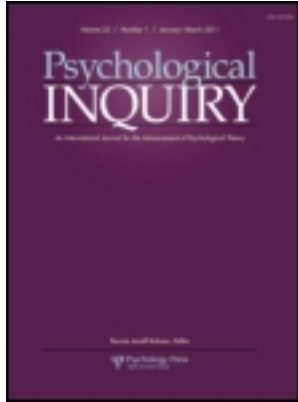


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Humans Are Dunnocks, not Peacocks: On Cause and Consequence of Variation in Human Mating Strategies

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In their article, Stewart-Williams and Thomas (2013) advocate what they call a mutual mate choice (MMC) model for understanding sex differences and similarities in human sexuality. The key features of this model include minimal sex differences in parental investment and the corollaries of reduced sexual dimorphism and mutual mate choice, in which male choice is seen as equally important as female choice. This model is contrasted with and favored over what they term the males compete, females choose (MCFC) model, which they argue is not a useful framework for understanding human sexuality; indeed, they suggest that it presents a distorted picture of human behavior. On this basis, they suggest that this presents two main issues: first, that there is a contradiction in the literature such that evolutionary psychologists sometimes incorrectly present humans as an MCFC rather than a MMC species, and second, that this leads to exaggeration in claims about sex differences within the evolutionary psychology literature, and relative neglect of certain aspects of human sexual behavior such as male choice and female competition over mates.

We agree with Stewart-Williams and Thomas on some points. Like them, we also think there is need for further work on male mate choice and female competitiveness in order to achieve a balanced and comprehensive view of human mating behavior, and we believe they make this point very clearly. In our view, however, the central premise of their article presents an unhelpful dichotomy between the MCFC and MMC models. We suggest instead that a comprehensive view of human sexuality in evolutionary perspective should (and does) contain elements of both models and that the extent to which each contribute insights into human nature is fluid and context dependent.

To set out this alternative view, we first revisit the implications of polygyny in ancestral and contemporary society, which Stewart-Williams and Thomas dismiss as relatively unimportant. We suggest instead that our heritage of frequent polygyny leaves important imprints in human mating psychology. In this light, past and present variability in human mating systems means that attempts to compartmentalize humans according to either MCFC or MMC models are unworkable. Finally,

we discuss how elements of both models are necessary to gain a full picture of human sexuality. We argue that greater focus on female than male choice, and on male than female competition, is not unreasonable but follows logically from this integrated view, notwithstanding the proposal that the balance is not yet right. Furthermore, only the integrated view can lead to a robust predictive framework for understanding patterns of sex differences in human mating psychology.

The Imprint of Polygyny

The basis for their argument is that “the pair bond is the most common setting for sex and reproduction in our species, that it has been for a long time, and that this has left a deep imprint on our evolved nature” (p. 145). Alongside this they argue that, for the MMC model to be favored as the appropriate scheme for human sexuality, it is only sufficient that pair bonding is common and that there is little difference in parental investment.

However, if we accept the argument that common and long-standing facets of human sexuality, such as pair-bonding, leave imprints on evolved sexuality, then this should be true of all facets of our sexuality. We also have a common and long-standing history of polygyny (and occasional polyandry), as they acknowledge. Applying their logic, then, we should not be surprised if this has also left a deep imprint on our nature.

Stewart-Williams and Thomas review a wealth of evidence for polygyny across societies, but they dismiss this aspect of human mating as rather unimportant. They conclude that it “should not exert a disproportionate influence on our picture of the evolved nature of our species” (p. 150) because, in those societies in which polygyny occurs (83% of societies), most relationships are monogamous. We do not dispute the data they cite, but the fact that in approximately 25% of polygynous societies more than one in five men are married polygynously would seem a rather more important phenomenon to consider than they appear to believe.

Socioecology of Mating Systems

Even more important, perhaps, is consideration of the origins and socioecology of polygyny. Behavioral ecological studies consistently show that mating systems are frequently related to ecology of particular populations and that if females gain net benefits from mating with an already mated male, they often do it. For example, the polygyny threshold model examines, in territorial species, the costs and benefits for females of mating with an already paired male or a single male in relation to the quality of their respective territories (Emlen & Oring, 1977). Although the nature and patterns of constraints and benefits vary across individual species, we frequently observe within-species variation in mating systems, similar to that seen in humans.

Origins of Monogamy

Researchers currently tend to agree that social monogamy may arise for several different reasons, of which paternal care is only one. Phylogenetic approaches reveal that the evolution of mammalian monogamy is better reflected by constraints on male mating strategies rather than the need for paternal care (Komers & Brotherton, 1997). Brotherton and Komers's (2003) analysis pointed to a sequential evolution of the two components, with pair-bonding evolving as a mating strategy (e.g., as a response to female dispersion and monopolizability) and paternal care evolving subsequently, if necessary. Indeed, numerous mammalian species which frequently form pair bonds do not show paternal care (Dobson, Way, & Baudoin, 2010), and often pair-bonding and within-pair behavior appears better explained by mate-guarding than paternal care (Brotherton & Rhodes, 1996; Roberts & Dunbar, 2000). Although the issue is still debated (e.g., Reno, Meindl, McCollum, & Lovejoy, 2003), data on postcranial sexual dimorphism in australopithecines indicate that polygyny has been prevalent for a considerable time and may be the ancestral mating system of modern humans (Gordon, Green, & Richmond, 2008). Indeed, based on findings such as these, Chapais (2013) recently proposed a sequential model of human social structure in which "social monogamy" arises out of polygyny (the ancestral state). In sum, this evidence suggests that humans are likely predisposed to polygyny but often constrained into monogamy by socioecological factors.

Monogamy, Polygyny, and Paternal Investment

Despite the preceding, it is conventionally assumed that paternal care is indispensable in humans and that it is the overarching cause of the evolution of monogamy

(Lovejoy, 1981). However, recent cross-cultural studies show that paternal investment is highly variable, and relatively low levels do not appear to exert marked effects on offspring survival (Sear & Mace, 2008). Instead, paternal absence may be buffered by efforts of other members of the extended family, making humans rather more like cooperative breeders than strictly pair-breeders, as proposed by Hrdy (2009). Stewart-Williams and Thomas thus arguably overemphasize paternal care as the evolutionary pathway to allomaternal care, because investment also comes from patrilineal kin (p. 20). In fact, the sequence might be the other way around (Chapais, 2013).

These arguments suggest that monogamy should not be equated with paternal investment, and that other explanations for frequent monogamy in humans must be sought. For instance, Marlowe (2000) argued that monogamy arises not because of dependence on paternal investment but due to constraints imposed by factors similar to the polygyny threshold (ecologically imposed monogamy) or by need for mate-guarding (socially imposed monogamy). Quinlan and Quinlan (2007) argued much the same, pointing out multiple reasons for evolution of pair-bonding. Indeed, they found a surprising result in that inequality between paternal and maternal investment is linked to pair bond instability, even when paternal investment accounts for disproportionately high levels of care. Such effects are further supported by field studies and mathematical modelling. For instance, in Tsimane, the impact of men's care on the survivorship and physical well-being of juvenile offspring is often unsubstantial. Winking, Gurven, and Kaplan (2011) therefore suggested that paternal involvement and low divorce rates might instead be explained by factors such as constraints imposed by female preferences and availability of alternative partners. Based on a modelling approach, Winking and Gurven (2011) came to the same conclusion: "Returns to paternal investment in terms of increased child survival are not substantial compared to those received by successfully practicing a serial mating strategy. This suggests that factors other than the ability to enhance child survival, such as female choice, are important to the evolutionary history and continued adaptive functioning of men's unique reproductive strategies" (p. 760).

In summary, this section makes several key points about variability in human mating systems. Across species, mating systems covary with social and ecological factors and individual strategies may vary within populations. The importance of polygyny in humans is judged not only by its prevalence across and within societies, but also phylogenetically, as the precursor to monogamy. Finally, the argument that pair-bonding is attributable to equitable parental investment rather than socioecological constraints may have been overstated.

As a result, we suggest that the evolutionary origins of polygyny, and its continued existence in contemporary societies, indicates that it may also have left a deep imprint on human mating psychology, in the same way that Stewart-Williams and Thomas propose for social monogamy.

A False Dichotomy in Mating Psychology

Due consideration of polygyny as an important component of mating psychology leads to our second point: that an attempt to define a species-typical model based on one component of evolved nature, while ignoring other components, is likely to lead to an incomplete picture. Stewart-Williams and Thomas argue that, despite many evolutionary psychologists acknowledging elements of the MMC model, the pervasiveness of the MCFC model subverts their thinking so that there appears to be a contradiction in the literature, with humans “sometimes presented as an MCFC species and sometimes presented as an MMC species” (p. 139). Our view is that this is only seen as a contradiction when one attempts to compartmentalize humans within one model or the other. In contrast, when one sees human mate choice and sexuality as representing a set of strategies that are expressed conditionally in different socio-ecological circumstances, as we have described, the apparent contradiction disappears. (For the sake of simplicity we do not consider cultural aspects here, although we acknowledge they may significantly, and to some extent independently, affect the outcomes of such decisions; see, e.g., Havlíček & Roberts, 2013.)

In other words, although Stewart-Williams and Thomas argue that it is sufficient for pair-bonding to be common in our evolutionary history in order to shape mating psychology to exhibit aspects consistent with the MMC model, the potential for adopting other mating strategies (e.g., polygyny) should also exert their own imprints on mating psychology, alongside those of pair-bonding.

An example to illustrate our point is the dunnock, *Prunella modularis*. The dunnock is a small passerine bird species found across temperate Europe, perhaps unremarkable in terms of its appearance, being small, brown, and relatively monomorphic. It is, however, anything but unremarkable in its mating socioecology. Both across and within populations, it exhibits a range of mating strategies from polygyny to monogamy and even polyandry (Davies, 1992). It has been argued that this variable mating system reflects the outcome of the interaction between competing interests of males and females within locally variable ecological constraints. Females benefit most from polyandry because they gain paternal care from two males, but males benefit most from polygyny. Local food distribution influences female range size, such that when food patches

are dense, female ranges are small and it is possible for males to monopolize access to one or more females. When food patches are less clumped or sparse, female ranges are larger and this swings the balance in favor of females and may lead to polyandry if the dominant male is unable to drive off a second male (Davies & Lundberg, 1984). In this case, the dominant male attempts to prevent the second male from copulating with the female, by mate-guarding, despite the female actively soliciting such copulations. Furthermore, males are capable of flexibly adjusting the degree of provisioning according to their likely proportion of paternity (Burke, Davies, Bruford, & Hatchwell, 1989).

No one would argue, we think, that dunnocks lack the cognitive repertoire to deal flexibly and adaptively with this range of mating system variability; they demonstrably do. But if we face the same diversity of strategies as dunnocks do, and if this approximately 20g bird can respond flexibly to these variable socio-ecological environments, it would be strange if we, with our relatively and absolutely large brains, cannot.

Thus an attempt to define humans as “an MMC species” is just as incorrect as it is to try to define humans as “an MCFC species.” We are both. Or, as we would prefer, humans display a range of behavioral strategies that are expressed conditionally, dependent on their costs and benefits within the constraints of both phylogenetic history and current socio-ecology.

Understanding Sex Differences in Mating Psychology

When seen in this integrated way, relative focus on female than male choice, and on male than female competition, is not unreasonable, misleading, or distorted, but follows logically from the different constraints acting on males and females. Just as a researcher who is interested in processes underlying obesity might choose a study population in, say, the United States or the United Kingdom rather than Japan, so a researcher interested in processes involved in human mate choice might choose to investigate women rather than men, and one interested in intrasexual competition might choose to investigate men rather than women. These decisions imply neither that obesity never occurs in Japan, nor that men never exercise choice, nor that women never compete over mates. Thus, we would argue that aspects of “MCFC phenomena” in humans remain a perfectly valid topic for research.

Furthermore, such studies arguably reveal greater sex differences than the authors choose to present, at least in traits reflecting differing costs and benefits for males and females. For illustration, we see this in their consecutive treatment of three areas of inquiry in their section on “Overlooking Male Mate Choice.” Here, their general point is that studies tend to explore issues

in female choice and that male choice is explored “as an afterthought.” For example, they criticize Wedekind and coworkers’ initial focus on women’s major histocompatibility complex (MHC) associated odor preferences. However, Wedekind, Seebeck, Bettens, and Paepke (1995) explicitly set out to test whether it was *possible* that humans could discriminate MHC by odor in the same way that female mice had been shown to do (see Wedekind & Seebeck, 1996). Focus on women rather than both sexes is then perfectly reasonable. Furthermore, if such an effect occurs, it would most likely occur in women (even if men also choose), because women systematically show higher olfactory acuity (Doty & Cameron, 2009) and attribute higher significance to body odors than men in a mate choice context (Havlicek et al., 2008). Note that in line with their aim to examine whether humans have the *capacity* to discriminate MHC-genotype from odor, Wedekind et al. also took care in several unusual aspects of experimental design, including asking odor raters to read a specific book (Patrick Suskind’s novel *Das Parfum*) to raise awareness of smell and providing them with a nasal spray to ensure their olfactory sense was in its best possible condition. Nonetheless, Stewart-Williams and Thomas then express no surprise to find that, in a subsequent paper (Wedekind & Furi, 1997), men were also shown to discriminate based on MHC-dissimilarity, saying that “this is exactly what one would expect given that males in our species typically invest in offspring and thus have well-developed mate preferences” (p. 158).

However, they do not treat the other studies in this section in the same way. For example, they neglect to mention the fact that sex differences do occur in discrimination of MHC-heterozygosity in their critique of Roberts et al. (2005), who had taken a similar approach as Wedekind and colleagues in addressing facial judgments. Had they addressed the facial literature as they did the odor studies, they would have discovered that in subsequent tests of male discrimination of female heterozygosity in faces, none of three studies conducted to date find an effect, whereas all three studies of female preferences for men report strong effects (Havlicek & Roberts, 2009). They also suggest that the focus on female choice by Roberts et al. (2005) “ignores the fact that we are a species with pair bonding and paternal care” (p. 157) but omit to mention the following statement contained in the abstract of that article: “In a relatively monogamous species like humans, evolutionary benefits from choosing heterozygous mates could include prolonged parental care and reduced risk of contracting disease for females and their offspring” (Roberts et al., 2005, p. 214).

Finally, and again in the same section, they argue that, had it not been for the MCFC focus, research on mate choice copying would have focused, from the outset, on male copying as much as female copy-

ing. Again, however, although they cite Little, Burriss, Jones, DeBruine, and Caldwell (2008), who suggested that men as well as women rate attractiveness of targets differently depending on attributes of supposed partners, they omit to mention research that does demonstrate sex differences. Thus women, but not men, are influenced by partner attributes when asked about willingness to date the target (Vakirtzis & Roberts, 2010), a measure more directly related to mate choice copying than attractiveness judgments. Indeed, far from being seen as “the default assumption from the start” that men should copy as much as women, it would be exceedingly strange if they did because the costs of copying are inherently different between sexes: There is no risk for female copiers that their target mate is already impregnated (Vakirtzis & Roberts, 2009).

In fact, once the literature is treated more comprehensively, the pattern of sex differences described in MHC-disassortative odor preferences, in preferences for MHC-heterozygosity in faces, and in mate choice copying, neatly demonstrates our main point in this article: That aspects of both MCFC and MMC models are required to gain a complete picture of mate choice and human sexuality. Of the three, the one (MHC-disassortative odor preference) in which men seem to choose in much the same way as women (i.e., the MMC model) is based on genetic compatibility between partners, which influences offspring fitness through increased heterozygosity, a trait that mutually benefits both parents (for reviews, see Havlicek & Roberts, 2009; Roberts & Little, 2008). In the other two, sex differences occur where the benefits (e.g., choosing heterozygous mates) and costs (e.g., mate choice copying) to males and females can be expected to differ, in ways that are better accounted for by the MCFC model.

Within this integrated view, we can certainly agree with Stewart-Williams and Thomas that men do exercise choice and that women compete over men, and that these elements are arguably relatively understudied. However, whereas they conclude that the existence of these elements in human mating makes “human beings an exception to the MCFC rule, and make us extremely unusual within the wider animal kingdom,” we would argue they are restricted neither to humans, nor to an MMC model of mating, nor even to sex-role reversed species. Indeed, they also exist in what Stewart-Williams and Thomas describe as MCFC species. In lizards, for example, female ornamentation can honestly advertise quality and lead to male choice, in the absence of paternal care and despite significant male competition (Weiss, 2006), and female vocalizations are involved in quality advertisement and competition over mates in birds that, like dunnocks, do not display exclusively monogamous mating systems (Langmore & Davies, 1997; Langmore, Davies, Hatchwell, & Hartley, 1996). Furthermore, at least until

recently, the argument that evolutionary psychologists do not address enough research attention on these elements can also, within the animal literature, be levelled at behavioral ecologists who have similarly been more interested in female choice and male competition, for reasons we outlined at the beginning of this section. Thus, despite early calls for more attention to selection on females (e.g., Berglund, Magnhagen, Bisazza, König, & Huntingford, 1993; Roberts, 1996), it is only within the past 5 or so years that serious interest in female selection has become manifest, with the emergence of a raft of papers tackling this subject. These studies are demonstrating that female intrasexual competition is more prevalent and complex than previously thought, and that female ornamentation and weaponry can arise for a variety of socio-ecological reasons such as cooperative breeding and female social hierarchies, not just due to monogamy and male mate choice (Clutton-Brock, 2007; Clutton-Brock et al., 2006; Rosvall, 2011; Rubenstein, 2012; Rubenstein & Lovette, 2009; Tobias, Montgomerie, & Lyon, 2012; Watson & Simmons, 2010), although certainly these are also important. If the article by Stewart-Williams and Thomas results in a similar ignition of interest in these elements within evolutionary psychology as has recently taken place within behavioral ecology, this can only be a positive outcome.

Conclusion

Stewart-Williams and Thomas argue that we are not an “MCFC species,” suggesting that humans lie somewhere on a continuum between peacocks and gibbons, and considerably closer to the latter, in terms of sexual dimorphism, paternal investment, and mating strategy. Peacocks are a highly dimorphic lekking species in which males have highly sexually selected characteristics and exhibit no paternal care. Gibbons are usually socially monogamous (although polyandry may not be uncommon in some gibbon species; Sommer & Reichard, 2000) and monomorphic (at least in size, they are often sexually dichromatic), but males of most gibbon species provide no direct paternal care (siamangs might be an exception; Lappan, 2008) and instead appear to be constrained into monogamy by female distribution and social factors such as infanticide risk and need for mate-guarding. One problem with their argument is that they seek to categorize humans according to one strategy or the other. Another is that both examples are of species in which there is little variability in mating strategy, due to either phylogenetic or socio-ecological constraints. In contrast, humans exhibit plasticity in mating strategy in ways that (if one were compelled to choose one species with which to compare humans) are more akin to a species like the dunnock. Thus their argument that interests of men and women are comparable and mutually compatible, sim-

ply because pair-bonding is the commonest strategy in human societies, belies both the inherent conflicts of interest between the sexes and the flexibility observed in actual human reproductive behavior, past and present (Borgerhoff Mulder & Rauch, 2009). Only minimal differences in interest between the sexes are needed to exert differential selection pressures on males and females that lead to different outcomes in terms of mating psychology. We agree that more research on male choice and female competition will be illuminating, but only if it is done within a framework that recognizes the full range and variability of human mating psychology.

Note

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