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OPINION PAPER

HUMAN REPRODUCTIVE EGALITARIANISM: A CATALYST FOR THE EVOLUTION OF PERSONALITY TRAITS

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Abstract

The human, species-typical reproductive system is distinctive and unique among the great apes. It involves pair-bonding and long-term mating as well as male investment in both mate and offspring. Studies have demonstrated that this mating system produces the lowest male reproductive skew known in primates as well as in mammals generally which entails the lowest level of reproductive failure among human males compared to other primate/mammalian species. It is argued that this low reproductive skew leads to an increase in the effective population size and to a greater diversification/variation in personality and behavioural traits in the population compared to other species. The implications of this Reproductive Egalitarian Model for human mating are discussed with regard to the emergence of human personality traits, social complexity, division of labour and risk of mental disorder.

Key words: human egalitarianism, human mating system, male reproductive skew, personality traits, division of labour

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1. Introduction

The study of human psychology encompasses both human universals as well as individual differences (Eysenck, 1981). Human personality is one of these core individual differences defined as differences in cognition, emotionality or behaviour that remain relatively stable over time (Hunt and Jaeggi, 2022). Individual differences in cognition have also been identified in non-human animals and studied within the recently developing field of animal personality (e.g. Delval et al., 2024). However, the literature on and interest in human personality is much older, and more extensive.

The question as to why such personality differences exist has been the focus of interest of some evolutionary theorists (e.g. Nettle, 2007) and there are multiple extant theories that attempt to answer this question. However, current evolutionary theories of personality apply in principle to all species and do not focus on the evolutionary peculiarities of *Homo sapiens* that have arguably led humans to become outliers and to stand out with particularly pronounced individual differences in personality. The current hypothesis purports to tackle and answer this question. The present hypothesis 'The Reproductive Egalitarianism Hypothesis' (RE) is based on the evolution of the distinctive human mating system that is likely to have played a pivotal and hitherto underappreciated role in shaping the human within-species diversity of personality traits and may have laid the ground for subsequent social complexity characteristic of all human societies. Importantly, the present model can serve as an overarching framework for the understanding of how personality differences could have emerged and flourished in humans and it can accommodate other evolutionary models acting at different selection levels or during different epochs of human evolutionary history. The RE model proposes that the distinctively low reproductive skew in human males compared to all other great apes and mammals generally that arises from the human mating system has facilitated the propagation of a greater diversity of personality traits (see **figure 1** for a summary flowchart of the RE Model).

2. The evolution of the human mating system

The first issue to note is that the human mating system differs radically from that of all other great apes and is notably a radical departure from that of the chimpanzees and bonobos, our closest ape relatives. This suggests that the system has emerged and evolved within the hominin lineage after the separation from the chimpanzee (and bonobo) line (Abed, 2024). Although human populations undoubtedly show a plurality of mating practices which include components of both short and long-term mating strategies (Schmitt, 2005),

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it is possible to identify certain common features that characterise a universal human, species-typical mating system. The human mating system (as is the case for other psychological traits) is neither endlessly malleable nor are the short and long-term mating strategies of equal importance in understanding human reproduction and human mating psychology.

In all human societies studied by anthropologists, the primary human mating strategy involves some variant of long-term mating. The distinctive characteristics of the human mating system includes pair-bonding, which is a ubiquitous feature of human mating relationships, as well as paternal investment (Alger et al., 2020; Schacht and Kramer, 2019). However, whereas paternal investment is highly variable between human populations in both extent and significance (Hrdy, 2024), alloparenting is both a ubiquitous and distinctive/ core feature of child care in human subsistence and traditional societies (Konner, 2005). Alloparenting is undertaken by a range of individuals including older siblings, grandmothers, other female relatives as well as fathers (Chaudhary et al., 2024).

Marriage, which is based on pair-bonding, is a unique human characteristic that is considered a universal, species-typical trait (Shenk, 2024). Also, while polygyny is permitted and/or tolerated in the majority of societies studied by anthropologists, monogamy is the dominant marriage system in all societies at any given moment in time (Shenk, 2024). In foragers, for example, on average, only 14% of married men are polygynous, and only 21% of married women have cowives (Marlowe, 2005). The egalitarianism of the human reproductive system should, perhaps, be viewed within the context of what has been described as the distinctly human 'Egalitarian Syndrome' (Gavrilets, 2012) (see section 6.5). Critically, it should be noted that this distinctively human mating system provides reproductive opportunities to a higher proportion of males than is the case in other primates and mammals generally and it is argued that this is the basis for the low reproductive skew among males and that it leads to the propagation of a wider diversity of personality traits down the generations.

This contention is supported by the findings of Ross et al (2023) who conducted the most extensive and comprehensive comparative, cross-species study to date on male and female reproductive skew. Their findings confirmed that human males indeed have the lowest male reproductive skew among the great apes, primates as well as mammals generally (while remaining within the mammalian range). They conclude that male skew increases with the intensity of polygyny and that sex differences in skew are higher in societies with normative polygyny than in societies with either normative monogamy or infrequent but permitted polygyny.

Interestingly, only a small minority of all mammals are socially monogamous (Kleiman, 1977; Lucas and Clutton-Brock, 2013; Olivier et al., 2024) and of these species, only a small fraction shows direct or indirect paternal care. Yet, paternal provisioning is common and widespread in human subsistence societies, while rare among primates and absent in the great apes (Alger et al., 2020). The prevalence of social monogamy in primate species is somewhat higher at around 15% but there are none among the non-human great apes (Diaz-Munoz & Bales, 2016; Olivier et al., 2024). This contrasts with 90% of birds being socially monogamous (Opie et al., 2013). Although nearly 85% of human societies studied by anthropologists permit polygyny, monogamy is the dominant marriage system in all societies (Shenk, 2024). In other words, the majority of marriages at any given time in all human societies are monogamous (Schacht and Kramer, 2019). So that across all human societies the predominant mating system is monogamous and humans are unique in this regard among the great apes (Conroy-Beam, Goetz & Buss, 2014).

While extra-pair paternity (which critically affects the reproductive importance of short-term mating strategies) is much debated (Scelza, 2024), current literature suggests that the levels are particularly low in humans at around 1-2% (Larmuseau et al., 2016) (although the Himba pastoralists are an outlier with exceptionally high rates of extra-pair paternity (Scelza et al., 2020) whereas it regularly exceeds 20% in monogamous birds (Schacht and Kramer, 2019).

As a result, the distinctive human mating system provides reproductive opportunities to a larger proportion of males and is instrumental in reducing reproductive skew, both male-male and male-female compared to the mating systems in all other great apes.

The human reproductive system shows other peculiarities. These include weaning before nutritional independence and short inter-birth-intervals (IBI) (Kaplan et al., 2000). It has been estimated that it takes 13 million calories to raise a single infant from birth to nutritional independence (Kaplan, 1994). Thus, unlike other great apes, human ancestral mothers would have found it impossible to provide this massive investment single-handedly and hence it needed to be supplemented by other adults within the group (Hrdy, 2009). To compound the provisioning problem, the human IBI is shorter than that of the other great apes and dependent offspring in need of provisioning are, therefore, 'stacked up' which multiplies the provisioning requirements (Hrdy, 2009). Two sources of this caloric investment stand out besides the mother: fathers and grandparents (Hooper et al 2015). As alluded to earlier, while men are high paternal investors compared to all other great apes and mammals generally, paternal care is facultative rather than obligatory and the significance of father presence to child survival varies across human societies, influenced by cultural and ecological factors (Marlowe, 2000; Lamb, 2004; Gray and Anderson, 2010; Shwalb et al., 2013). Nevertheless, unlike other great apes and most mammals, men produce a considerable level of surplus calories (primarily through hunting) during their peak adult years and, a proportion of this surplus is available for investment in mate and offspring (Kaplan et al., 2000).

Arguing against the significance of paternal provision, Hawkes (1991) suggested that men's caloric production and hunting prowess was more 'showing off' and a costly display rather than paternal investment, suggesting that men's caloric production can be viewed as mating effort as opposed to parental effort. While this question remains the subject of heated debate (Hrdy, 2024) and its resolution awaits further empirical research there is evidence to the contrary in the current literature. For example, Wood and Marlowe (2013) in their study of the Hadza suggest that their data on men's behaviour support paternal investment rather than 'showing off' or costly display and Marlowe (2001) showed that the greater the man's provisioning the shorter is the IBI. Also, genetic fathers have been shown to provide greater paternal care than stepfathers (Marlowe, 1999). Also, there is evidence that men work extra-hard on provisioning when they have a small infant to support and their wife cannot forage (Marlowe, 2003) all of which favour the paternal investment interpretation. On the other hand, men appear to invest less when they have increased mating opportunities suggesting that paternal investment is indeed sensitive to the costs and benefits of the different mating strategies (Marlowe, 1999). Hence, rather than being mutually exclusive, male provisioning can consist of both components i.e. parental and mating effort (costly signalling) depending on ecological and social circumstances (Smith and Bird, 2005).

3. Reproductive skew in humans compared to chimpanzees and other mammals

Studies of common chimpanzees show that position in the hierarchy is a crucial determining factor for reproductive success in males and to a lesser extent in females. This is also true in bonobos and while also true in humans, it is much less pronounced, as male status, however achieved in a given culture is significantly associated with fitness, but less strongly than in other primates (von Rueden and Jaeggi, 2016). It is of interest that the male reproductive skew in humans is smaller than that in other primates and in mammals generally and is more similar to species with monogamous mating systems (von Rueden and Jaeggi, 2016; Ross et al., 2023).

For example, in chimpanzees the alpha male can sire 30-50% of all offspring within the group consistent with the 'priority of access model' (Boesch et al., 2006; Wroblewski et al., 2009) depending on the number of competitors. Also, subordinate male chimpanzees increase their reproductive success through close alliance with alpha males (Feldblum et al., 2021). High ranking female chimpanzees also have greater reproductive success through better offspring survival, most probably as a result of better access to food resources and lower levels of stress rather than differential access to mates (Pusey et al., 1997). Rather unexpectedly (given their supposedly more egalitarian and less aggressive nature), the male reproductive skew was found to be even higher in bonobos (more than 60% sired by alpha male) compared to common chimpanzees (Surbeck et al., 2017).

Hence, the reproductive skew between men across human societies has been found to be particularly low compared to all other mammals, a fact that stands out as an important human, species-typical characteristic. This finding is a cornerstone of the present Reproductive Egalitarian model and represents a fundamental characteristic of the human species-typical mating system (von Rueden, 2024). However, human male reproductive skew has varied according to ecological, social and economic circumstances across human history (see section 5).

4. Reproductive egalitarianism as a generator of individual personality/behavioural differences

The human species-typical mating system referred to as the Reproductive Egalitarianism model has been noted in the literature as an explanation for the reduced reproductive skew in humans compared to other great apes and mammals generally (Ross et al., 2023; von Rueden, 2024). Importantly, reference to egalitarianism in this context should not be understood as all members of the group being equal, having equal access to vital resources or equal reproductive success (Kelly, 2013). Inequalities existed to varying degrees in human hunter-gatherer societies, with many even being characterised as non-egalitarian (Kelly, 2013). Such inequalities became particularly stark following the Neolithic where sedentism, food storage and increased population density were important factors (Kelly, 2013; Kohler et al 2017). Nevertheless, compared to other great apes and to mammals generally, humans continue to show a greater degree of reproductive egalitarianism. However, it is proposed that the corollary of the reduction of reproductive skew is the greater reproductive success of a wider range (greater diversity) of individuals (especially males who suffer far more catastrophic reproductive failure than do females) hence the present novel proposal that RE is a plausible explanation for the accentuation/diversification of human personality traits and individual differences. It is argued that the unique human characteristic of reproductive egalitarianism that has enabled a greater proportion of men to reproduce than in any other primate or mammalian species, has enabled a greater variation in personality traits to be propagated/maintained and the human personality traits/individual differences to emerge and/or be accentuated.

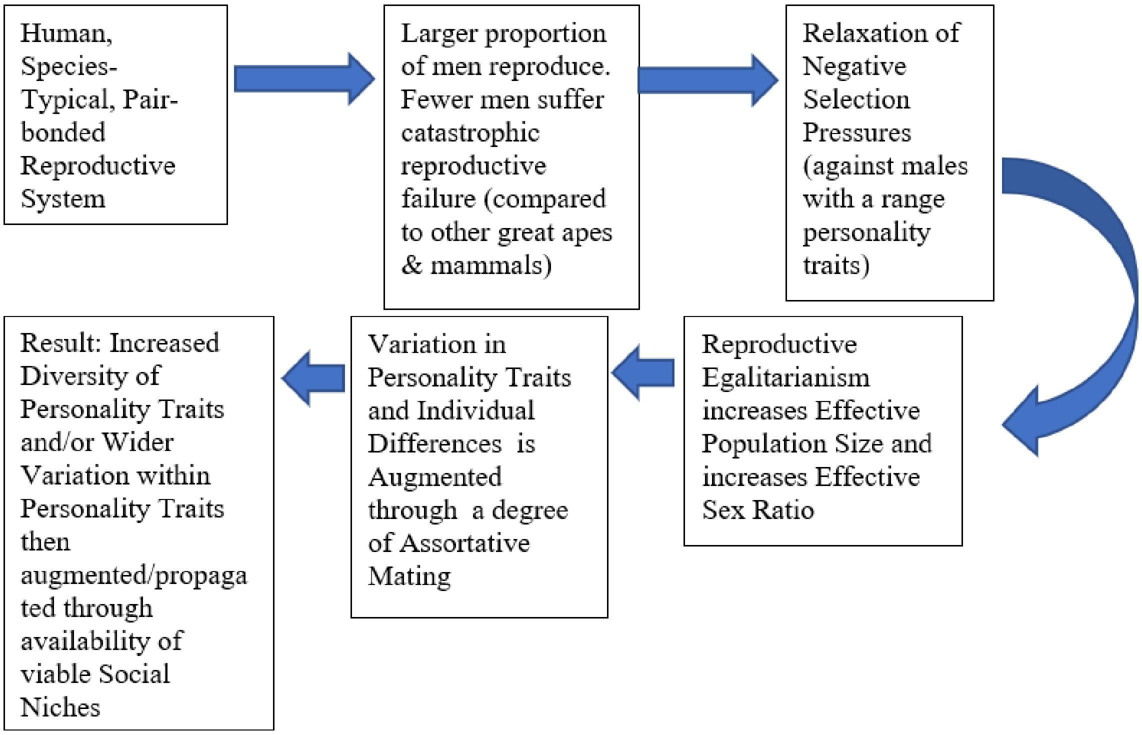
It is hypothesised that the way that individual differences in personality have been accentuated and propagated as a result of RE and the low levels of skew is as follows: The low levels of skew among males entail fewer males suffering complete failure to reproduce. This led to an increase in the effective population size through increasing the number of breeding males and increasing the effective sex ratio. This leads to a relaxation of the negative selection pressures against males with certain personality/ behavioural traits that would have led to failure to reproduce under alternative mating systems that would have characterised the last common ancestor with the chimpanzees such as the promiscuous or extreme polygynous mating system (in chimpanzees or gorillas respectively). The RE system which involves pair-bonding can further augment this process through a degree of assortative mating (which is only possible in monogamous mating systems) where personality similarity has been shown to enhance success in pair-bonding and increase reproductive success in monogamous matings in other species (e.g. Common et al., 2024). This can lead to a runaway process which can, in turn, lead to further magnification of a range of personality traits. It is of interest that such assortative mating has been proposed as a risk factor for certain psychiatric disorders such as autism spectrum disorders (Baron-Cohen, 2020).

Hence, it is hypothesised that the RE mating system facilitates the emergence of individual differences in personality in a two-step process. The first step involves the relaxation of negative selective pressures against males with a range of traits that would have led to failure to reproduce under alternative mating systems and this can be augmented by a degree of assortative mating. This can lead to an increase of both cryptic genetic variation (see section 6) as well as to genetic variation with ancestrally neutral phenotypic effects. The increased genetic variation/diversity emerging from this first step represent potential pre-adaptations that are then subjected to positive or negative selection as well as developmental/plastic effects in step-two of the process as a result of trait adaptiveness to available social niches in more complex human societies (see section 5).

5. The distinctively human division of labour as a producer of diverse adaptive niches

Although humans may not be the only mammals that have evolved a division of labour within their societies, the complexity and degree of specialisation created

Figure 1. *Flowchart summarising the reproductive egalitarianism model for personality variation*



by humans is, without doubt, unique and unparalleled (Pagano, 2020). The only other organisms with an elaborate and complex division of labour that may rival that of humans are the social insects. However, social insects are phylogenetically distant from humans and form a division of labour that is genetically programmed, fixed and species-specific whereas in humans its form is culturally based, ever-changing and is highly variable in time and place.

The most ancient division of labour that is claimed to exist more or less universally in human societies is that between males and females and has its evolutionary roots within the mammalian line in pregnancy and lactation (Low, 2015), leading to further differences in parental investment. Interestingly, although human males and females differ relatively little physically i.e. show relatively low sexual dimorphism, it is claimed that they are one of the most sexually dimorphic species behaviourally (Low, 2015; Ridley, 1993). However, more recently, anthropological surveys have challenged the claimed human division of labour with evidence that women have, in fact, practiced hunting over human evolutionary history to a greater extent than hitherto acknowledged in the literature (e.g. Anderson et al., 2023). Nevertheless, women's caloric returns in foraging societies is highly influenced by their child care responsibilities and number of dependents (Hurtado et al., 1992). This is a female-specific phenomenon that leads to major fluctuations in caloric returns and does not apply to men.

Furthermore, it is of interest that detailed surveys of human populations worldwide have identified a range of economic roles/activities, within the wider phenomenon of division of labour, as exclusively or predominantly male (but not the reverse). Examples include hunting large aquatic and land fauna, smelting, lumbering, metalworking, stone-working to name but a few (Murdock and Provost, 1973). It should be noted, however, that sex-role differentiation was greatly strengthened under post-Neolithic despotic systems characterised by the monopolising of control of resources by elite males (Betzig, 1986; Summers, 2005).

It is clear that the evolutionary roots of the unique and complex division of labour are multi-faceted. However, it is argued here that while the RE human mating system has had an important and hitherto under-appreciated role, it acted in conjunction with other uniquely human characteristics. Hence, RE not only enabled personality types to emerge (through low male reproductive skew and increased genetic variation) but also enabled and enhanced the division of labour in more complex human societies (together with other factors). It is proposed that the emergence of variations in personality and behavioural traits were pre-adaptations that enabled the division of labour which had its early beginnings in hunter-gatherers and semi-settled societies through the creation of viable social niches suited to certain personality types more than others (Kelly, 2013). This led to positive selection of a range of personality traits that were particularly suited to specific social niches.

Human social and cultural evolution has involved progressively increasing complexity starting with hunter-gatherers and progressing further with more settled agricultural societies. The division of labour which had its beginnings in hunter-gatherer populations took off in more extensive ways in the Neolithic and has continued to complexify into the present. This has led to a feedback loop whereby socio-economic niches particularly suitable for certain personality types, led to the selection and propagation of particular personality/behavioural traits enabling greater diversity of personality to be maintained and this in turn enabled more elaborate and complex division of labour.

It is noted, however, that there was a drop in the reproductive egalitarianism in association with farming and settled living whereby wealthy and powerful men practiced extreme polygyny under some circumstances fathering many children, resulting in an increase in reproductive skew (Betzig, 2012). Nevertheless, normative/social monogamy made a major comeback spreading through Europe and subsequently throughout the rest of the world over the past several centuries due to a range of important intra and inter-group benefits where the shifting of male effort from seeking wives to paternal investment increases child investment and economic productivity thus improving competitiveness versus rival nations/groups (Henrich, Boyd and Richerson, 2012). An alternative model for the predominance of monogamy has been proposed by Ross et al (2018) that does not require inter-group competition. They propose that increasing wealth inequality decreases the frequency of individuals with sufficient wealth to secure polygynous marriage, and this leads to diminishing marginal fitness returns to additional wives and this prevents extremely wealthy men from obtaining as many wives as their relative wealth would otherwise predict. These conditions jointly lead to a high population-level frequency of monogamy (Ross et al., 2018). Thus, it appears that the normative human, species-typical RE mating system has made a comeback following a period in human history of extreme polygyny by a few despotic and powerful men.

6. Evolutionary mechanisms relevant to the reproductive egalitarianism model

- RE and reduced male reproductive skew increases the Effective Population Size (Ne) (Hedrick, 2005). Ne refers to the proportion of the population who are contributing to the next generation's gene pool (Charlesworth, 2009). Low Ne (e.g. under extreme polygyny) can lead to loss of alleles due to random sampling effect. Thus, rare alleles carried by reproductively less successful males may be lost entirely reducing the genetic diversity of the population. Hence, the larger the Ne is, the greater the genetic diversity. As RE reduces male skew and increases Ne, this should increase genetic diversity compared with alternative mating systems. Male skew directly affects the effective sex ratio in a given population so that a low male skew leads to a higher effective sex ratio and a greater balance in the number of breeding males and females that contribute to future gene pool. This leads to an increase in effective population size and lowers the probability of inbreeding thus leads to higher genetic variation (Charlesworth, 2009).
- The effect of RE on Cryptic Genetic Variation (CGV) and other ancestrally neutral (phenotypically manifest) genetic variation: CGV refers to genetic variation that does not produce manifest phenotypic effects under normal conditions but can become phenotypically expressed under certain environmental or genetic changes. While CGV is invisible under normal conditions it can fuel evolutionary change when circumstances change (Paaby and Rockman, 2014). These hidden variations can be revealed under specific conditions, contributing to evolutionary potential and adaptability. Importantly, CGV increases with the increase in effective population size (Ne) associated with reduced male skew as explained above. However, see Teixeira and Huber (2021) for a contrary view on CGV.
- Low reproductive skew (increasing reproductive success of wider proportion of males) can lead to variation/diversification as a result of relaxation of negative selective pressures against alleles carried by males who would fail to reproduce under alternative mating systems e.g. promiscuous or extreme polygynous systems that characterize chimpanzees/bonobos and gorillas respectively.
- Mutation-selection balance: Mutation rates increase with the increase in effective population size and selection removes the deleterious ones and it is argued that RE produces this effect. However, in complex traits like those involved in human behaviour and cognition the constant influx of small mutations may create persistent heritable variation even under selection (e.g. Plomin et al., 2018).
- Additional human-specific evolutionary factors that may have co-evolved with and augmented the effect of RE:

  It should be clear that the human RE mating system did not emerge and evolve in isolation but co-evolved with other human characteristics which would have influenced each other in complex ways. It is proposed that a number of specifically human traits and conditions, all of which contribute to a relaxation of natural selection pressures would have acted synergistically to magnify the effects of RE in increasing the variation/diversification of human personality/behaviourial traits. These include:

  Human ecological dominance: Ecological dominance refers to 'the exertion of a major controlling influence of one or more species upon all other species by virtue of their number, size, productivity or related activities' (United Nations, 1997, p. 25). It is notable that the extent of human ecological dominance i.e. humans' control over other species, habitats, and resources impacting all areas and ecosystems of the Earth's environment far exceeds that of any other organism (Uenal et al., 2022; Vitousek et al., 1997) and has greatly accelerated social, cultural, technological, and economic progress (Flinn et al., 2005). Furthermore, the human ecological dominance appears to have deep evolutionary roots predating the emergence of *Homo sapiens* and may be traced back to the emergence of Homo erectus (Flinn et al., 2005). Importantly, the ecological dominance that has been attained by humans entails a reduction of a whole range of environmental hazards (e.g. predation) which itself leads to a relaxation of a range of natural selection pressures and personality/behavioural diversification.

  Observers have long been intrigued by the human display of an egalitarian tendency and a set of moral intuitions that sets them apart from other species. This has been characterized as a Human Egalitarian Syndrome (Gavrilets, 2012). Although there is no agreement as to exactly when these traits evolved in the human lineage, a number of factors and processes have been proposed to explain their emergence. One can speculate, however, on the reasons for its onset that also offer some insights on why it did not happen in other animals. These include an increased efficiency of coalitionary aggression and decreased uncertainty in evaluating fighting skills of group members. Both could have followed the evolution of better cognitive abilities and the development of better coordination skills and especially projectile weapons as a result of cooperative big-game hunting (Gavrilets, 2012). Additional processes and factors have been implicated in the evolution of human egalitarianism including moralistic punishment, internalization of culturally enforced norms, symbolic language and gossiping as well as social selection for altruism and self-restraint applied by groups to its members need to be considered (Boehm, 2012). Wrangham (2019) also argues that the elimination of bullies through effective coalitionary action and the use of projectile weaponry has led to what he has termed the human 'Goodness Paradox'.

In addition, the all-pervasive role of human culture in the evolution of *Homo sapiens* and creating the conditions for aspects of human uniqueness cannot be over-emphasised. These include the unique characteristics of cumulative cultural evolution and gene-culture co-evolution (Henrich, 2016 & 2020).

7. Studies of animal personality

Although there is no current clear evidence that humans exhibit more heritable variation in behavioural traits than other species, human behaviour is unique in its complexity, with an extensive role for the environment, culture and learning (e.g. Sterelny, 2012). Nevertheless, it has been proposed that human personality traits exhibit a greater range compared to other species but there is no agreement as to its origin (Delval, et at, 2024).

While a validated personality instrument has been developed and has been applied to 16 different species of primates (Hominoid Personality Questionnaire) (King & Figueredo, 1997) a range of methodological and conceptual difficulties remain that affect cross-species comparisons. These include (Delval et al., 2024):

- The fact that a test for one species may not apply to another.
- Definitions of behavioural traits are not uniform.
- A given standard test could be measuring two or more personality traits.

A further difficulty in making cross-species comparisons is that personality traits are bound to be species-typical. For example, timidness and boldness will not be the same for prey and predator species.

The fact remains that knowledge of animal personality remains scarce both in terms of commonalities and differences in personality structure in different species as well as variability within each species (Fernandez-Bolanos et al., 2020).

Hence, clear comparative evidence of similarities and differences in personality structure in humans and animals must await further theoretical developments and empirical studies.

8. The compatibility of the model with other evolutionary models of personality

It is argued that RE and its consequences for human genetic variation and individual differences may be an important missing link that augments rather than contradicts many existing models for the origin of human personality differences. Hence, the Reproductive Egalitarianism hypothesis is compatible with a range of evolutionary models of personality including the 'Niche Diversity Model' (Durkee et al., 2022; Lukaszewski et al., 2017; Smaldino et al., 2019) that assumes that individuals possess a large number of behavioural traits (Smaldino et al., 2019) that act as a source of inter-individual variation and that these behaviourial traits become organized into personality types as a result of developmental plasticity in response to socioeconomic niche availability. In the present hypothesis the low skew and wider range of men who succeed in reproducing results in a wider range of behavioural traits that are available to form into personality types.

Furthermore, the RE Model describes a set of traits and characteristics that are uniquely human whereas other evolutionary models of human personality apply universally to all species and thus have limited scope for explaining the multiple aspects of human uniqueness (e.g. Bingham, 1999). The RE model explains the emergence of a greater diversity of behavioural traits as a result of a range of distinctively human evolutionary characteristics that led *Homo sapiens* into a distinctive set of social developments and achievements.

The RE model is a high-level explanatory hypothesis for understanding why individual differences that had arisen originally as ancestrally neutral pre-adaptations or cryptic genetic variations may have led to a greater range of personality traits and/or a wider range of within trait diversity to be more prevalent in humans and it does not exclude other evolutionary models that explain the propagation of personality traits at other levels or during subsequent evolutionary epochs. This applies particularly to the Fluctuating Selection Model (Nettle, 2007) and the Fitness Indicator Model (Miller, 2009) but not so much to the Random Quantitative Variation Model (Tooby & Cosmides, 1990; Kanazawa, 2010) that does not consider the potential adaptiveness of human personality traits.

9. Studies of the fitness of personality traits

The fitness contribution of various personality traits has been examined in a number of studies. However, the question of the role of relaxation of of negative selection pressures has not been directly investigated. This is partly due to the fact that the RE model has not been previously proposed but also, due to the fact that the question can only be properly addressed comparatively, either with other species with different mating systems or between human societies with radically different levels of polygyny.

Hence, while current available studies show definite (positive or negative) effects of personality traits on fertility, especially in men, these do not necessarily have a direct bearing on the RE model.

For example, Bailey et al (2013), in their study of the Ache or Paraguary, a natural fertility population, found that Extroversion in men predicted higher fertility. They concluded that assortative mating and selective neutrality were possible processes for maintaining personality variance which are consistent with the RE model.

Gurven et al (2014), in their study of another natural fertility population, the Tsimane of Bolivia found that the most consistent trait associated with increased fertility among males was Industriousness. However, several other traits were also associated with increased fertility in men including Extroversion, Agreeableness, Concientiousness and Openness whereas Neuroticism had a negative effect on fertility. It is notable that Industriousness is only significant as a personality trait in a pair-bonded system where paternal investment is an important determinant of fitness. Also, the finding of multiple personality traits having a positive effect on fertility may be supportive of relaxation of negative selection pressures.

Mededovic (2025), examined the effects on fertility of the 'Dark Tetrad' (psychopathy, narcissism, Machiavelianism, Sadism) in a population of Serbian prisoners and found a negative effect on fertilityfor psychopathy and Sadism mediated through a criminal career. Whereas narcissism had a consistely positive effect on fertility.

Ene et al (2022), in their review of the effect of psychopathic traits on fertility proposed that these traits present potential adaptive trade-offs between fertility and mortality and between offspring quantity and quality. They conclude that psychopathic traits contribute to fitness in different ways across cultures but they predict that such traits are likely to inflict fitness costs in hunter-gatherer contexts. The latter prediction would be entirely consistent with the RE model where the dominant human, long-term mating strategy can be subverted by a parasitic, cheater strategy, which is frequency-dependent and contributes only a very small proportion of total human reproduction.

10. The potential cost and downside of high levels of behavioural and personality trait diversity/variation

It has been argued throughout this paper that RE leads to both the propagation of individual differences in personality/behavioural traits as well as to the extension of the range of these traits. A further question, therefore, arises as to whether this diversification/variation plays a causal role in the unique human vulnerability to mental disorder and psychopathology? Based on the RE model, it is predicted that the extremes of the range of individual differences would indeed be expected to be associated with certain vulnerabilities.

Accordingly, a meta-analysis of studies of the relationship of the five-factor personality model with symptoms of clinical disorders has, in fact, found evidence of a consistently significant relationship between four personality factors and a wide range of psychiatric disorders. These are: high Neuroticism, low Conscientiousness, low Agreeableness, and low Extraversion (Malouf et al., 2005).

Also, neuroticism has been found to correlate with the risk of a range of both psychiatric and physical disorders (Lahey, 2009). In addition, current evidence suggests that depression is linked to neuroticism/negative emotionality, extraversion/positive emotionality, and conscientiousness and, importantly, that personality characteristics appear to contribute to both the onset and course of depression through a variety of pathways (Klein et al., 2012).

It has also been suggested that psychopathology can be broadly categorised into three general areas: (1) internalizing disorders, indexed by internal distress (e.g., sadness and anxiety), (2) externalizing disorders, indexed by externally disinhibited behaviours (e.g., aggression and substance use), and (3) thought disorders, indexed by cognitive and perceptual disturbances and that these three categories map onto models of normal personality in robust and meaningful ways (Tackett et al., 2021). Hence, it appears that the whole area of personality and psychopathology has been a rapidly growing field over the past decade and it is contended here that the RE mating system that has contributed to the diversification of these traits would have played a hitherto overlooked but pivotal role in the unique human vulnerability to mental disorders and psychopathological states generally.

These ideas and findings are consistent with a previous proposal that the cultural niche that has shielded humans from a wide range of environmental hazards have led to a relaxation of natural selection pressures and to the diversification of psychological and behavioural traits creating the vulnerability to mental disorders (Fuchs, 2018).

11. Conclusions

Pair-bonding together with other human characteristics including romantic love and alloparenting have been identified by other authors as playing a pivotal role in the evolution of *Homo sapiens* (e.g. Fletcher et al., 2015).

However, this paper seeks to draw attention to the significance of the human mating system in understanding the origins of human personality and, potentially, the origins of psychopathology. It is contended that the RE human species-typical reproductive system has had a pivotal and hitherto unappreciated role in the evolution of the human personality/behavioural pre-adaptations that enabled the evolution of greater personality/behavioural diversity and plasticity and subsequently enabled the creation of social complexity in human societies with their multiple (and progressively multiplying) specialised social niches . Importantly, the model proposes plausible evolutionary mechanisms that have produced such complexity.

Therefore, while the human, species-typical mating system has been extensively studied by evolutionists (psychologists, anthropologists, behavioural ecologists etc.) the angle discussed in this paper is both novel and important.

The RE model is epistemically significant for the study both human psychology and psychopathology as it:

- Helps in the study and understanding of human uniqueness generally by drawing attention to the peculiarities and distinctiveness of the human mating system and its wide-ranging implications.
- Prompts evolutionary psychiatrists to shift their focus from the exclusive study of universal evolutionary causes/processes for vulnerability to mental disorders and more towards human, species-specific causes/factors.
- Prompts psychiatrists (including evolutionary psychiatrists) to consider personality factors more seriously and systematically (both in populations and in individuals) as aetiologically important factors for mental disorders.

Furthermore, the RE model is testable and refutable in principle, although the tests may be indirect and difficult to design. Nevertheless, it should be possible, in principle, to discard the model or modify it based on future empirical evidence. Here are some predictions:

1. Animal studies of personality: While it may be difficult at present to make direct comparisons between human and animal personality studies for the reasons outlined in section 7, it should become possible at some stage in the future. The RE model predicts that humans would show greater diversity of personality compared to other species mainly in the range of individual traits but also in the number and variety of the traits.

2. Based on the RE model, it is expected that there would be a reduction in the range and variation of behavioural/personality traits in societies with extreme and prolonged/persistent polygyny (which also have high levels of male reproductive skew). And that there would be a gradient of personality variation in societies based on the degree of male reproductive skew (the lower the skew, the higher personality variation).
3. Genetic variation, both cryptic and phenotypically manifest in a population should increase with the reduction of male reproductive skew.

Finally, the RE model proposes that Humanity and human society have been shaped and defined by Reproductive Egalitarianism (despite the existence of setbacks and fluctuations during certain periods of human history) that has helped propagate diverse behavioural traits and individual differences, enabling and creating the foundations for increasingly complex human social systems. It should be noted that RE is the diametric opposite of eugenics which advocates reproductive elitism and a reduction of diversity. Hence, according to the Reproductive Egalitarian Model, eugenics represents a fundamentally flawed understanding of the evolutionary history of our species that is based on a relatively egalitarian and not an elitist past. Hence, the advocation and practice of eugenics represents a reversal of an evolutionarily ancient human characteristic that is distinctive and species-typical.

References

Abed, R. (2024). Evolutionary Perspectives on eating disorders. In L. Al-Shawaf & T. Shackelford (Eds), *The Oxford Handbook on Evolution and the Emotions* (pp. 1172-1196). OUP.

Alger, I., Hooper, P. L., Cox, D., Stieglitz, J., & Kaplan, H. S. (2020). Paternal provisioning results from ecological change. *Proceedings of the National Academy of Sciences*, *117*(20), 10746–10754. https://doi.org/10.1073/pnas.1917166117

Anderson, A., Chilczuk, S., Nelson, K., Ruther, R., & Wall-Scheffler, C. (2023). The Myth of Man the Hunter: Women's contribution to the hunt across ethnographic contexts. *PLoS ONE*, *18*(6), e0287101. https://doi.org/10.1371/journal.pone.0287101

Bailey, D. H., Walker, R. S., Blomquist, G. E., Hill, K. R., Hurtado, A. M., & Geary, D. C. (2013). Heritability and fitness correlates of personality in the Ache, a Natural-Fertility population in Paraguay. *PLoS ONE*, *8*(3), e59325. https://doi.org/10.1371/journal.pone.0059325

Baron-Cohen, S. (2020). *The Pattern Seekers: How Autism Drives Human Invention*. Basic Books.

Betzig, L. (1986). *Despotism and Differential Reproduction: A Darwinian View of History*. Aldine de Gruyter.

Betzig, L. L. (2012). Means, Variances, and Ranges in Reproductive Success: Comparative Evidence. Evolution and Human Behavior, 33, 309-317. http://dx.doi.org/10.1016/j.evolhumbehav.2011.10.008

Bingham, P. M. (1999). Human Uniqueness: A General Theory. *The Quarterly Review of Biology, 74*, 133 - 169.

Boehm, C. (2012). *Moral Origins: The Evolution of Virtue, Altruism, and Shame*. Basic Books.

Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2005). Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology*, *130*(1), 103–115. https://doi.org/10.1002/ajpa.20341

Charlesworth, B. (2009). Effective population size and patterns of molecular evolution and variation. *Nature Reviews Genetics*, *10*(3), 195–205. https://doi.org/10.1038/nrg2526

Chaudhary, N., Salali, G. D., & Swanepoel, A. (2023). Sensitive responsiveness and multiple caregiving networks among Mbendjele BaYaka hunter-gatherers: Potential implications for psychological development and well-being. *Developmental Psychology*. https://doi.org/10.1037/dev0001601

Common, L. K., Katsis, A.C., Frigerio, D., & Kleindorfer, S. (2024). Effects of assortative mating for personality on reproductive success in greylag geese, Anser anser. *Animal Behaviour, 216*, 141-153. https://doi.org/10.1016/j.anbehav.2024.08.0

Conroy-Beam, D., Goetz, C. D. Buss, D. M. (2016). What predicts romantic relationship satisfaction and mate retention intensity: mate preference fulfillment or mate value discrepancies? *Evolution and Human Behavior*, *37*, 6480-4, 44. https://doi.org/10.1016/j.evolhumbehav.2016.04.003.

Delval, I., Fernández-Bolaños, M., & Izar, P. (2023). Towards an integrated concept of personality in human and nonhuman animals. *Integrative Psychological and Behavioral Science*, *58*(1), 271–302. https://doi.org/10.1007/s12124-023-09759-y

Díaz-Muñoz, S. L., & Bales, K. L. (2015). "Monogamy" in Primates: Variability, Trends, and Synthesis: Introduction to special issue on Primate Monogamy. *American Journal of Primatology*, *78*(3), 283–287. https://doi.org/10.1002/ajp.22463

Durkee, P. K., Lukaszewski, A. W., Von Rueden, C. R., Gurven, M. D., Buss, D. M., & Tucker-Drob, E. M. (2022). Niche diversity predicts personality structure across 115 nations. *Psychological Science*, *33*(2), 285–298. https://doi.org/10.1177/09567976211031571

Ene, I., Wong, K. K., & Salali, G. D. (2022). Is it good to be bad? An evolutionary analysis of the adaptive potential of psychopathic traits. *Evolutionary Human Sciences*, *4*. https://doi.org/10.1017/ehs.2022.36

Eysenck, H. J. (1981) Aim and scope. *Personality and Individual Differences*, *1*, 1-2.

Feldblum, J. T., Krupenye, C., Bray, J., Pusey, A. E., & Gilby, I. C. (2021). Social bonds provide multiple pathways to reproductive success in wild male chimpanzees. *iScience*, *24*(8), 102864. https://doi.org/10.1016/j.isci.2021.102864

Fernndez-Bolanos, M., Delval, I., De Oliveira, R. S., & Izar, P. (2020). Assessing the personality of wild capuchin monkeys (Sapajus xanthosternos) using trait rating and behavioral coding. *Journal of Comparative Psychology*, *134*(3), 349–360. https:// doi. org/ 10. 1037/ com00 00219

Fletcher, G. J. O., Simpson, J. A., Campbell, L., & Overall, N. C. (2015). Pair-Bonding, romantic love, and evolution. *Perspectives on Psychological Science*, *10*(1), 20–36. https://doi.org/10.1177/1745691614561683

Flinn, M. V., Geary, D. C., & Ward, C. V. (2005). Ecological dominance, social competition, and coalitionary arms races. *Evolution and Human Behavior*, *26*(1), 10–46. https://doi.org/10.1016/j.evolhumbehav.2004.08.005

Fuchs, I. (2019). *The Evolutionary Mechanisms of Human Dysfunctional Behavior*. Radius Book Group.

Gavrilets, S. (2012). On the evolutionary origins of the egalitarian syndrome. *Proceedings of the National Academy of Sciences*, *109*(35), 14069-14074. https://doi.org/10.1073/pnas.1201718109

Gurven, M., Von Rueden, C., Stieglitz, J., Kaplan, H., & Rodriguez, D. E. (2013). The evolutionary fitness of personality traits in a small-scale subsistence society. *Evolution and Human Behavior*, *35*(1), 17–25. https://doi.org/10.1016/j.evolhumbehav.2013.09.002

Gray, P. B., & Anderson, K. G. (2010). *Fatherhood: Evolution and human paternal behavior*. Harvard University Press.

Hawkes, K. (1991). Showing off: Tests of an hypothesis about men's foraging goals. *Ethology & Sociobiology, 12*(1), 29–54. https://doi.org/10.1016/0162-3095(91)90011-E

Hedrick, P. W. (2005) Genetics of Populations 3rd Edition. Jones and Bartlett Publishers.

Henrich, J. (2016). *The Secret of Our Success: How Culture is Driving Human Evolution, Domesticating our Species, and Making us Smarter.* Princeton University Press.

Henrich, J. (2020). *The Wierdest People in the World: How the West Became Psychologically Peculiar and Particularly Prosperous.* Penguin.

Henrich, J., Boyd, R., & Richerson, P. J. (2012). The puzzle of monogamous marriage. *Philosophical Transactions of the Royal Society B Biological Sciences*, *367*(1589), 657–669. https://doi.org/10.1098/rstb.2011.0290

Hooper, P. L., Gurven, M., Winking, J., & Kaplan, H. S. (2015). Inclusive fitness and differential productivity across the life course determine intergenerational transfers in a small-scale human society. *Proceedings of the Royal Society B Biological Sciences*, *282*(1803), 20142808. https://doi.org/10.1098/rspb.2014.2808

Hrdy, S. (2009). *Mothers and Others: The Evolutionary Origins of Mutual Understanding*. The Belknap Press of Harvard University Press.

Hrdy, S. (2024). *Father Time: A Natural History of Men and Babies*. Princeton University Press.

Hunt, A. D., & Jaeggi, A. V. (2022). Specialised minds: extending adaptive explanations of personality to the evolution of psychopathology. *Evolutionary Human Sciences*, *4*. https://doi.org/10.1017/ehs.2022.23

Hurtado, A.M., Hill, K., Hurtado, I., & Kaplan, H. (1992). Trade-Offs between female food acquisition and child care among hiwi and ache foragers. *Human Nature, 3*(3), 185–216. https://doi.org/10.1007/BF02692239

Kaplan, H. (1994). Evolutionary and wealth flows theories of fertility: Empirical tests and new models. *Population and Development Review, 20*, 4, 753-791.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology*, *9*(4), 156-185. https://doi.org/10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.0.CO;2-7

Kelly, R.L. (2013). *The Lifeways of Hunter-Gatherers 2nd Edition.* CUP.

King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality, 31*(2), 257-271. https://doi.org/10.1006/jrpe.1997.2179

Kleiman, D. G. (1977). Monogamy in Mammals. *The Quarterly Review of Biology, 52*, 39 - 69.

Klein, D. N., Kotov, R., & Bufferd, S. J. (2011). Personality and Depression: Explanatory models and Review of the evidence. *Annual Review of Clinical Psychology*, *7*(1), 269–295. https://doi.org/10.1146/annurev-clinpsy-032210-104540

Kohler, T. A., Smith, M. E., Bogaard, A., Feinman, G. M., Peterson, C. E., Betzenhauser, A., Pailes, M., Stone, E. C., Marie Prentiss, A., Dennehy, T. J., Ellyson, L. J., Nicholas, L. M., Faulseit, R. K., Styring, A., Whitlam, J., Fochesato, M., Foor, T. A., & Bowles, S. (2017). Greater post-Neolithic wealth disparities in Eurasia than in North America and Mesoamerica. *Nature, 551*, 619–622. https://doi.org/10.1038/nature24646

Lahey, B. B. (2009). Public health significance of neuroticism. *American Psychologist, 64*(4), 241–256. https://doi.org/10.1037/a0015309

Lukas, D., & Clutton-Brock, T. H. (2013). The evolution of social monogamy in mammals. *Science*, *341*(6145), 526–530. https://doi.org/10.1126/science.1238677

Lamb, M. E. (2004). *The role of the father in child development* (4th ed.). John Wiley & Sons, Inc

Larmuseau, M. H., Matthijs, K., & Wenseleers, T. (2016). Cuckolded fathers rare in human populations. *Trends in Ecology & Evolution*, *31*(5), 327–329. https://doi.org/10.1016/j.tree.2016.03.004

Low, B. S. (2015). *Why Sex Matters: A Darwinian Look at Human Behavior.* Princeton University Press.

Lukaszewski, A. W., Gurven, M., von Rueden, C. R., & Schmitt, D. P. (2017). What explains personality covariation? A test of the socioecological complexity hypothesis. *Social Psychological and Personality Science, 8*(8), 943-952. https://doi.org/10.1177/1948550617697175

Malouff, J. M., Thorsteinsson, E. B., & Schutte, N. S. (2005). The Relationship between the Five-Factor model of personality and Symptoms of Clinical Disorders: A Meta-Analysis. *Journal of Psychopathology and Behavioral Assessment*, *27*(2), 101–114. https://doi.org/10.1007/s10862-005-5384-y

Marlowe, F. (1999). Showoffs or providers? The parenting effort of hadza men. *Evolution and Human Behavior, 20*(6), 391–404. https://doi.org/10.1016/S1090-5138(99)00021-5

Marlowe, F. (2000). Paternal investment and the human mating system. *Behavioural Processes*, *51*(1–3), 45–61. https://doi.org/10.1016/s0376-6357(00)00118-2

Marlowe, F. W. (2001). Male Contribution to Diet and Female Reproductive Success among Foragers1. *Current Anthropology, 42*, 755-759.

Marlowe, F. W. (2003). A critical period for provisioning by Hadza men: Implications for pair bonding. *Evolution and Human Behavior, 24*(3), 217–229. https://doi.org/10.1016/S1090-5138(03)00014-X

Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology Issues News and Reviews*, *14*(2), 54–67. https://doi.org/10.1002/evan.20046

Međedović, J. (2025). Reproductive ecology of dark personalities: Dark Tetrad traits, criminal career, and fertility, *Personality and Individual Differences*, *233*, 112883, https://doi.org/10.1016/j.paid.2024.112883.

Miller, G. F. (2009). *Spent: Sex, Evolution and Consumer Behavior.* Viking.

Murdock, G. P., Provost, C. (1973). Factors in the division of labor by sex. *Ethology, 12*, 203-225.

Nettle, D. (2007). *Personality: What Makes You the Way You Are*. OUP.

Olivier, C., Martin, J. S., Pilisi, C., Agnani, P., Kauffmann, C., Hayes, L., Jaeggi, A. V., & Schradin, C. (2023). Primate social organization evolved from a flexible pair-living ancestor. *Proceedings of the National Academy of Sciences*, *121*(1). https://doi.org/10.1073/pnas.2215401120

Opie, C., Atkinson, Q. D., Dunbar, R. I. M., & Shultz, S. (2013). Male infanticide leads to social monogamy in primates. *Proceedings of the National Academy of Sciences*, *110*(33), 13328–13332. https://doi.org/10.1073/pnas.1307903110

Paaby, A. B., & Rockman, M. V. (2014). Cryptic genetic variation: evolution's hidden substrate. *Nature Reviews Genetics*, *15*(4), 247–258. https://doi.org/10.1038/nrg3688

Pagano, U. (2020). Why only humans and social insects have a division of labour. *Cambridge Journal of Economics*, 44, 1-15. https://doi.org/10.1093/cje/bez026

Plomin, R., DeFries, J. C., McClearn, G. E., & McGuffin, P. (2008). *Behavioral genetics* (5th ed.). Worth Publishers.

Pusey, A., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, *277*(5327), 828–831. https://doi.org/10.1126/science.277.5327.828

Ridley, M. (1993). *The Red Queen: Sex and the Evolution of Human Nature.* Viking.

Ross, C. T., Mulder, M. B., Oh, S., Bowles, S., Beheim, B., Bunce, J., Caudell, M., Clark, G., Colleran, H., Cortez, C., Draper, P., Greaves, R. D., Gurven, M., Headland, T., Headland, J., Hill, K., Hewlett, B., Kaplan, H. S., Koster, J., . . . Ziker, J. (2018). Greater wealth inequality, less polygyny: rethinking the polygyny threshold model. *Journal of the Royal Society Interface*, *15*(144), 20180035. https://doi.org/10.1098/rsif.2018.0035

Ross, C. T., Hooper, P. L., Smith, J. E., Jaeggi, A. V., Smith, E. A., Gavrilets, S., Zohora, F. T., Ziker, J., Xygalatas, D., Wroblewski, E. E., Wood, B., Winterhalder, B., Willführ, K. P., Willard, A. K., Walker, K., Von Rueden, C., Voland, E., Valeggia, C., Vaitla, B., . . . Mulder, M. B. (2023). Reproductive inequality in humans and other mammals. *Proceedings of the National Academy of Sciences*, *120*(22). https://doi.org/10.1073/pnas.2220124120

Scelza, B. A. (2024). Mating. In J. Koster, B.A. Scelza & M.K. Shenk (Eds), *Human Behavioral Ecology* (pp. 203-229). CUP.

Schacht, R., & Kramer, K. L. (2019). Are we monogamous? A review of the evolution of Pair-Bonding in humans and its contemporary variation Cross-Culturally. *Frontiers in Ecology and Evolution*, *7*. https://doi.org/10.3389/fevo.2019.00230

Schmitt, D. P. (2005). Fundamentals of Human Mating Strategies. In D. M. Buss ed., *The Handbook of Evolutionary Psychology* . John Wiley & Sons, Inc. pp. 258–291.

Shenk, M. K. (2024). Marriage. In J. Koster, B.A. Scelza & M.K. Shenk (Eds), *Human Behavioral Ecology* (pp. 230-255). CUP.

Shwalb, D. W., Shwalb, B. J., & Lamb, M. E. (2013). *Fathers in cultural context.* Routledge/Taylor & Francis Group.

Smaldino, P. E., Lukaszewski, A., von Rueden, C., & Gurven, M. (2019). Niche diversity can explain cross-cultural differences in personality structure. *Nature Human Behaviour*. doi:10.1038/s41562-019-0730-3

Smith, E. A., & Bird, R. B. (2005). Costly Signaling and Cooperative Behavior. In H. Gintis, S. Bowles, R. Boyd, & E. Fehr (Eds), *Moral sentiments and material interests: The foundations of cooperation in economic life* (pp. 115–148). MIT Press.

Sterelny, K. (2012). *The Evolved Apprentice: How Evolution Made Humans Unique.* MIT Press.

Summers, K. (2005). The evolutionary ecology of despotism. *Evolution and Human Behavior, 26*(1), 106-135. https://doi.org/10.1016/j.evolhumbehav.2004.09.001

Surbeck, M., Girard-Buttoz, C., Boesch, C., Crockford, C., Fruth, B., Hohmann, G., Langergraber, K. E., Zuberbühler, K., Wittig, R. M., & Mundry, R. (2017). Sex-specific association patterns in bonobos and chimpanzees reflect species differences in cooperation. *Royal Society Open Science*, *4*(5), 161081. https://doi.org/10.1098/rsos.161081

Tackett, J. L., & Mullins-Sweatt, S. N. (2021). Personality and psychopathology. In O. P. John & R. W. Robins (Eds.), *Handbook of personality: Theory and research* (4th ed., pp. 743–754). The Guilford Press.

Teixeira, J. C., & Huber, C. D. (2021). The inflated significance of neutral genetic diversity in conservation genetics. *Proceedings of the National Academy of Sciences of the United States of America, 118*(10), e2015096118. https://doi.org/10.1073/pnas.2015096118

Tooby, J., & Cosmides, L. (1990). On the universality of human nature and the uniqueness of the individual.: The role of genetics and adaptation. *Journal of Personaity*, *58*, 17-67.

Uenal, F., Sidanius, J., Maertens, R., Hudson, S. T., Davis, G., & Ghani, A. (2022). The roots of ecological dominance orientation: Assessing individual preferences for an anthropocentric and hierarchically organized world. *Journal of Environmental Psychology*, *81*, 101783. https://doi.org/10.1016/j.jenvp.2022.101783

United Nations. (1997). Glossary of environment statistics. In *Studies in methods, series F*. No. 67. New York, NY, US.

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science, 277*(5325), 494–499. https://doi.org/ 10.1126/science.277.5325.494

von Rueden, C. R., & Jaeggi, A. V. (2016). Men's status and reproductive success in 33 nonindustrial societies: Effects of subsistence, marriage system, and reproductive strategy. *PNAS, 113*(39), 10824–10829. https://doi.org/10.1073/pnas.1606800113

von Rueden, C. R. (2024). Status. In J. Koster, B.A. Scelza & M.K. Shenk (Eds), *Human Behavioral Ecology* (pp. 153-179). Cambridge University Press.

Wood, B. M., & Marlowe, F. W. (2013). Household and kin provisioning by Hadza Men. *Human Nature, 24*(3), 280–317. https://doi.org/10.1007/s12110-013-9173-0

Wrangham, R. (2019). *The Goodness Paradox: How Evolution Made Us Both More and Less Violent.* Profile Books.

Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, Pan troglodytes schweinfurthii. *Animal Behaviour*, *77*(4), 873-885. https://doi.org/10.1016/j.anbehav.2008.12.014