*
Males							
Lifetime sexual partners	7.66	5.00	8.29	1	60	-0.17	0.02
One-night stands	3.03	1.00	5.78	0	50	0.31	0.04
EPC partners	0.91	0.00	2.03	0	15	-0.42	0.05
Having been an EPC partner	0.79	0.00	1.64	0	15	-0.64	0.07
Females							
Lifetime sexual partners	7.82	6.00	7.90	1	50		
One-night stands	2.83	2.00	5.44	0	45		
EPC partners	1.03	0.00	2.78	0	31		
Having been an EPC partner	0.99	0.00	3.46	0	40		

Note: EPC = extra-pair copulation; N=141 males, N=143 females. p > .05 for all t-tests.

Table 3. Zero-order Spearman correlations between the three indicators of developmental stability and outcome variables.

Spearman's ρ	FA_{body} (m.-c.)	FA_{body} (PCA)	MPAs	FA_{atd}	Sexual partners	One-night stands	EPCs	Been an EPC
FA_{body} (mean-centered)	-	-	.08	.10	.08	.08	.04	.00
FA_{body} (PCA)	-	-	.05	.15	.10	.11	-.05	.03
MPAs	.04	-.07	-	.10	-.04	-.05	.19*	.09
FA_{atd}	-.13	-.05	.00	-	.10	-.03	-.03	.01
Lifetime sexual partners	.03	-.02	-.01	.12	-	.78***	.55***	.46***
One-night stands	-.04	-.07	.00	.09	.81***	-	.47***	.44***
EPCs	.02	-.03	-.01	.04	.57***	.42***	-	.41***
Having been an EPC	-.06	-.02	-.04	-.09	.52***	.39***	.37***	-

Note: FA_{body} = fluctuating asymmetry in body traits; MPAs = minor physical anomalies; FA_{atd} = fluctuating asymmetry in palmar atd angles; EPC = extra-pair copulation. Females (N=143, for FA_{atd} n=102) in the top-right, males (N=141, for FA_{atd} n=111) in the bottom-left. *p<.05, **p<.01, ***p< .001.

3.2 Confounding variables

First, the role of the potential confounding variables relationship status, age and BMI will be considered. Both male and female singles indicated higher numbers of lifetime sexual partners than partnered participants (male singles *M*=9.31, *SD*=7.85, partnered males *M*=5.41, *SD*=5.10, t_{139}=3.51, *p*<.01, *d*=0.59; female singles *M*=9.33, *SD*=7.19, partnered females *M*=5.69, *SD*=5.58, t_{141}=3.38, *p*<.01, *d*=0.57). No association was found with FA_{body} (both *p*s>.44 and >.61 for mean-centered and PCA-based FA_{body}). A positive link was found between age and the number of lifetime sexual partners (ρ=.28, *p*<.01 for males; ρ=.27, *p*<.01 for females), but not between age and FA_{body} (unsigned ρs<.16, *p*s>.06 for mean-centered FA_{body} and ρs<.14, *p*s>.10 for PCA-based FA_{body} for both males and females). Regarding BMI, a significant positive correlation was found with FA_{body} (ρ=.22, *p*<.01 and ρ=.19, *p*=.02 for mean-centered FA_{body}, ρ=.20, *p*=.02 and ρ=.30, *p*<.001 for PCA-based FA_{body}, for males and females, respectively). Correlations of BMI with the number of lifetime sexual partners were non-significant (ρ<.04, *p*>.72 for males and females). These results are comparable to previous studies (Manning, 1995; Hume & Montgomerie, 2001; but see Rikowski & Grammer, 1999). Since age, relationship status and BMI appeared to be linked to at least one of either FA_{body} or number of sexual partners, we included them as control variables in further analyses, hence providing more robust results (see Table 4 and Tables S1, S2 and S3 in the supplementary).

3.3 Mating outcomes and FA_{body}

For men, no significant associations between FA_{body} and any of the four mating outcome variables emerged. This was true for mean-centered and PCA-based correction for DA in FA_{body}, and in both model 1 and when including the three confounding variables (all unsigned *B*s < 1.35, *p*s > .07; see Table 4, and S1 in the supplementary). In line with our hypotheses, coefficients were mostly negative for the number of lifetime sexual partners, one-night stands and times having been an EPC partner, though clearly statistically non-significant.

For women, positive associations emerged between FA_{body} and the number of lifetime sexual partners and one-night stands. This held for both mean-centered and PCA-based correction for DA in FA_{body}, and both models (all *B*s > 0.32, *p*s < .03; see Table 4, and Table S1 in the supplementary). No effect of FA_{body} with either DA correction was found on women's number of EPC partners (all *B*s < 1.37, *p*s > .09). For the number of times having been an EPC partner, positive effects were detected for both mean-centered and PCA-based corrections for DA in FA_{body} (models 1 only, *B*s > 0.91, *p*s < .01; for all others, unsigned *B*s < 0.05, *p*s > .88). Thus, we found rather consistent evidence for an unexpected positive association of FA_{body} with the number of lifetime sexual partners and one-night stands in women: More asymmetric women reported higher numbers of lifetime sexual partners and one-night stands.

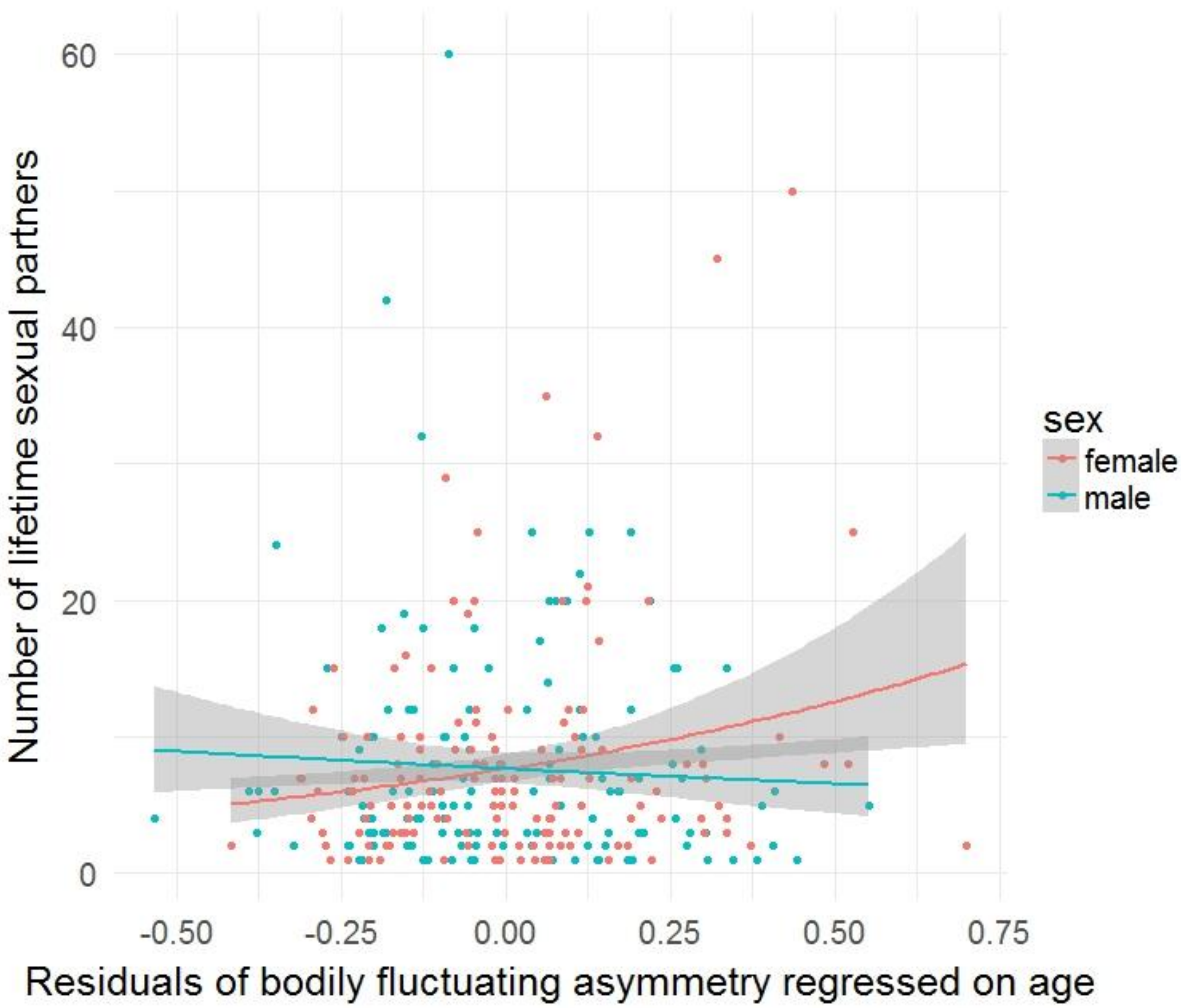
The odds ratio *Exp(B)* can be interpreted as follows: in model 1, taking women's mean age of 23.1 years, for each increase in one unit of PCA-based FA_{body} (i.e., unsigned factor score, mean of all twelve traits), the natural logarithm of the predicted number of lifetime sexual partners is expected to increase by 1.05, on average. That is, for example, for an FA_{body} score of 0.78 (mean of PCA-based FA_{body}), the lifetime number of sexual partners is expected to be 7.57, and for an FA_{body} score of 0.98 (mean plus one standard deviation) the expected value increases to 9.33. In the following, coefficients can be interpreted accordingly.

Table 4. Negative binomial models predicting the four mating success indicators from bodily fluctuating asymmetry (FA_{body}).

	Males				females			
	B	*SE*	*Exp(B)*	*p*	*B*	*SE*	*Exp(B)*	*p*
DV: lifetime sexual partners								
model 1	-0.55	0.40	0.58	.17	1.05	0.34	2.85	.002
model 2	-0.48	0.38	0.62	.22	0.98	0.37	2.66	.001
DV: one-night stands								
model 1	-1.34	0.74	0.26	.07	2.23	0.50	9.25	<.001
model 2	-1.15	0.68	0.32	.09	1.78	0.58	5.91	.002
DV: EPC partners								
model 1	0.38	1.02	1.46	.71	0.92	0.77	2.52	.23
model 2	0.43	1.01	1.54	.67	1.36	0.81	3.88	.09
DV: been an EPC								
model 1	-0.23	0.55	0.79	.67	2.33	0.64	10.23	<.001
model 2	-0.42	0.52	0.66	.43	-0.10	0.76	0.91	.90

Note: EPC = extra-pair copulation; model 1: only bodily fluctuating asymmetry (corrected for directional asymmetry based on principal component analyses) as IV; model 2: additionally including age, BMI and relationship status; *N*=141 males, *N*=143 females.

Figure 1. Scatterplot for the negative binomial regressions model, predicting the number of lifetime sexual partners from bodily fluctuating asymmetry (FA_{body}), controlling for age.



Note: *N*=141 males, *N*=143 females. Bodily fluctuating asymmetry corrected for directional asymmetry based on principal component analyses. Independent variable is residuals from bodily fluctuating asymmetry regressed on age.

3.3.1 Equivalence tests

In order to examine whether the effect sizes in our sample on associations between FA_{body} and mating success are statistically different from previously reported mean effect sizes, we conducted equivalence tests using R package TOSTER (Lakens, 2017). As the effect sizes of interest (equivalence bounds) we used the mean from the range of plausible mean estimates reported in a recent meta-analysis by Grebe, Falcon and Gangestad (2017). The reported range was from .11 to .17, hence we used the midpoint of .14 (i.e., -.14 as the negative and .14 as the positive bound). Moreover, for robustness, we conducted the same analyses using the mean effect sizes for reproduction outcomes from an earlier meta-analysis by Van Dongen & Gangestad (2011), namely r=.17 for men (k=8 samples, overall N=1071) and r=.13 for women (k=4 samples, overall N=526). We converted odds ratios from our Negative Binomial models (model 1; incl. the confound age) to Pearson correlation coefficients as suggested by Borenstein, Hedges, Higgins and Rothstein (2009; see supplementary S4 for a sample calculation). Table 5 shows Pearson correlation coefficients for all four outcome variables, separately for men and women.

Equivalence tests revealed that for men, the effect sizes' confidence intervals for three of the four outcome variables included the negative bound of r=-.14 (based on mean effect size reported in Grebe, Falcon, & Gangestad, 2017). That is, for the lifetime number of sexual partners, one-night stands and number of times having been an EPC partner, our effect size was not statistically different from the previously reported mean effect size. Figure 2 illustrates this for the outcome lifetime number of sexual partners: The confidence interval around our converted effect size (r=-.05) includes the lower bound (r=-.14), hence it is not statistically different from the previously reported average effect size. In contrast, for the number of EPCs, our effect size (converted r=.05) turned out to be statistically different from the negative bound. Thus, for this outcome variable, we provide evidence for a potential absence of a negative association with FA_{body}, contrary to previous studies (e.g., Gangestad & Thornhill, 1997b).

For women, three effect sizes' confidence intervals did not include the previously reported mean effect size (*r*=.14; Grebe, Falcon, & Gangestad, 2017). Hence, for the number of lifetime sexual partners, one-night stands and EPC partners (converted effect sizes in our study: *r*=.11, *r*=.21 and *r*=.16, respectively), we provide evidence that the association with FA_{body} may not be as has been reported previously. In turn, for the number of times having been an EPC partner, our effect size's (converted *r*=-.01) confidence interval did include the mean effect size, so that we can draw no clear conclusion here. Results were virtually identical when conducting equivalence tests with the effect sizes reported in Van Dongen and Gangestad (2011; for men: *r*=-.17, women: *r*=-.13) Thus, overall even though our effect sizes are mostly statistically non-significant (except for women's number of lifetime sexual partners and one-night stands), they are not statistically different from and hence in the ballpark of previous findings (for men and women, the number of times having been an EPC partner; for men only, for the number of lifetime sexual partners and one-night stands). For number of EPCs (both men and women), number of lifetime sexual partners and one-night stands (women), we provide evidence for a statistically significant difference of our effect sizes from previously reported effect size (Grebe, Falcon, & Gangestad, 2017; Van Dongen & Gangestad, 2011).

Table 5. Pearson correlation coefficients between fluctuating asymmetry (FA_{body}) and the four mating outcome variables converted from the Negative Binomial models' odds ratios (model 2).

	Males	Females
Lifetime sexual partners	-.05	.11
One-night stands	-.13	.21
Extra-pair copulations	.05	.16
Having been an EPC partner	-.05	-.01

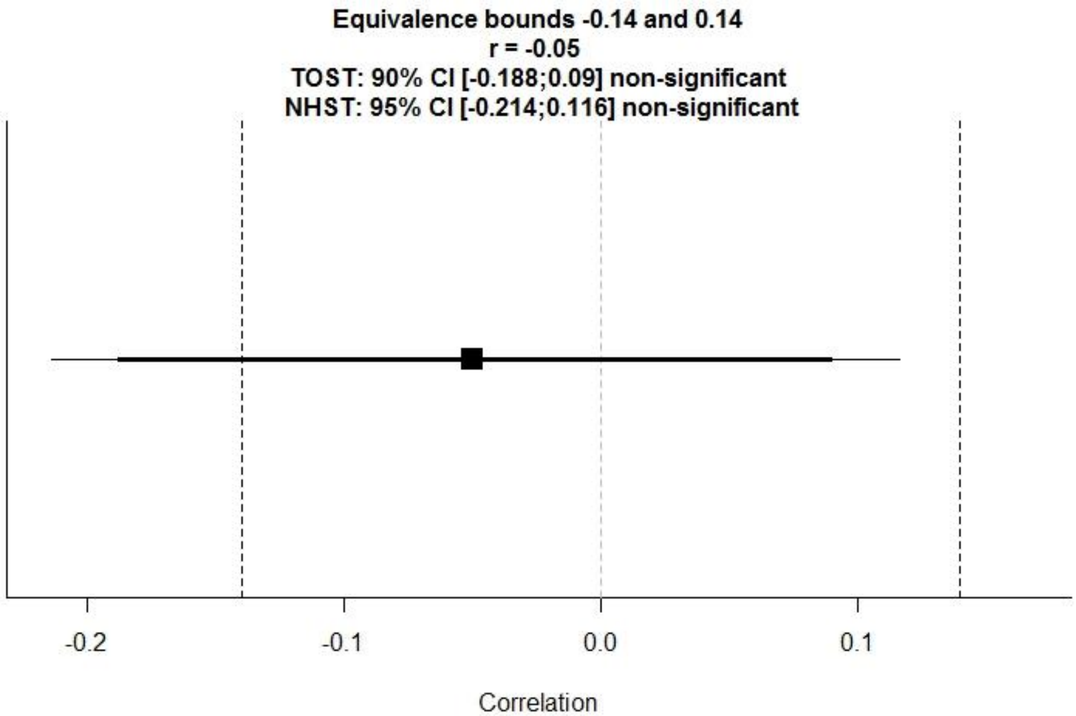
Note: *N*=141 males, *N*=143 females.

Table 6. Results of equivalence tests between our study's and previous meta-analyses effect sizes.

	Males				Females			
90% confidence intervals	*ES*	*LL*	*UL*	*p*	*ES*	*LL*	*UL*	*p*
Lifetime sexual partners	-0.05	-.19	.09	.14	0.11	-.03	.24	<.01**
One-night stands	-0.13	-.26	.01	.45	0.21	.07	.34	<.001***
Extra-pair copulations	0.05	-.09	.19	.01*	0.16	.02	.29	<.001***
Having been an EPC partner	-0.05	-.19	.09	.14	-0.01	-.15	.13	.06

Note: *ES*=our study's effect size converted from odds ratio, *UL*=upper limit, *LL*=lower limit, *p*-value for equivalence tests; *N*=141 males, *N*=143 females. Equivalence bound for males and females *r*=-.14/.14 (based on Grebe, Falcon, & Gangestad, 2017).

Figure 2. Equivalence test for the lifetime number of sexual partners; males only.



Note: *N*=141 males.

3.3.2 Correcting for limited validity of FA_{body}

Since the validity of an FA_{body} aggregate for measuring shared DI is less than perfect, correlations between FA_{body} and mating success underestimate real associations between DI and outcome measures, such as mating success. This attenuation can be corrected for by taking into account the estimated validity of FA_{body}. We calculated the validity of our FA_{body} aggregate using the formula provided by Van Dongen and Gangestad (2011). Taking the square-root of our twelve traits' internal consistency (Cronbach's α=.144 for PCA-based FA_{body}), revealed an estimated validity of .38. Consequently correcting the correlations (from Table 3) by an attenuation factor of 2.63 (1/.38) yielded estimated correlations for associations between underlying DI and mating outcome variables of between ρ=-.18 and .08 for men, and between ρ=-.13 and .29 for women (men/women, lifetime sexual partners: ρ=-.05/.26**; one-night stands: ρ=-.18*/.29***; EPC partners: ρ=.08/-.13; times having been an EPC partner: ρ=-.05/.08).

Thus, only one statistically significant correlation in the expected (negative) direction emerged for associations between DI and mating success, namely for the number of one-night stands in men (and two significant positive correlations for women, number of lifetime sexual partners and one-night stands). To conclude, even after correcting for limited validity of our FA_{body} aggregate in estimating underlying DI, these still represent small effects of DI on mating success.

3.4 Mating success, MPAs, and FA_{atd}

No significant association of MPAs were detected with any of the mating success outcome variables for men or women (all *p*s > .21 and > .11, respectively; see Table S2 in the supplementary). Regarding FA_{atd}, no significant effects emerged, neither for men nor for women (all *p*s > .36 and > .10, respectively; see supplementary Table S3).

4. Discussion

This study examined the relationship between different, carefully assessed indicators of developmental instability (DI) and several indicators of mating success implicated in human sexual selection, drawing on a comparatively large and well-controlled data set. Contrary to previous studies, no significant associations emerged between any of the three indicators of DI (bodily fluctuating asymmetry (FA_{body}), aggregate minor physical anomalies (MPAs), dermatoglyphic fluctuating asymmetry in palmar atd angles (FA_{atd})) and mating success in men. Rather consistent positive relationships between FA_{body} and two facets of mating success, numbers of lifetime sexual partners and one-night stands, were found for women. No effects on mating success were detected for two other indicators of DI, MPAs and FA_{atd}, in women as well. We hence did not find support for an association between low DI and quantitative mating success in humans, as predicted by 'good genes' models of sexual selection (Gangestad & Simpson, 2000).

4.1 Bodily fluctuating asymmetry and mating success

Although most of the effects of bodily fluctuating asymmetry on mating success were nominally in the expected negative direction in men (except for number of EPC partners), all results were statistically clearly non-significant, even after correcting for limited validity of the FA_{body} aggregate as a measure of shared DI. Thus, if there is a real association between FA_{body} and mating success in men in our sample, it is very weak at best. We hence were unable to support previous findings, such as an inverse relationship between FA_{body} and the number of lifetime sexual partners (Thornhill & Gangestad, 1994; Van Dongen, Cornille & Lens, 2009), and EPC partners or times having been an EPC partner (Gangestad & Thornhill, 1997b). Nor did we find significant results for an additional mating outcome, the number of one-night stands, which to our knowledge has not been studied in relation to FA_{body} before.

In women, FA_{body} was related to the number of lifetime sexual partners and one-night stands. However, the effects of FA_{body} were in the opposite direction as previously found in the meta-analysis by Van Dongen and Gangestad (2011), though it has to be noted that the meta-analytic estimate was based on only four studies and not theoretically expected (see Gangestad et al., 1997b). Given that the positive associations we found for women were unexpected, they should be treated with care, as it is always possible that they represent false positives. If real, they could be interpreted as women who are less attractive due to their asymmetry (Hume & Montgomerie, 2001) being less choosy when it comes to sexual partners. Since access to female sexuality is a limited resource on the mating market (Baumeister & Vohs, 2004), less attractive women might compensate for their lower mating market value by making their sexuality more accessible. This strategy might avoid the reproductive costs of not finding a mating partner at all, increase the chance of securing a long-term partner despite their competitive disadvantage, or allow them to extract resources from multiple mates that might not be willing to engage in investing long-term relationships with them. Alternatively, the high number of sexual partners of more asymmetric women might be indicative of repeated failures to secure long-term partners, which is generally the preferred reproductive strategy of women (Buss & Schmitt, 1993). This would underline the adaptive benefits of low FA.

Even though most of our study's effect sizes of FA_{body} on mating outcomes were statistically non-significant (except for women's number of lifetime sexual partners and one-night stands), equivalence tests showed that for the number of lifetime sexual partners and one-night stands (men only) and times having been an EPC partner (men and women), effect sizes were not statistically significant from previously reported effect sizes (Grebe, Falcon, & Gangestad, 2017; Van Dongen & Gangestad, 2011). Only for the number of EPCs (both men and women) as well as lifetime sexual partners and one-night stands (women), our effects were significantly larger than previously reported, so that we provide clear evidence against negative associations with FA_{body}. Compared to the studies in the meta-analysis by Van Dongen and Gangestad (2011), which showed robust small-to-moderate negative effects of FA_{body} on number of sexual partners for both sexes, we employed a slightly larger sample of both men and women, and a larger number of traits for the FA_{body} aggregate, so that our results can be seen at least as robust as previous findings. Thus, our study questions the suggested association between FA_{body} and mating success in humans. Alternatively, one could argue that an FA_{body} aggregate of twelve traits is still not sufficient and that the number of traits needs to be increased. For example, Penke and colleagues (2009) used an aggregate facial FA consisting of 35 traits and found associations with elderly men's cognitive decline. Even higher aggregated, spatially dense FA indicators have been assessed from 3D face scans using geometric morphometrics (Claes, Walters, Vandermeulen, & Clement, 2011; Hill et al., 2017). This technique holds much potential for approaching DI better and should be used to check the robustness of published correlates of FA in future studies.

4.2 Three indicators of developmental instability

FA_{body}, MPAs and FA_{atd} arise in slightly different periods of early development. MPAs and FA_{atd} mainly arise during the first trimester of gestation, the former due to developmental deviations, the latter under genetic control and further affected by environmental influences in this period of gestation, after which both show high temporal stability (Chintamani et al., 2007; Yeo, Gangestad & Daniel, 1993). FA_{body}, in contrast, is related to variability in growth rates across the whole period of pregnancy, to perinatal complications such as prematurity or low birth weight (Livshits, Davidi, Kobyliansky, Ben-Amitai, Levi, & Merlob, 1988) and to environmental influences during early postnatal developmental, such as illnesses or oxidative stress (Gangestad, Merriman & Thompson, 2010; Kowner, 2001; Van Dongen & Gangestad, 2011). Thus, these three measures tap into somewhat different manifestations of DI, differentially affected over phenotypic development. Assuming these are not false positives, female mating success outcomes might be more related to manifestations of DI that emerge at later developmental stages, like FA_{body}, but not at earlier stages of prenatal development, like MPAs and FA_{atd}. For men, in turn, we present converging null-results for all three indicators of DI, FA_{body}, MPAs and FA_{atd}, so that speculations about potentially differential associations between indicators of DI and mating success are not warranted based on our findings.

Still, DI may well be related to outcomes in other domains. For example, in a meta-analysis Banks, Batchelor and McDaniel (2010) showed an overall robust negative association between FA_{body} and general intelligence. Moreover, in their meta-analysis Van Dongen and Gangestad (2011) found small-to-medium-sized associations of FA_{body} with maternal risk factors for malicious fetal outcomes, the development of schizophrenia and associated personality variations (e.g., schizotypy), and facial attractiveness (the latter for facial FA only). Somewhat smaller effects were found for infectious diseases and other major illnesses, sexually dimorphic reproductive hormones (testosterone in men, estrogen in females) and masculine/feminine features. Comparing the relationships with different indicators of DI could provide an avenue to unravel at which developmental stages DI impacts such outcomes.

4.3 Strengths and limitations

This study had some considerable advantages compared to previous studies. First of all, for MPAs and FA_{body} we assessed a large number of traits (26 and twelve, respectively), whereas comparable studies on FA_{body} only used between six and ten traits (Gangestad & Thornhill, 1997b; Hughes, Harrison & Gallup Jr, 2002; Thornhill & Gangestad, 1994, 1999; Van Dongen, Cornille, & Lens, 2009; Van Dongen & Gangestad, 2011). Moreover, Van Dongen (2011) noted that most studies on FA and mating success used student samples. In our large sample, in contrast, only 59.5 % were students, rendering our findings more generalizable, at least within the young age range of our study (18-30 years). Finally, we took into account three indicators of DI to get a more complete picture. However, given that even aggregated FA measures estimate underlying DI only very imperfectly, further research in even larger samples and with FA_{body} composites of an even larger number of traits is required to clarify whether there is no significant association between FA and mating success, and a positive relationship for some of the mating outcomes in women. Concerning the study's limitations, firstly, we did not assess fitness outcome directly (i.e., reproductive outcome in terms of the number of children and grandchildren and their subsequent health and reproduction). Rather, we asked for our participants' mating success (both numbers of short-term and lifetime sexual partners), which is generally assumed to closely map the number of offspring individuals produced over human's evolutionary history, and hence a large part of biological fitness. In contemporary societies, however, this relationship might not be as direct anymore, due to contraceptive control and the prevalence of humans' extended sexuality (i.e., sexual activity not only during the fertile phase of females' menstrual cycle; Thornhill & Gangestad, 2008). Thus, we do not know participants' actual reproductive success.

Furthermore, regarding the mating success indicators such as the number of lifetime sexual partners, we used self-reported data. Such data have been shown to be slightly inaccurate in some cases, especially for men exaggerating their numbers of sexual partners (e.g., Smith, 1992). However, in our study no sex difference in reported lifetime sexual partners became apparent (men: M=7.35, women: *M*=7.52), suggesting that a large exaggeration by men, compared to women, is not present in our sample. Still, future research could aim at yielding more accurate numbers of sexual partners by explicitly asking participants to enumerate their sexual partners rather than giving a rough estimate (Brown & Sinclair, 1999).

While the sample of the current study was more representative than in prior studies, it was still restricted demographically. All participants reported prior sexual and romantic relationship experience, were unmarried, without children, and German native speakers. Thus, an increased variance in participants' prior sexual experience and current family status (e.g., being married and/or father or mother of a child) might have led to larger effects of FA_{body} on mating success (Lakes, 2013).

4.4 Conclusion

To conclude, in this study we examined the relationship between three presumed indicators of DI (FA_{body}, MPAs, FA_{atd}) and different facets of mating success, using a larger sample and more complete assessment and analysis of FA_{body} than most previous studies. A differential pattern for males and females with regards to the relationship between indicators of DI and the mating success measures emerged. Whereas more asymmetric women indicated higher numbers of lifetime sexual partners and one-night stands, but not EPCs or times having been an EPC partner, we found no significant relationship of FA_{body} with mating success in men. Thus, our results contradict previous findings of an inverse relationship of fluctuating asymmetry, and hence DI, with mating success (Gangestad & Simpson, 2000; Van Dongen & Gangestad, 2011). The positive findings for women similarly appear unexpected, since based on previous results we predicted either negative or null associations (Van Dongen & Gangestad, 2011). Nevertheless, equivalence tests revealed our effect sizes still to be in the ballpark of previously reported mean effect sizes of a negative association between FA_{body} and mating outcomes. At least for men’s number of lifetime sexual partners and one-night stands, as well as both men’s and women’s times having been an EPC partner, our effect sizes are not significantly different from previously reported mean effect sizes (Grebe, Falcon, & Gangestad, 2017; Van Dongen & Gangestad, 2011). Only for men's and women's number of EPC partners we provide evidence against a negative association with FA_{body}. Thus, further replication studies are warranted to examine whether effects are of smaller magnitude indeed (as in our study), or if our study represents a false negative (since, at least for men, effects were mostly statistically significant in previous studies). Two other indicators of developmental instability, minor physical anomalies and fluctuating asymmetry in palmar atd angles, were unrelated to mating success. However, it needs to be emphasized that our study was still slightly underpowered for finding associations with FA_{body}, despite its relatively large sample size compared to previous studies. Thus, further studies employing large samples and more highly aggregated measures of bodily fluctuating asymmetry are warranted for a clear picture of the association between developmental stability and human mating success.

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Online supplement

Table S1. Negative binomial models predicting the four mating success indicators from bodily fluctuating asymmetry (FA_{body}).

	Males				females			
	B	*SE*	*Exp(B)*	*p*	*B*	*SE*	*Exp(B)*	*p*
DV: lifetime sexual partners								
model 1	-0.14	0.16	0.87	.38	0.38	0.14	1.46	.01
model 2	-0.10	0.15	0.91	.52	0.33	0.14	1.40	.02
DV: one-night stands								
model 1	-0.45	0.30	0.63	.13	0.74	0.21	2.09	<.001
model 2	-0.33	0.27	0.72	.22	0.52	0.22	1.68	.02
DV: EPC partners								
model 1	0.10	0.40	1.10	.81	0.26	0.33	1.29	.43
model 2	0.14	0.40	1.15	.73	0.32	0.33	1.37	.33
DV: been an EPC								
model 1	-0.20	0.22	0.82	.36	0.91	0.29	2.48	.002
model 2	-0.29	0.22	0.75	.18	0.04	0.30	1.04	.89

Note: EPC = extra-pair copulation; model 1: only bodily fluctuating asymmetry (corrected for directional asymmetry by mean-centering FA values) as IV; model 2: additionally including age, BMI and relationship status; *N*=141 males, *N*=143 females.

Table S2. Negative binomial models predicting the four mating success indicators separately from minor physical anomalies (MPAs) and confounding variables.

	males				females			
	B	*SE*	*Exp(B)*	*p*	*B*	*SE*	*Exp(B)*	*p*
DV: lifetime sexual partners								
model 1	-0.01	0.04	0.99	.82	-0.06	0.04	0.95	.12
model 2	0.01	0.04	1.01	.87	-0.04	0.03	0.96	.21
DV: one-night stands								
model 1	-0.01	0.07	0.99	.93	-0.07	0.06	0.93	.27
model 2	0.04	0.07	1.04	.61	-0.05	0.06	0.95	.43
DV: EPC partners								
model 1	-0.04	0.09	0.97	.69	0.13	0.08	1.14	.11
model 2	-0.03	0.09	0.98	.78	0.12	0.08	1.13	.14
DV: been an EPC								
model 1	-0.10	0.08	0.91	.21	-0.03	0.09	0.97	.72

model 2	-0.06	0.06	0.94	.28	0.07	0.07	1.07	.32

Note: EPC = extra-pair copulation; model 1: MPAs as the only IV; model 2: additionally including age, BMI and relationship status; *N*=141 males, *N*=143 females.

Table S3. Negative binomial models predicting the four mating success indicators separately from fluctuating asymmetry in atd angles (FA_{atd}).

	males				females			
	B	*SE*	*Exp(B)*	*p*	*B*	*SE*	*Exp(B)*	*p*
DV: lifetime sexual partners								
model 1	0.01	0.01	1.01	.40	0.02	0.02	1.02	.29
model 2	0.01	0.01	1.01	.36	0.01	0.02	1.01	.76
DV: one-night stands								
model 1	-0.01	0.02	0.99	.59	0.04	0.03	1.04	.10
model 2	-0.01	0.02	0.99	.76	0.02	0.02	1.02	.41
DV: EPC partners								
model 1	0.01	0.04	1.01	.72	0.01	0.03	1.01	.81
model 2	0.02	0.04	1.02	.63	0.01	0.03	1.01	.88
DV: been an EPC								
model 1	0.00	0.02	1.00	.89	0.01	0.05	1.01	.79
model 2	0.00	0.02	1.00	.99	-0.05	0.04	0.96	.22

Note: EPC = extra-pair copulation; model 1: FA_{atd} as the only IV; model 2: additionally including age, BMI and relationship status; *n*=110-111 males, *n*=101-102 females.

S4. Sample conversion of odds ratios to Pearson correlation coefficients.

Odds ratios (*Exp(B)*) from our Negative Binomial models (model 2) were converted to Cohen's *d* and then to Pearson correlation coefficients using the following formula (Borenstein, Hedges, Higgins, & Rothstein, 2009):

$$d = LogOddsRatio \times \frac{\sqrt{3}}{\pi}$$

$$r = \frac{d}{\sqrt{d^2 + a}}$$

The correction factor α was set to 4, since equal sample sizes are assumed. Sample calculation for male participants and the dependent variable lifetime sexual partners:

LogOddsratio = log(0.62) = -0.21

d = -0.21 * $\frac{\sqrt{3}}{\pi}$ = -0.11

r = $\frac{-0.11}{\sqrt{-0.11^2+4}}$ = -0.05