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Sex ratio dynamics and fluctuating selection on personality

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ABSTRACT

Fluctuating selection has often been proposed as an explanation for the maintenance of genetic variation in personality. Here I argue that the temporal dynamics of the sex ratio can be a powerful source of fluctuating selection on personality traits, and develop this hypothesis with respect to humans. First, I review evidence that sex ratios modulate a wide range of social processes related to mating and parenting. Since most personality traits affect mating and parenting behavior, changes in the sex ratio can be expected to result in variable selection on personality. I then show that the temporal dynamics of the sex ratio are intrinsically characterized by fluctuations at various timescales. Finally, I address a number of evolutionary genetic challenges to the hypothesis. I conclude that the sex ratio hypothesis is a plausible explanation of genetic variation in human personality, and may be fruitfully applied to other species as well.

1. Introduction

Various theorists have pointed at balancing selection as a plausible explanation of genetic variation in personality (e.g., Figueredo et al., 2011; MacDonald, 1995; Nettle, 2005, 2006a, 2011; Penke et al., 2007; Wilson, 1998; Wolf et al., 2007, 2008). Balancing selection regimes – whereby the phenotype with the highest fitness changes at different times, in different places, or in different individuals – include heterozygote advantage, antagonistic pleiotropy, negative frequency-dependent selection, and spatial and temporal heterogeneity in environmental parameters.

Recurrent fluctuations in the environment can potentially affect a broad range of traits, and their impact on personality evolution has been demonstrated in nonhuman animals (e.g., Dingemanse et al., 2004; Dingemanse and Réale, 2005; Boon et al., 2007). The environmental factors that may give rise to fluctuating selection on personality include basic life history-related parameters such as environmental risk, predictability, and resource availability (see Ellis et al., 2009). These qualities of the environment can easily select for differences in specific personality traits; for example, a dangerous environment is likely to favor traits such as high anxiety and fearfulness (Nettle, 2011). At a larger scale, the behavioral correlations engendered by life history trade-offs (e.g., Belsky et al., 1991; Figueredo et al., 2005; Figueredo and Gladden, 2007; Stamps, 2007; Wolf et al., 2007) may give rise to selection for correlated variation in a broad cluster of traits, including mating styles, parental investment, risk-taking, status competition, aggression, and so on. More generally, behavioral traits that reinforce the effects of one another in a given context (*synergistic behaviors*; Nettle, 2011) should select for correlated variation in personality. Nomadism, migration, and variation in foraging tasks have been proposed as other sources of fluctuating selection on personality (Penke et al., 2007; Nettle, 2011).

So far, the environmental factors proposed in the literature mainly concern the *physical* environment; however, given the profound implications of personality traits for social interaction, it would also make sense to look for possible sources of fluctuating variation in the *social* environment. To qualify as a plausible source of fluctuating selection, a given feature of the social environment would need to show considerable heterogeneity, and a pattern of temporal change likely to select for genetic variation instead of (or in addition to) developmental plasticity. In this paper, I argue that the temporal dynamics of the sex ratio provide a plausible, pervasive source of fluctuating selection on personality. I call this the *sex ratio hypothesis* of personality evolution.

1.1. The sex ratio hypothesis of personality evolution

1.1.1. Sex ratios and animal behavior

Sex ratios play a crucial role in mating-related processes, and affect behavior in multiple, interconnected ways. The *adult sex ratio* (ASR; also called the *tertiary sex ratio*) is simply the ratio of adult males to adult females; the *operational sex ratio* (OSR) is defined as the ratio of sexually active males to receptive females in a population, or, alternatively, the ratio of male to female individuals that are "ready to mate" at a given time (Emlen and Oring, 1977; Clutton-Brock and Parker, 1992). Obviously, the OSR

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depends on the ASR; but while the ASR can be calculated in a straightforward way from population demographics, the OSR is affected by factors such as the mating system, the stability of pair-bonds, the potential reproductive rate of the two sexes, sex differences in maturation rates and reproductive longevity, and so on. In this paper, I use the generic term "sex ratio" to include both the ASR and the OSR.[1]

The OSR contributes to determine the intensity and type of competition for mates in a given population. As a general rule, the more abundant sex faces stronger competition for access to individuals of the opposite sex. In some species, changes in the OSR may induce sex role reversals, shifting the burden of mating competition from males to females and vice versa; in other species, sex roles remain fixed but the intensity of competition changes dramatically (Kvarnemo and Ahnesjö, 1996; Pettersson et al., 2004). In a recent meta-analysis, Weir and colleagues (2011) found that male-biased OSRs (>1) tend to (a) increase male–male competition (up to a value of about 2, after which the costs of competition may become too high and competition decreases); (b) decrease male courtship displays; and (c) increase female guarding by males in a range of nonhuman species.

Above and beyond this general pattern, the behavioral effects of sex ratios can change considerably depending on the details of a species' ecology. A key element is the presence of paternal care; if males can increase their fitness by caring for their offspring, the increased male competition engendered by high sex ratios can actually prompt males to *decrease* their mating effort and invest more in parental care (Kokko and Jennions, 2008). Also, responses to increased competition may involve delaying reproduction, so as to accumulate competitive skills and/or resources for future mating attempts. As I discuss in Section 2, the effects of sex ratios on human behavior seem to follow a complex pattern of this kind.

1.1.2. Logic of the sex ratio hypothesis

The logic of the sex ratio hypothesis is straightforward. Sex ratios strongly affect a wide range of social behaviors ultimately related to mating and parenting, in humans as well as other animals. Since many personality traits have direct implications for mating- and parenting-related processes, variable sex ratios are likely to exert multiple selective pressures on personality. The key insight is that, as I discuss in this paper, the temporal dynamics of the sex ratio are intrinsically characterized by fluctuations at various levels and timescales, potentially making the sex ratio a pervasive source of fluctuating selection on personality.

Some of the processes driving sex ratio fluctuations are quite general, while others depend on the specific features of a species' demography and mating system. Here I will identify five such processes: (a) the ASR is subject to stochastic fluctuations, which are especially strong in small populations of up to a few hundred individuals; (b) when mating age differs between the sexes, OSR fluctuations arise following population expansion and contraction; (c) changes in sex-specific mortality and dispersal can act as delayed feedback mechanisms, counteracting changes in the ASR after they take place; (d) shifts in life history-related behavior result in delayed negative feedback on the OSR, further reinforcing the fluctuating nature of sex ratio dynamics; and (e) oscillatory OSR dynamics can be amplified and destabilized when younger and older individuals compete with each other for mates.

In summary, the sex ratio hypothesis of personality evolution is the hypothesis that fluctuating selection driven by sex ratio dynamics contributes to explain the maintenance of genetic variation in personality. The extent to which the hypothesis applies to a given species depends on the strength and pervasiveness of sex ratio fluctuations, as well as other factors (such as the presence of overlapping generations with multiple life stages) that make it more or less tenable from the evolutionary genetic standpoint.

1.1.3. Challenges to fluctuating selection models

While explanations invoking fluctuating selection are intuitively powerful, they are not without problems. To begin with, a classic finding of evolutionary genetic models is that temporally fluctuating selection is much less effective than *spatially* variable selection in maintaining genetic polymorphism (Frank and Slatkin, 1990). Thus, there is no guarantee that sex ratio dynamics will be able to maintain a significant amount of genetic variation in a given species.

In humans, fluctuating selection models must overcome a number of additional empirical challenges. Human personality traits are moderately heritable (typically in the 0.30–0.60 range; Plomin et al., 2008); however, they appear to lack the genetic signatures one would expect from balancing selection regimes (Penke et al., 2007; Miller, 2011). Mathematical models indicate that balancing selection should typically result in asymmetric genetic architectures, whereby most of the trait variance is controlled by a small number of polymorphic genes of moderate to large phenotypic effects. Moreover, genetic polymorphism should be limited to relatively few alleles at intermediate frequencies (Bürger, 2002a,b; Turelli and Barton, 2004; Keller and Miller, 2006; Kopp and Hermisson, 2006; Van Doorn and Dieckman, 2007). As I discuss later (Section 4), these predictions should not be taken as "iron rules", since they depend on assumptions that may or may not hold in real organisms. Granting them for now, it is noteworthy that molecular genetic research has clearly failed to identify major single-gene effects on personality traits (e.g., Munafò et al., 2003; Shifman et al., 2007; Gillespie et al., 2008; Terracciano et al., 2008; de Moor et al., 2010; Verweij et al., 2010). Taken together, these results are highly consistent with a lack of major-effect genes, although the many copy number variations (CNVs) recently discovered in the human genome may eventually explain a larger portion of heritability than single-nucleotide variants (see Gangestad, 2010, 2011).

The lack of major-effect genes is not the only empirical stumbling block for balancing selection models. The first genome-wide searches for polymorphic genes with moderate-frequency alleles – the other expected signature of balancing selection – yielded largely negative results (Bubb et al., 2006), suggesting that long-term balancing selection has been rare in human evolution. This type of analysis, however, suffers from low detection power, and a more recent study has identified dozens of genes displaying strong signatures of long-term balancing selection (Andrés et al., 2009). In the next few years, improved methodology and larger samples are likely to yield more results of this kind. The negative results of early studies, and especially the apparent lack of major-effect genes, have led some (notably Miller, 2011) to forcefully question the plausibility of balancing selection accounts of personality evolution.

1.2. Overview of the paper

In the remainder of the paper, I apply the logic of the sex ratio hypothesis to the evolution of human personality. On the one hand, the decision to focus on humans reflects my own research interest in evolutionary psychology; on the other hand, the life

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[1] This paper is not concerned with the *primary sex ratio* (i.e., the sex ratio at conception) nor with the *secondary sex ratio* (i.e., the sex ratio at birth).

history and demographic characteristics of the human species make it an especially good candidate for the sex ratio hypothesis. Readers whose primary interests lie in other species should treat the following sections as an extended "case study."

In Section 2, I review evidence that the sex ratio is a powerful determinant of human social behavior. I also argue that most personality traits have important implications for mating and parenting, and are thus likely to undergo variable selective pressures as sex ratios changes over time. Since empirical studies of natural selection on human personality are extremely sparse (Eaves et al., 1990; Alvergne et al., 2010; Jokela et al., 2011), Section 2 has the form of a plausibility argument rather than a watertight demonstration. In Section 3, I discuss the main sources of sex ratio fluctuation in humans, and use a simple simulation approach to quantify the strength of stochastic sex ratio fluctuations in ancestral human populations. In Section 4, I address the main theoretical and empirical challenges to fluctuation selection models, and argue that the sex ratio hypothesis stands as a plausible explanation of genetic variation in human personality. In the conclusion, I briefly consider how the hypothesis might apply to non-human species, and suggest directions for future research.

2. Sex ratios and personality in humans

2.1. Sex ratios and human behavior

2.1.1. Social and behavioral outcomes

The first systematic analysis of the role of sex ratios in human behavior was performed by Guttentag and Secord (1983) in a sociological perspective. In Guttentag and Secord's analysis, the rarer sex enjoys increased bargaining power on the mating market ("dyadic power"), and can thus obtain its preferred type of relationship from the other sex. In female-biased populations (low sex ratio), men should become reluctant to commit to marriage; divorce rates are predicted to increase, together with casual sexual relationships and births outside marriage. On the contrary, in male-biased populations (high sex ratio) women can obtain higher commitment from men, resulting in earlier marriage, high relationship stability, and low divorce rates, especially if men maintain privileged access to valuable resources ("structural power" in the authors' terminology).

Pedersen (1991) reframed Guttentag and Secord's analysis in the context of sexual selection theory. In an evolutionary framework, biased sex ratios simultaneously modulate the intensity of mating competition and the constraints on mate choice faced by the two sexes. For example, a high sex ratio constrains men's mate choices and, at the same time, intensifies some aspects of male–male competition. Pedersen (1991) made several additional predictions concerning the effects of biased sex ratios. Low sex ratios should encourage permissive sexual mores, striving for economic independence by women, and increased engagement by women in health-promoting and appearance-enhancing behaviors (i.e., behaviors that increase female mate value). In contrast, high sex ratios should lead to greater resource provision and engagement in parenting activities by men, increased fertility, and higher levels of male violence. Male violence in high sex ratio societies can be directed towards other men, but also towards women; for example, a large proportion of unmated men can increase the incidence of rape, and marital violence may increase as a form of mate guarding. Note that male competition can also take place *between* social groups; indeed, high sex ratios are associated with a higher likelihood of war in pre-agricultural human groups (Divale and Harris, 1976).

Empirical research has supported the main predictions of Guttentag and Secord (1983) and Pedersen (1991); furthermore, later studies have extended and refined the theory, and we now have a fairly detailed understanding of the effects of sex ratio changes in human populations. Both male-biased and female-biased sex ratios can increase violence and crime, although for different reasons. High sex ratios clearly increase male competition, bust most of the competition may take place by *indirect* means (e.g., by gaining access to economic resources; Barber, 2009). Indeed, in male-biased environments violence and aggression can be expected to be strongly condition-dependent: most of the violence should come from unmated men of low status, rather than from high-status men who are able to find a partner and marry. Also, part of the violence in high sex ratio contexts may simply depend on having more young males around (Messner and Sampson, 1991). Whatever the causal pathways, high sex ratio at maturity has been found to predict higher male mortality in the US (Jin et al., 2010). A longitudinal study of sex ratio variation in three English-speaking nations (Barber, 2003) found that violent crime was predicted by high sex ratios.[2]

Female-biased sex ratios tend to decrease relationship commitment and increase sexual promiscuity; this is expected to increase *direct* mating competition among men, with a predictable increase in violent crime (Barber, 2011). Furthermore, marital instability and family disruption can shift children's development toward antisocial trajectories (Messner and Sampson, 1991; Barber, 2001; see also Avakame, 1999; O'Brien, 1991). Accordingly, several studies have found cross-national associations between low sex ratios and higher rates of violent crime (see Barber, 2000, 2009, 2011). At least in modern societies, the net effect of low sex ratios seems to be that of increasing male violence.

The effects of sex ratio variation on mating and marriage are also complex, but consistent with a sexual selection framework. Studies of US cities show that, where the sex ratio is low, men are less likely to marry when they are young but *more* likely to marry when they get older, indicating that they are deferring long-term commitment in the pursuit of short-term mating (Kruger and Schlemmer, 2009a, b). High sex ratios correlate with earlier age at marriage for women, but not for men; however, male *variance* in marital age increases (Kruger et al., 2010; see also South, 1996). This suggests the simultaneous action of two distinct effects: in high sex ratio populations, men are willing to marry younger; however, women become choosier with respect to status and wealth, which ends up favoring older men. Indeed, a study of US states showed that, where sex ratios are male-biased, the positive effect of socioeconomic status on male marriage prospects increases considerably (Pollet and Nettle, 2008). In other words, men with lower SES may have an especially difficult time finding a marriage partner in male-biased environments. This conclusion is further supported by the results of a US study by Lichter and colleagues (1995), showing that a high sex ratio increased women's odds of marrying a high-status man rather than a low-status one. Another finding consistent with Pedersen's predictions is that, across US cities, low sex ratios are associated with higher proportions of women in high-paying careers (Durante et al., in press).

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[2] Barber (2003) computed two variables: (a) the sex ratio of individuals aged 15–44, and (b) a measure of "marital opportunity of women", i.e., the ratio of single men to women at peak age of marriage. The former correlated positively, and the latter negatively, with violent crime. The "marital opportunity" variable exhibited a strong negative correlation with the sex ratio variable (from -0.46 to -0.70), and its precise meaning can be questioned. A reasonable alternative interpretation is that a high ratio of single men to women at the typical age of marriage actually reflects male non-commitment, possibly driven by low OSR, rather than increased marital opportunity.

In foraging societies, and in modern societies until recently, low sex ratios are associated with relationship instability and higher divorce rates (Guttentag and Secord, 1983; Trent and South, 1989; Pedersen, 1991; Blurton Jones et al., 2000). In contrast, a US study by South and Lloyd (1992) showed higher divorce rates (as well as higher marriage rates) in *male*-biased environments. In contemporary Western societies, women have unprecedented control over economic resources, and divorce can be initiated by women as well as men (see Guttentag and Secord, 1983, pp. 233–239); when many men are available as potential marriage partners, women may marry early, but then divorce easily if the opportunity to secure a better mate arises (see Kruger et al., 2010). Finally, high sex ratios generally predict a lower incidence of teen pregnancies (Barber, 2001), although the evidence is somewhat mixed (South, 1996; discussed in Barber, 2001).

2.1.2. Psychological processes

Whereas most studies of sex ratio focus on behavioral outcomes (such as violence, marriage, and divorce), some researchers have started to investigate the psychological processes that mediate behavioral responses to sex ratio variation. Schmitt (2005) showed that, across nations, high sex ratios predict restricted sociosexuality (i.e., lower interest in, and pursuit of, short-term mating with multiple partners). This result was replicated, albeit with a smaller effect size, in an Internet-based study by Lippa (2010, p. 648).

Stone et al. (2007) correlated cross-national sex ratios with self-reported preferences for long-term mates; they found that, in male-biased countries, both males and females tend to report less stringent mate choice criteria, with the exception of women placing a higher value on male chastity. Although the result for chastity is consistent with a sexual selection perspective, the general finding of relaxed mate choice criteria by women in high sex ratio environments goes against expectations, and is inconsistent with the evidence that high sex ratios favor high-status men (Lichter et al., 1995; Pollet and Nettle, 2008; Kruger et al., 2010). Further research is needed to resolve this contradiction.

Finally, two recent studies investigated real-time psychological responses to experimentally manipulated perceptions of the local sex ratio. Decreasing the perceived sex ratio led females to increase their preferences for high-paying careers, and to prioritize career relative to family. The same shift was observed in males when *increasing* the perceived SR. Moreover, the effect was more pronounced in males of high self-perceived mate value and women of *low* self-perceived mate value (Durante et al., in press). Taken together, these findings suggest that males in high sex ratio contexts prioritize career as a response to increased mate competition, whereas females in low sex ratio contexts prioritize career as a way to economically support themselves and their future family. In another study, increasing the perceived sex ratio led males (but not females) to prefer immediate over delayed monetary rewards, decreased their motivation to save money, and increased their motivation to borrow money. Moreover, both sexes expected males to spend more for courtship when the perceived sex ratio was male-biased (Griskevicius et al., in press). These findings suggest that young, unmarried men (such as the students tested in the experiments) may respond to increased mate competition by spending more resources in order to attract a romantic partner; it is likely that the results would be quite different were the study replicated in samples of older, married men. Although more studies of this kind are needed, and should be performed in different socioeconomic contexts and different cultures, the fine-grained experimental study of the psychological effects of sex ratios is a promising research avenue.

2.1.3. A note on measurement

Obtaining a faithful measure of the OSR in human populations is a daunting task. Strictly speaking, calculating the OSR would require researchers to know the reproductive and relational status of each individual at a given point in time; thus, all the empirical studies so far have employed approximate measures of the OSR, which are often closer to the ASR. As noted by Kokko and Jennions (2008), this frequently happens in studies of other species as well. A typical way of approximating the OSR is to put an upper age limit on the ASR, in order to exclude non-reproductive older individuals. I propose to label this index the *reproductive adult sex ratio* (RASR), so as to distinguish it from the OSR proper. Age brackets for the RASR typically go from 15–44 years to 15–59 years (e.g., Barber, 2003; Messner and Sampson, 1991; Stone et al., 2007; Kruger et al., 2010). Closer to the original definition of the OSR, Kruger and colleagues (2010) operationalized it as the ratio of unmarried men to unmarried women aged 18–64. In a study of sex ratios in hunter-gatherers, Blurton Jones and colleagues (2000) calculated the ratio of men aged 20–55 to females aged 15–40, that is, a variation on the RASR; in addition, they followed Hurtado and Hill (1992) and derived a measure of “fertility units per male” (FU/m) by multiplying the RASR by the total fertility rate. This derived measure tracks the potential reproductive benefits for males who desert their current partner, thus capturing some of the implications of the OSR better than the RASR alone (Blurton Jones et al., 2000, p. 87). Future research in this area would benefit from increased precision in terminology; researchers should explicitly state whether they measured the ASR, the RASR, the OSR, or some approximation of the latter.

2.2. Sex ratios and selection on personality traits

The evidence just reviewed shows that sex ratio variation powerfully modulates the social dynamics of human groups. Male-biased and female-biased sex ratio contexts tend to favor different patterns of behavior, and can be expected to increase the reproductive fitness of individuals whose behavioral dispositions are consistent with the local sex ratio. When the sex ratio is male-biased, there are fewer mating opportunities for men, and marriage becomes the royal road to reproductive success; restricted sociosexuality, relationship stability and long-term commitment should be favored in both sexes. Furthermore, some aspects of social competitiveness and status-seeking (particularly those concerned with resource accumulation) should be favored in men, as they improve the likelihood of becoming a desirable marriage partner. As the stability of pair-bonds increases and sociosexuality becomes more restricted, there is also a premium on high paternal investment; indeed, couple stability is one of the strongest predictors of reliable investment in human fathers (see Furstenberg and Nord, 1985; Betzig, 1989; Draper, 1989; Anderson, 2011). In contrast, female-biased sex ratios open up many opportunities for short-term mating, increase female competition for attractive sexual partners, and favor unrestricted sociosexuality and low relationship stability in both sexes. Accordingly, the expected return of paternal investment should decrease, favoring behavioral dispositions that promote reduced investment and faithfulness in men. Of course, this general pattern of selection pressures will not act uniformly on the whole population; both assortative mating and behavioral trade-offs are likely to create adaptive niches for individuals with a range of different dispositions. Still, the net effect of selection can be expected to reverse sign when a population shifts from high to low sex ratio and vice versa.

Individual behavior can match sex ratio variation in at least four different ways. First of all, people clearly respond in real time to perceived sex ratio variation, as shown by the experimental studies described in Section 2.1; such contingent, rapid changes in behavioral dispositions may be called *adaptive conditional adjustments* (Penke, 2011). Second, mechanisms of adaptive developmental plasticity (West-Eberhard, 2003; Hagen and Hammerstein, 2005) can adaptively match children's developmental trajectories to their local environment. If the sex ratio is stable enough, a child can use the sex ratio observed during the first years of life (and/or its consequences, for example family stability) to estimate the one he/she will likely encounter at sexual maturity, about ten years in the future. Third, stochastic bet-hedging may be favored when the environment is difficult to predict (Svardal et al., 2011). Fourth and most relevant to the present paper, sex ratio fluctuations are likely to exert directional selective pressures on stable, genetically influenced personality traits, thus leading to changes in gene frequencies across generations. These options are not mutually exclusive; even among plastic individuals, those with an additional tendency to display higher levels of a favored trait (i.e., with upward-shifted developmental reaction norms) will, on average, enjoy increased reproductive success. Furthermore, people differ considerably in their level of plasticity (Belsky and Pluess, 2009; Ellis et al., 2011); in the less plastic share of the population, genetic selection on personality traits is likely to be stronger and to elicit a faster directional response.

2.2.1. *The mating–parenting trade-off as an organizing principle*

Male-biased and female-biased environments favor different patterns of behavior in a number of related areas, including short-term mating and sociosexuality; long-term commitment and couple stability; status- and resource-seeking; resource provisioning and parenting effort; and intra- and intersexual aggression. Crucially, most of these behaviors can be seen as manifestations of individual differences in life history strategy, and specifically in the *mating–parenting* trade-off (Figueredo et al., 2004; Penke, 2011; Wolf et al., 2007).

When interpreted in a narrow sense, life history strategies concern traits such as maturation timing, age at first reproduction, number and quality of offspring, and so forth. In social species, however, the key life history trade-offs (current versus future reproduction, quality versus quantity of offspring, and mating versus parenting effort) can be expected to affect a much broader range of traits and behaviors. For example, males engaging in early reproduction and high mating effort typically require a highly competitive disposition, heightened status-seeking, and considerable investment in attractive traits and displays. In addition, the trade-off between current and future reproduction engenders correlated variation in risk-related traits such as boldness and aggression (Wolf et al., 2007). In humans, the correlated traits that can be ultimately connected to life history strategies include impulsivity and risk-taking, relationship stability, and sociosexuality, but also cooperativeness, altruism, and so forth (see Figueredo et al., 2004, 2005, 2007; Figueredo and Jacobs, 2010).

In humans, low sex ratios favor increased mating effort, whereas high sex ratios favor increased parenting effort. This behavioral shift is observed in both sexes (Section 2.1), even if the specifics (as well as the overall mating–parenting balance) can differ between men and women. The main behavioral correlates of mating-oriented life history strategies are unrestricted sociosexuality and sexual promiscuity, reduced commitment in long-term relationships, couple instability, and low parental involvement. Parenting-oriented strategies are marked by restricted sociosexuality, commitment in long-term relationships, couple stability, and high parental involvement. Of course there are substantial sex differences in the costs and benefits associated with this trade-off, and men tend to invest more than women in mating effort, especially when they are attractive as partners and control lots of resources (Heath and Hadley, 1998; Geary, 2002, 2005; Schmitt, 2005; Penke, 2011).

2.2.2. *Personality traits and the mating versus parenting trade-off*

In humans, most personality traits are functionally linked to the mating versus parenting trade-off. The most widely adopted taxonomy of personality traits is the *five-factor model* (Costa and McCrae, 1995). The broad traits described by the five-factor model are *extraversion*, *neuroticism* (i.e., emotional instability), *conscientiousness*, *agreeableness*, and *openness to experience*, collectively known as the "Big Five." Cross-culturally, extraversion correlates with unrestricted sociosexuality, and consistently predicts short-term mating success, relationship instability, and cheating (Schmitt and Buss, 2000; Nettle, 2005; Orzeck and Lung, 2005; Markey and Markey, 2007; Schmitt and Shackelford, 2008). The opposite holds for agreeableness and conscientiousness (Schmitt and Buss, 2000; Schmitt, 2004; Schmitt and Shackelford, 2008). Moreover, high extraversion and low agreeableness are associated with dominance, antisocial tendencies, and risk-taking (Wiebe, 2004; Nettle, 2007; Ashton et al., 2010). These findings can be better understood by noting that, in the five-factor model, extraversion is a heterogeneous factor, involving facets related to dominance and venturesomeness as well as traits related to warmth and affiliation (Lucas et al., 2000). MacDonald (1995, 2005) has argued that, from an evolutionary and neurobiological standpoint, a more meaningful factorial solution can be obtained by rotating agreeableness and extraversion to yield a *dominance/sensation seeking* factor and a *nurturance/love* factor. Dominance/sensation seeking would then predict short-term mating, sexual promiscuity, dominance, risk-taking, and antisocial tendencies, thus capturing the association of these variables with extraversion and agreeableness (MacDonald, 1995, 2005; see also Linton and Wiener, 2001).

Cross-culturally, openness tends to correlate with short-term mating interests and behaviors, although a study by Schmitt and Shackelford (2008) showed a sex-specific effect in North America, with openness increasing short-term mating in women but decreasing it in men. However, the effects of openness may be confounded with those of *schizotypy* (i.e., proneness to psychotic-like symptoms), a trait that positively correlates with openness, although the exact functional relation between the two is still unclear (see Nettle, 2011; Watson et al., 2008). Positive schizotypy (characterized by unusual cognitive and perceptual experiences, magical ideation, and reference/paranoid thoughts) and openness predict artistic creativity as well as larger numbers of sexual partners (Haselton and Miller, 2006; Nettle, 2006b; Nettle and Clegg, 2006; Miller and Tal, 2007; Rawlings and Locarnini, 2008). Positive schizotypy is also associated with unrestricted sociosexuality and reduced investment in long-term couple relationships (Del Giudice et al., 2010). The last of the Big Five traits, neuroticism, tends to be associated with increased short-term mating in women but reduced short-term mating in men, although there are national differences in this respect (Schmitt and Shackelford, 2008). Personality traits are also good predictors of divorce: high neuroticism, low conscientiousness, and (to a smaller extent) low agreeableness all contribute to increase the likelihood of divorce in married couples (Bentler and Newcomb, 1978; Kelly and Conley, 1987).

The Big Five and schizotypy are not the only traits relevant to the mating versus parenting trade-off. For example, a recent study (Del Giudice et al., 2010) showed that *autistic-like traits* predict reduced interest in short-term mating and higher investment in long-term couple relationships. The personality traits of the "dark triad" (*narcissism*, *psychopathy*, and *Machiavellianism*) also consistently predict short-term mating and sexual promiscuity in addition to antisocial tendencies (Jonason et al., 2009). Finally, the *honesty–humility* trait in the six-factor HEXACO model (Ashton and Lee, 2007, 2008) exhibits strong negative correlations with the dark triad (Ashton et al., 2000), and is associated with restricted sociosexuality, low seductiveness, relationship exclusivity, and reduced risk-taking (Lee et al., 2005; Bourdage et al., 2007; Ashton et al., 2010).

2.2.3. Higher-order personality factors

Although they are often treated as orthogonal dimensions, personality traits are in fact moderately correlated with one another. The Big Five tend to cluster in two higher-order factors (Digman, 1997; DeYoung, 2006) called *alpha* or *stability* (high conscientiousness and agreeableness, low neuroticism) and *beta* or *plasticity* (high extraversion and openness). At the top of the personality hierarchy, a *general factor of personality* (GFP) can be identified (Musek, 2007). The GFP is currently the subject of a heated methodological debate, and there is still no consensus in the literature as to whether it represents a methodological artifact or a real feature of human personality (see Just, 2011; Rushton and Irwing, 2011). The GFP represents a socially desirable personality profile characterized by high sociability and stable, positive emotionality.[3] Agreeableness, conscientiousness, extraversion, and openness have positive loadings on the GFP, whereas neuroticism has a negative loading. Like other personality traits (Gangestad, 2010, 2011), the GFP is substantially heritable, and displays a certain amount of non-additive genetic variance in most studies (Just, 2011; but see Loehlin and Martin, 2011). While not diagnostic, this finding is at least consistent with a history of fluctuating selection.[4] The GFP has been proposed as a correlate of slow life history strategies and high parenting effort (Rushton et al., 2008; Rushton and Irwing, 2011); indeed, the *K-factor* (a measure of the behavioral correlates of slow life history strategies in humans) shows moderate correlations with the GFP (Dunkel and Decker, 2010; Olderbak and Figueredo, 2010), and both load on a single “super-factor” that accounts for their shared genetic variance (Figueredo et al., 2007; Figueredo and Rushton, 2009). Interestingly, attempts to recover the GFP from personality ratings of nonhuman primates have failed so far (Weiss et al., 2011).

How do these higher-level personality factors relate to sex ratio variation? Male-biased environments should favor parenting effort and, consequently, higher levels of the GFP, while female-biased environments should favor lower GFP levels. A problem arises, however, with the mating-oriented correlates of extraversion and openness, two traits that load positively on the GFP (and beta). A possible solution lies in the fact that both extraversion and openness are Janus-faced traits composed of functionally distinct facets. The two components of extraversion discussed above (dominance/venturesomeness and warmth/affiliation) are clearly functional to different types of strategy. Likewise, openness has two main components, *intellect* and *imagination* (see Nettle, 2011); only the latter is associated with schizotypy and, consequently, with short-term mating tendencies. Thus, only some facets of extraversion and openness may actually load on the GFP and be selected for in male-biased environments. Similarly, alpha is likely to be consistently selected for in male-biased environments (and selected against in female-biased environments); in contrast, only some facets of beta (i.e., those associated with increased parenting effort) can be expected to follow this pattern.

3. Fluctuating sex ratio dynamics in human populations

3.1. Stochastic ASR fluctuations

Every time a child is conceived, its sex is the outcome of a largely stochastic process. In the long run, the human sex ratio at birth (or *secondary sex ratio*) converges to a value close to one (1.05 is a typical estimate), but large deviations from one can be expected in the short run. In small populations, stochastic fluctuations in the sex ratio at birth can substantially shift the ASR in either direction. This is the most basic source of fluctuation in the sex ratio, and one that becomes more powerful as the population size gets smaller. Since humans have lived in relatively small groups until a few millennia ago, stochastic ASR fluctuations must have played a major role in the course of human evolution.

3.1.1. The size of human populations

In order to quantify the impact of stochastic fluctuations on sex ratio dynamics, one needs a reasonable estimate of the modal population size. How large was the typical ancestral population of *Homo sapiens*? Based on studies of modern foragers, Birdsell (1973) proposed the tribe as the basic human demographic unit or *deme* (i.e., a local population of individuals that interbreed and share the same gene pool), with an estimated modal size of about 500 individuals. Birdsell’s estimate was used by Eller et al. (2004) to model human population size in the Pleistocene. Dunbar (1993) and Aiello and Dunbar (1993) showed that, in foragers and horticulturalists, it is usually possible to identify three levels of social organization: the band (30–50 individuals), the tribe (500–2500 individuals), and an intermediate level of about 100–200 individuals, often organized in a clan or village. Tribes are often defined by linguistic homogeneity (Dunbar, 1993), but a given member is unlikely to have access to every opposite-sex member of the tribe as a potential mate, because of limits imposed by marriage rules, kinship, and geographic distance. Thus, the typical deme size of ancestral humans ought to lie between that of the clan/village (100–200) and that of Dunbar’s tribe (500–2,500). Finally, Wobst (1974) described a model of the human “maximum band”, defined as a marriage network composed of loosely interlocking bands (a close approximation of the human deme). By applying realistic demographic constraints to the model, Wobst found that the *minimum* size of a maximum band should lie between about 175 and 475 individuals, depending on the mating system (e.g., monogamy vs. polygyny) and other demographic factors. Taken together, these studies converge in indicating 500 as a good estimate of the modal population size, with 250 and 1000 as reasonable bounds accounting for phases of population growth and shrinkage.

3.1.2. A simulation of stochastic ASR fluctuations

Having estimated the typical population size in human evolution, the stochastic component of sex ratio fluctuations can be quantified with the help of a simple simulation model (see the Appendix for details). The model simulates a population of constant size, in which age-specific mortality rates reflect those observed in hunter-gatherer populations (Denham, 1974; Weiss, 1973). At each iteration, the sex of new population members is randomly determined (assuming an even sex ratio at maturity), and the ratio of individuals aged 15–49 (i.e., the RASR; see Section 2.1) is computed.

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[3] Note that it would be a fallacy to assume that, just because high levels of the GFP are socially desirable, the GFP must be an artifact caused by socially desirable responding. For example, Uziel (2010) reviewed evidence that people who score high in “impression management” scales (typically assumed to measure socially desirable response styles) *are* in fact more prosocial, emotionally stable, and socially skilled than low scorers. For further discussion of this issue see Figueredo et al. (2011) and Just (2011).

[4] The presence of non-additive genetic variance is not a diagnostic signature of balancing selection; it is also consistent with a history of strong directional selection, as originally hypothesized for the GFP by Rushton et al. (2008). See Keller et al. (2011).

A generation is assumed to last 25 years, as a compromise between the typical estimate of 20–25 years (Fenner, 2005) and the more recent estimate of about 30 years advanced by Matsumura and Foster (2008). As is typical in hunter-gatherer populations, the male:female mortality ratio between 15 and 49 years of age is set at 1.5 (Hill and Hurtado, 1996; Kruger and Nesse, 2006). Predictably, this level of male-biased mortality results in a decidedly female-biased RASR (about 0.80 on average); however, it should be noted that the focus of the simulation is not the average SR value, but rather the pattern of sex ratio change across generations. The RASR is only an approximation of the OSR, and the exact relation between the two depends on several factors, including the mating system; for example, even a female-biased RASR can translate into a male-biased OSR in a highly polygynous society.

Simulation results show that, with a population size of 500, the mean absolute change in RASR from one generation to the next is $\Delta=0.11$, with 90% of changes lying between -0.23 and $+0.23$. For $N=250$, the mean absolute change increases to $\Delta=0.16$, with 90% of changes lying between -0.33 and $+0.33$; whereas for $N=1000$, $\Delta=0.08$, and 90% of the distribution lies between -0.16 and $+0.16$. These are not trivial fluctuations; especially in populations of small to average size ($N=250$–500), the RASR can change considerably from one generation to the next, and can shift from significantly male-biased to significantly female-biased in the span of two or three generations. Fig. 1a shows RASR changes across 50 generations in a typical simulation; the unpredictably fluctuating dynamics of the RASR are clearly visible. Fig. 1b shows sex ratio fluctuations at a finer scale, highlighting the balance between stability and change within the span of a single generation.

A complementary tool for quantifying sex ratio stability is provided by r_g, the autocorrelation of the RASR with a lag of one generation (25 years). In the present simulation, $r_g=0.16$ regardless of population size. Thus, stochastic fluctuations make the sex ratio change rather unpredictably from one generation to the next. Another useful statistic is r_d, the autocorrelation of the RASR with a lag of 10 years, that is, the approximate developmental interval between the end of early childhood and the attainment of reproductive maturity. The r_d statistic is important because it constrains the evolution of adaptive developmental plasticity; an individual can use the sex ratio observed in childhood as an estimate of the sex ratio he/she will face at maturity only if the correlation between the two is sufficiently large. In this simulation, $r_d=0.56$, regardless of population size; thus, the sex ratio experienced in childhood provides a moderately valid (but far from perfect) estimate of the expected sex ratio at sexual maturity. In other words, the stability of the sex ratio within a single generation is sufficiently strong (i.e., there is enough short-term inertia) that developmental plasticity can potentially evolve in addition to the potential for immediate conditional adjustment (Section 2.2). At the same time, it is not so strong that it precludes genetic selection on the relevant personality traits.

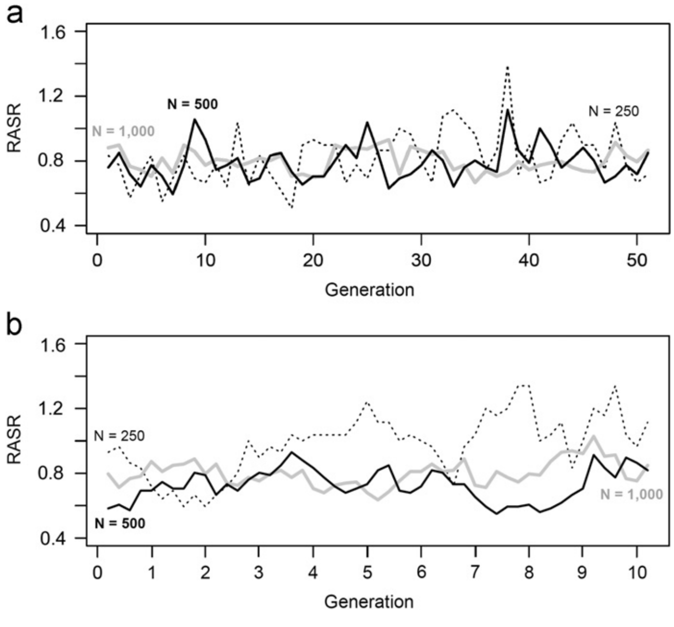

Fig. 1. Stochastic sex ratio fluctuations in a typical simulation, shown for three human populations of different size. Panel (a) shows 50 generations, with a resolution of 1 generation; panel (b) shows 10 generations, with a resolution of 5 years. RASR: reproductive adult sex ratio (15–49 years). *Note*: generation time is set at 25 years, and the male:female adult mortality ratio is fixed at 1.5. See Appendix for details.

I performed a sensitivity analysis to explore the effects of age distribution on the simulation results. Simulations were re-run with a more bottom-heavy distribution (higher proportions of younger people) and with a more top-heavy distribution (higher proportions of older people; see the Appendix for details). Age distribution had little effect on the mean absolute change (Δ), which stayed within ± 0.01 of the original values. Predictably, the effect on autocorrelations was more apparent, although it did not alter the qualitative pattern of results: with the bottom-heavy distribution, $r_g=0.11$ and $r_d=0.48$; whereas with the top-heavy distribution, $r_g=0.20$ and $r_d=0.64$.

3.2. Demographic fluctuations affecting the OSR

The simulation presented above assumes a population of constant size, so as to isolate the contribution of stochastic fluctuations. When population size varies, however, additional sources of fluctuation come into play. Because of universal sex differences in the preferred age of mates, and the associated sex differences in age at marriage (e.g., Buss, 1989; Kenrick and Keefe, 1992; Kenrick et al., 1996), human females enter the mating market a few years before their male peers. Thus, phases of demographic expansion produce an excess of marriageable women and a shortage of marriageable men as "baby boom" children grow up, resulting in a decrease in the population OSR. Conversely, demographic contraction results in an excess of marriageable men and increased population OSR (Pedersen, 1991). In this way, fluctuations in population size are translated into OSR fluctuations with a delay of one-two decades. Cycles of population expansion and contraction determine cyclical changes in the OSR, possibly extending across several generations. Also, demographic expansion and contraction alter the age distribution of the population, making it more bottom-heavy (expansion) or top-heavy (contraction); as shown in Section 3.1, this is expected to affect the autocorrelation parameters of stochastic RASR fluctuations.

3.3. Mating competition between age groups and OSR oscillations

Caswell and Weeks (1986) developed a sophisticated model of human population dynamics, taking into account a number of demographic constraints, including sex differences in maturation and mortality rates. In this model, the ASR converges to a stable equilibrium value if there is no mating competition between age groups—a highly unrealistic assumption. When Caswell and Weeks allowed for mating competition between individuals in different age groups, the equilibrium was destabilized, often resulting in strong oscillatory sex ratio dynamics. Oscillations could be periodic, quasi-periodic or chaotic, depending on the intensity of mating competition and other parameters in the model. These results suggest that mating competition between individuals in different age groups tends to drive the sex ratio out of equilibrium, which may result in sustained oscillatory dynamics.

3.4. Negative feedback on the ASR via sex-specific mortality and dispersal

As noted above (Section 2.1), high sex ratios can increase some forms of intrasexual male violence and – even more importantly – predict the occurrence of war in traditional societies. Conflict between groups leads to increased male mortality, thus acting as negative feedback mechanisms on the ASR. Increases in male mortality can be expected to follow increases in ASR with a delay of a few years, allowing for competition to build up and for intergroup tensions to accumulate. Another possible outcome of heightened competition is sex-specific dispersal; when the prospects for mating are dire, some individuals of the more abundant sex may leave their deme and migrate to other demes with better mating opportunities. From the standpoint of the ASR, the outcome would be equivalent to that of increased mortality. Whereas the long-term effect of delayed negative feedback on the sex ratio is a stabilizing one, its short-term effect is to make the sex ratio fluctuate, as change in one direction induces a delayed reaction of opposite sign. As long as "pulses" of sex ratio change are constantly supplied by other mechanisms (such as stochastic fluctuations and demographic changes), delayed negative feedback cannot extinguish sex ratio oscillations by progressively dampening them, and instead results in increased short-term fluctuations.

The simulation presented in Section 3.1 can be modified so that the male:female mortality ratio at a given time depends on the RASR at the previous iteration (i.e., five years earlier in simulation time). Introducing sex ratio-dependent mortality has small effects on between-generation changes in RASR, but results in substantially lower autocorrelation values. As an example, consider a population $N=500$ in which the male:female mortality ratio linearly depends on the RASR (so that a RASR of 1.2 at T_i results in a m:f mortality ratio of 2 at T_{i+1}, and a RASR of 0.4 at T_i results in a m:f mortality ratio of 1 at T_{i+1}). In this population, the mean absolute change in the RASR is $\Delta=0.10$ (compared with $\Delta=0.11$ when the mortality ratio is constant), with 90% of changes lying between -0.20 and $+0.20$ (compared with $-0.23/+0.23$). By contrast, $r_g=0.08$ (compared with $r_g=0.16$), and $r_d=0.42$ (compared with $r_d=0.56$). Thus, the negative feedback on the ASR due to increased male competition tends to decrease the stability of the ASR, without a comparable reduction in the amplitude of fluctuations.

In order to check the robustness of this result, I performed a sensitivity analysis by systematically varying the strength of the relationship between the RASR and the male:female mortality ratio (see Appendix). Across a range of plausible values, the mean absolute change (Δ) stayed within a range of ± 0.02, whereas autocorrelations ranged from $r_d=0.56$ to $r_d=0.28$ and from $r_g=0.16$ to $r_g=0.05$. These results further show that delayed negative feedback decreases autocorrelations but has little effect on the amplitude of fluctuations.

3.5. Negative feedback on the OSR via life history-related behavioral changes

Life history-related shifts in behavior provide another, subtler source of negative feedback on the OSR. When the OSR is female-biased, men tend to invest less in parenting and couple relationships become unstable. As a consequence, the number of unmated individuals in the population will increase; however, women will continue to invest substantially in their offspring (at the very least through pregnancy and lactation). The net result will be a proportionally larger increase in the number of ready-to-mate men compared with ready-to-mate women, and the OSR will increase accordingly. Symmetrically, the behavioral changes driven by a male-biased OSR (higher parental investment by men, couple stability) eventually tend to reduce the OSR itself (Kokko and Jennions, 2008). Thus, life-history related behavioral adjustments tend to counteract changes in the OSR and introduce another source of delayed negative feedback on sex ratio dynamics.

3.6. Other hypothetical factors

(Lummaa and colleagues, 1998; Ranta et al., 2000) advanced the hypothesis that human mothers automatically adjust the sex ratio of their offspring based on the local OSR, for example by giving birth to more females when there is an excess of males in neighboring regions. Clearly, such a mechanism would affect sex ratio dynamics in human populations, either by providing an additional source of delayed feedback or (under very restrictive conditions) by reducing the amplitude of sex ratio fluctuations. However, the evidence in support of this hypothesis is scant and rather mixed, as summarized by Helle and colleagues (2008). Given the equivocal evidence for adaptive adjustment of the sex ratio at birth in humans (reviewed in Helle et al., 2008; Del Giudice and Belsky, 2011), this potential mechanism should be treated with skepticism until more data become available.

In contrast to secondary sex ratio adjustment, sex-specific infanticide in foraging populations is a well documented phenomenon (see Dickemann, 1979; Helm, 1980; Smith and Smith, 1994). However, cultural patterns of infanticide tend to target a specific sex (usually females) rather than the more common sex in the population, so this mechanism is unlikely to have significant effects on sex ratio dynamics. Although it has been suggested that female infanticide in Inuit populations may have worked to keep the adult sex ratio balanced by counteracting adult male mortality, the supporting evidence is extremely weak (see Smith and Smith, 1994). Moreover, there is no evidence of flexible adjusting of infanticide following sex ratio changes over time. In absence of such a flexible mechanism, sex-specific infanticide would result in a mean shift toward the favored sex, but would otherwise have no effect on sex ratio fluctuations.

4. Evolutionary genetic challenges

4.1. Overcoming the limitations of fluctuating selection

The classic models showing that fluctuating selection is ineffective in maintaining genetic polymorphism (Hedrick et al., 1976; Hedrick, 1986; Frank and Slatkin, 1990) were all based on the assumption of discrete, nonoverlapping generations. Under this assumption, all population members simultaneously undergo the effects of environmental change, and alleles that become unfavorable at a given point in time are quickly removed from the gene pool. The results change dramatically, however, in species with (a) overlapping generations in which juveniles and adults coexist, and (b) multiple life stages, at least of which is temporarily "shielded" from the effects of environmental change. When these conditions are met, temporally fluctuating selection becomes extremely effective in maintaining genetic variation, as multiple life stages store genetic variation and maintain it as the environment changes (Ellner and Hairston, 1994; Hedrick, 1995; Ellner, 1996; Ellner and Sasaki, 1996). In addition, Hedrick (1995) showed that (c) reducing the autocorrelation between environmental states *increases* the potential for polymorphism under fluctuating selection.

Crucially, the human species meets all the above conditions. Our species is characterized by highly overlapping generations (the life course of an individual may span three, even four generations), and sex ratio fluctuations exert a selective pressure on personality by virtue of their effects on mating and parenting behaviors; thus, children are largely shielded from the *direct* selective action of sex ratio dynamics. Imagine for example a child, born in a generation with a male-biased sex ratio, who carries an allele favored in female-biased contexts. There is a nontrivial probability that, by the time the child becomes an adult, the sex ratio will have become female-biased again, and the probability increases if one considers the whole future reproductive span of the child. As shown by Ellner and Hairston (1994), these conditions considerably increase the number of alleles that persist in the gene pool. Finally, the negative feedback mechanisms discussed in Section 3 reduce autocorrelations in the sex ratio, thus enhancing the ability of fluctuating selection to maintain genetic polymorphism.

Sex ratio dynamics have another property that should make them an especially effective agent of evolutionary change. All else being equal, the genetic response to selection increases with population size, so that in smaller populations the pace of evolutionary change is slower (e.g., Robertson, 1960; Falconer and Mackay, 1996). However, ASR fluctuations become larger as population size becomes smaller (Section 3.1; see Fig. 1). As a result, sex ratio dynamics will exert stronger selective pressures in smaller populations, partly counteracting their weaker response to selection.

4.2. *Fluctuating selection may not produce major-effect genes*

Models of balancing selection typically predict the evolution of asymmetric genetic architectures, with a few polymorphic genes of major effect determining most of the phenotypic variance. As noted in Section 1.1.3, no such genes have been found in relation to human personality, which casts doubts on the plausibility of fluctuation selection models. However, it should be stressed that standard theoretical models (e.g., Bürger, 2002a,b; Kopp and Hermisson, 2006; Van Doorn and Dieckman, 2007) assume from the outset that a single gene is capable of covering the whole phenotypic spectrum by evolving arbitrarily large effects. This assumption is unlikely to hold if personality results from the interplay of multiple neural pathways, each regulated by different neurotransmitters. Redundancy in the neurobiological systems and the existence of protective “buffering” mechanisms further reduce the opportunity for a single gene, however important, to take control of the whole phenotypic variance in a personality trait. When a single gene is *not* allowed to evolve arbitrarily large phenotypic effects, models predict the evolution of several polymorphic genes, each with a smaller effect (Bürger, 2002a,b; Kopp and Hermisson, 2006).

The statistical distribution of environmental fluctuations may be another important (and overlooked) factor determining the number of polymorphic genes maintained by fluctuating selection. In the model by Ellner and Sasaki (1996), polymorphism is predicted to evolve at *all* loci influencing the trait if the distribution of fluctuations is leptokurtic (broad-tailed); the classical result (i.e., a few genes of major effect) is only found with platykurtic distributions. In summary, fluctuating selection does not necessarily produce major-effect genes, and the lack of such genes cannot be taken as strong evidence against a history of fluctuating selection.

A further reason to treat the predictions of formal models with caution is that asymmetric genetic architectures seem to evolve rather slowly: in Kopp and Hermisson’s (2006) model, asymmetry typically started to appear after about 5000 generations of balancing selection, and only stabilized after about 30,000 generations. On a human scale, this corresponds to roughly 750,000 years. Even if major-effect genes could evolve without constraints, only traits with a *really* long-term history of balancing selection should be expected to show asymmetric genetic architectures.

If the sex ratio hypothesis of personality evolution is correct, association studies may be unable to detect genes of major effect even under the standard theoretical assumptions. As discussed above (Section 4.1), sex ratio fluctuations (and the selective pressures they create) become stronger as populations get smaller. This paradoxical effect may result in different genes “taking the lead” of phenotypic variation in different micro-populations, provided that they remain reproductively isolated for long enough. Imagine for example that 10 genes can influence a given trait, and that each is capable of producing a full phenotypic response to fluctuating selection. Standard models predict that, in any given population, only one (or a few) of those genes will become polymorphic and evolve a large phenotypic effect, while the remaining ones will become monomorphic. Thus, gene *A* may become polymorphic and acquire a major effect in population A, gene *B* may become polymorphic and acquire a major effect in population B, and so on. Even in small, reproductively isolated populations, fluctuating selection driven by sex ratio changes can be strong enough for an asymmetric genetic architecture to evolve. If reproductive isolation between micro-populations breaks down (as it likely happened in humans), the macro-population will look like a patchwork of many genes of small effect, even if (consistent with model predictions) a single major-effect gene has in fact evolved in each micro-population. The resulting genetic architecture would be evolutionarily unstable; still, it would likely persist for many generations, given the slow evolution of asymmetric genetic architectures (Kopp and Hermisson, 2006).

4.3. *The distribution of polymorphic alleles*

In theoretical models of balancing selection, genetic structures evolve so that polymorphism is typically limited to few alleles at intermediate frequencies. Of course, the caveats about model assumptions still apply, even if this prediction appears to be more robust than those concerning the evolution of major-effect genes (Ellner and Sasaki, 1996). It is probably too early to take stock of the empirical support for this prediction; studies of allele distribution have low statistical power, and the results of the few genome-wide scans performed in humans have been contradictory (Bubb et al., 2006; Andrés et al., 2009). Also, no specific study of personality-related genes has been attempted yet. In summary, the jury is still out on this point, though an increasing amount of relevant data may become available within a few years.

5. Conclusion

In this paper I advanced the hypothesis that fluctuating selection driven by sex ratio dynamics contributes to explain the maintenance of genetic variation in personality traits. I then applied the hypothesis to human evolution, and concluded that it represents a promising (if partial) explanation of genetic variation in personality (see Fig. 2). Of course, this is just the first step toward a full understanding of the mechanisms involved. In Section 3, I presented converging theoretical findings showing that sex ratios are intrinsically fluctuating. However, it would be extremely useful to develop an integrated formal model of sex ratio dynamics, thus capturing the full interplay of the various processes described here. A general model would also provide more information on the likely statistical distribution of

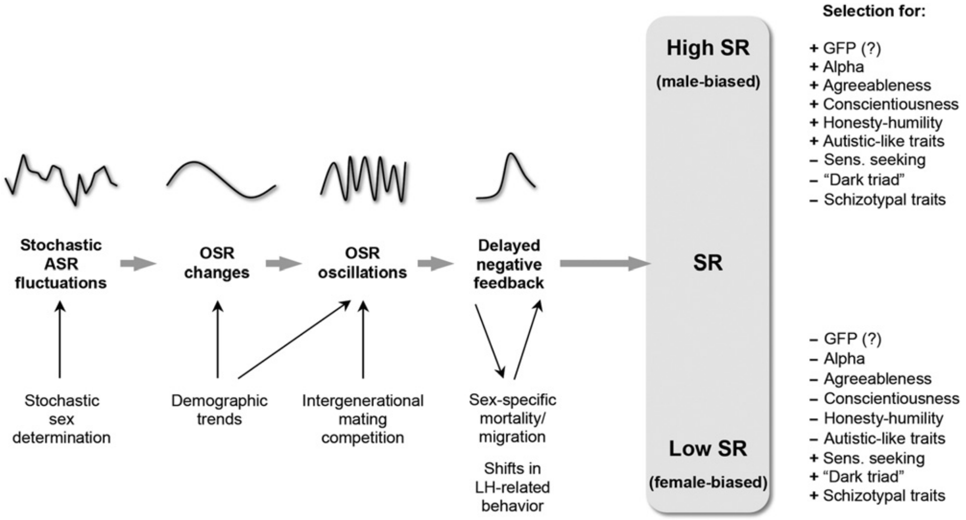

Fig. 2. Fluctuating sex ratio dynamics and hypothesized selection pressures on human personality traits. SR: sex ratio, ASR: adult sex ratio, OSR: operational sex ratio, LH: life history, GFP: general factor of personality.

fluctuations, a crucial parameter in many evolutionary genetic models (Section 4.2).

The field of human personality evolution is thin on empirical data, but it should be relatively easy to gather initial evidence for or against the sex ratio hypothesis. Indeed, the sex ratio is a universal feature of the social landscape; especially in small populations with limited mobility, it should be possible to estimate the reproductive success of individuals with different personality profiles, and to make comparisons between neighboring villages with different sex ratios. Also, long time series of sex ratio fluctuations can be easily reconstructed from demographic and anthropological records. Although a complete assessment of the sex ratio hypothesis will inevitably require many lines of converging evidence, its assumptions are eminently testable even in absence of molecular data.

How does the hypothesis apply to nonhuman species? While this is an open question, the present paper hints at a number of factors that may make the hypothesis more or less plausible in a given species. The first is a species' demographic structure. Stochastic fluctuations are strongest in small populations, and species with demes comprising many thousands of individuals will experience little stochastic variation in the sex ratio (Section 3.1). The spatial clustering of populations and the migration rate are also important, as spatial and temporal variation (Section 4) can have independent effects on the maintenance of genetic polymorphism. Furthermore, age-specific mortality and population size critically determine the "inertia" of the sex ratio. If sex ratios are too volatile with respect to generation time, the selection pressures they induce may not last long enough to determine genetic change, and the response to changing sex ratios may only take place at the level of conditional adjustment and/or developmental plasticity.

The next factor to consider is the mating and reproductive system of the target species. In humans, sex differences in mating age (Section 3.2) and competition between age groups (Section 3.3) contribute to destabilize the operational sex ratio; of course, this may or may not apply to other species. In contrast, the negative feedback processes driven by sex-specific mortality/dispersal (Section 3.4) and life history-related behavioral changes (Section 3.5) are likely to apply more generally across species. The ability of some animals to facultatively adjust the sex ratio at birth (e.g., West and Sheldon, 2002) should be factored in as well. Finally, the plausibility of the hypothesis at the evolutionary genetic level depends on the structure of an organism's life history. Fluctuating selection can be expected to be most effective in species with overlapping generations and multiple life stages, at least some of which are temporarily shielded from the selective effects of variable sex ratios (Section 4.1).

In conclusion, the sex ratio hypothesis is a promising addition to the theory of personality evolution. The heuristic value of the sex ratio hypothesis is increased by its generality, as the sex ratio is an ubiquitous feature of the social environment of sexually reproducing species. Moreover, the deep connection between sex ratios and life history strategies may help elucidate the logic of correlated selection on personality traits. Indeed, life history strategies may turn out to function as a "common pathway" for the effects of many different sources of fluctuating selection, including environmental risk, unpredictability, and resource availability (Stamps, 2007; Wolf et al., 2007). The evolution of individual differences is still a largely uncharted terrain, and we are only beginning to understand the processes that drove the evolution of the amazing behavioral diversity we observe today. To succeed in this task, researchers will need to creatively explore all the options, while at the same time keeping their hypothesis as plausible, rigorous, and testable as possible. The present work aspires to make a small step in this direction.

Acknowledgments

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Appendix A. Simulation of stochastic sex ratio fluctuations

A1. Simulation parameters

The following is a simulation of stochastic fluctuations in the reproductive adult sex ratio (RASR) of a population of size N. Each iteration corresponds to a 5-year interval. The subpopulation of interest (adults from 15 to 49 years of age) is divided into seven age classes, each spanning 5 years. Following Denham (1974), the proportion of individuals in the seven age classes (youngest to oldest) is $P_i = \{0.10, 0.09, 0.07, 0.06, 0.05, 0.04, 0.03\}$.

The idealized population described by Denham (1974) is based on demographic data from Australian aboriginal hunter-gatherers, and is virtually identical to the idealized population of Eskimo/Alaskan hunter-gatherers described by Weiss (1973). This suggests that the demographic parameters of the simulation are highly generalizable across hunter-gatherer populations.

The basic male:female adult mortality ratio is set at $k=1.5$, based on the Ache data in Kruger and Nesse (2006; from Hill and Hurtado, 1996). Two additional parameters, α and β, determine how the male:female mortality ratio varies depending on the RASR (see Section A3.1).

A2. Simulation set-up

At the beginning of the simulation ($T=0$), the male:female mortality ratio is set at $K_T=k$. The number of males and females in the youngest age class ($i=1$) is given by

$$M_{1,T}=F_{1,T}=\tfrac{1}{2}NP_1 \tag{1}$$

while for the remaining age classes

$$\begin{cases} M_{i,T}=N\left[P_{i-1}-(P_{i-1}-P_i)\frac{K_T}{K_T+1}\right] \\ F_{i,T}=NP_i-M_{i,T} \end{cases} \tag{2}$$

(results are rounded to the nearest integer). The total number of reproductive adults, which is kept constant throughout the simulation, is

$$N_A=\sum_i (M_{i,0}+F_{i,0}) \tag{3}$$

and the RASR is simply the ratio of reproductive males to females:

$$R_T=\frac{\sum_i M_{i,T}}{\sum_i F_{i,T}} \tag{4}$$

A3. Iteration

A3.1. Update of the male: female mortality ratio

At the beginning of each iteration (starting from $T=1$), K_T is updated:

$$K_T=k+\alpha(R_{T-1}-\beta) \tag{5}$$

so that the male:female mortality ratio at time T linearly depends on the RASR at time $T-1$ (i.e., 5 years earlier). In the simulation presented in Section 3.1, the mortality ratio was fixed at 1.5 by setting $\alpha=0$. In the main simulation presented in Section 3.4, $\alpha=1.2$ and $\beta=0.8$; with this choice of parameters, $K_T=1.5$ when $R_{T-1}=0.8$ (i.e., the average RASR when the mortality ratio is fixed at $k=1.5$).

A3.2. Age change and death

For all age classes except the youngest one, the number of males (females) in class i at time T is given by the number of males (females) that were in class $i-1$ at time $T-1$ (age change), minus a randomly determined number D (death). D is binomially distributed, with probability equal to the mortality rate calculated for each sex/age class. Each class must contains at least one individual, in order to avoid infinite sex ratios and other problems. Thus, for $i=\{2\ldots7\}$,

$$\begin{cases} M_{i,T}=\max\left\{1,\left[M_{i-1,T-1}-D_M\sim B\left(M_{i-1,T-1},\left(1-\frac{P_i}{P_{i-1}}\right)\frac{K_T}{K_T+1}\right)\right]\right\} \\ F_{i,T}=\max\left\{1,\left[F_{i-1,T-1}-D_F\sim B\left(F_{i-1,T-1},\left(1-\frac{P_i}{P_{i-1}}\right)\frac{1}{K_T+1}\right)\right]\right\} \end{cases} \tag{6}$$

A3.3. Replenishment of the youngest age class

For the youngest age class ($i=1$), the number of males at time T is a binomially distributed random variable with probability 1/2 (i.e., even sex ratio at maturity). The size of the youngest age class at time T is chosen so as to keep the number of reproductive adults constant. Thus

$$\begin{cases} M_{1,T}\sim B\left(N_A-\sum_{i=2}^{7}(M_{i,T}+F_{i,T}),\frac{1}{2}\right) \\ F_{1,T}=N_A-\left[\sum_{i=2}^{7}(M_{i,T}+F_{i,T})+M_{1,T}\right] \end{cases} \tag{7}$$

A3.4. Update of the sex ratio

At the end of each iteration, the updated RASR is computed and stored (Eq. (4)). The simulation output is a RASR time series with a 5-year resolution, as shown in Fig. 1b.

A4. Sensitivity Analyses

The sensitivity analysis described in Section 3.1 explored the effects of population age structure on the simulation results. Two different age structures were employed: a bottom-heavy distribution $P_i=\{0.12, 0.10, 0.08, 0.05, 0.03, 0.03, 0.03\}$ and a top-heavy distribution $P_i=\{0.08, 0.08, 0.07, 0.07, 0.06, 0.05, 0.04\}$. The sensitivity analysis described in Section 3.4 explored the effects of α on the simulation results. Higher values of α indicate that the male:female mortality ratio K_T depends more strongly on the sex ratio R_{T-1}. In the analysis, α was varied from 0.5 to 2.5, in steps of 0.5.

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