

Dissertation drafts and notes

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Introduction

1. Sexual selection theory and human mating strategies

The Darwin-Bateman paradigm. Until a relatively recent diversification of approaches, sexual selection theory has long been used to assert that sexually antagonistic selection on interest in mating may give rise a fundamental and near-universal dichotomy between “coy females” and “promiscuous males” - sometimes characterised as the “Darwin-Bateman paradigm” (Moniq Borgerhoff Mulder 2021; Dewsbury 2005). As the name would suggest, it is rooted in Darwin (1981) ’s early assertion that males in almost all animal species are more eager and less discriminate than females when it comes to reproduction. This, Darwin continues, makes them the primary target of evolution via sexual selection - either through male-male competition or through female choice, the inverse processes of which (e.g. female-female competition, etc.) he largely neglects (but see Bonduriansky 2009). Darwin, of course, could only speculate about the origin of these sex differences, which he tentatively reasoned to be driven by the fact that insemination requires males to closely approach females, thus selecting for an “eagerness” in males to seek out the opposite sex (Darwin 1981). But the brevity with which this, entirely non-empirical, explanation is offered in *The Descent of Man* perhaps speaks to the lack of confidence Darwin had in this line of reasoning. In any case, Darwin’s ideas on sexual selection and the associated coy female-ardent male dichotomy largely languished in scientific no-man’s land until the latter half of the eponymous paradigm, Angus J. Bateman, published an article titled “Intra-sexual selection in *Drosophila*” in *Heredity* in 1948. Here, Bateman (1948) publishes three key findings that would prove very influential for the science of mating systems: For one, he found that males show greater variability in fertility or “reproductive success” than females across his experiments. Similarly, mating success in males was significantly more variable than mating success in females. This held both on a group level, with 1 in 5 males failing to reproduce where for females, it was only 1 in 25, as well as on the individual level, where number of partners varied much more between individual males than between individual females. The third finding was that, additionally, reproductive success of males seemed to increase linearly with number of mates - indicating that males should strictly prefer more mating opportunities (i.e. promiscuity), within the constraints of Bateman’s experiments. Female reproductive success, on the other hand, did not seem to benefit from additional mates beyond the first one. When visualised as a two-dimensional line graph, this relationship between number of mates (or “mating success”) and reproductive success is referred to as Bateman’s gradient, the slope of which, after Bateman, is often posited to be steeper for males than for females (Gerlach et al. 2012). Collectively, Bateman’s results were enshrined in modern sexual-selection research as “Bateman’s principles,” seemingly offering an elegant explanation for sex differences in sexual selection that had eluded Darwin (Arnold 1994), and which continue to exert considerable influence on contemporary sexual selection research (e.g. Janicke et al. 2016). Bateman (1948) explained these results by invoking anisogamy - male sex cells (gametes) are comparatively small and metabolically inexpensive, making the number of matings the limiting factor of male reproductive success, whereas female gametes are expensive and thus themselves constitute the limiting factor on female reproduction. Like his results, the idea of anisogamy as an underlying cause was later picked up by Trivers (1972), who in his landmark chapter on parental investment (cited 15940 times according to Google Scholar) argued that sex differences in post-zygotic parental investment (i.e. parental care) followed logically from anisogamy, which he recognises as a

form of pre-zygotic parental investment itself. Subsequently, in circumstances under which males and females differ in their parental investment, they ought to differ in their reproductive strategies, with the least invested sex being more promiscuous (Trivers 1972). Simply put, their relatively small parental investment affords males with a higher potential reproductive rate, which should bias them toward promiscuous mating (T. H. Clutton-Brock and Vincent 1991). Interestingly, invoking anisogamy as the ultimate cause for sex-differences in mating behaviour poses the corollary question of what, ultimately, causes anisogamy, which similarly has been subject of much scientific interest, notably by Geoff Parker and researcher influenced by him (Parker, Baker, and Smith 1972; Lehtonen and Kokko 2011). This is why the aforementioned “Darwin-Bateman paradigm” is sometimes more completely, but rather confusingly, described as the “Darwin-Bateman-Trivers-Parker paradigm” of sexual selection and the evolution of sex roles (Hoquet 2020). This paradigm, or derivations thereof, remains at the basis of much sexual-selection research in non-human animals (e.g. Arnold 1994; T. H. Clutton-Brock 2019).

It is worth noting that, in his original paper, Bateman (1948) himself only alludes in passing to generalising his results to humans, though he seemed convinced that his results would extend to many species in which anisogamy holds. Similarly, while Trivers (1972) is more explicit in terms of applying his parental investment principles to humans, overall he also takes a broad, cross-specific view of the subject. Nevertheless, and albeit firmly rooted in theoretical evolutionary biology, Trivers’ treatment of Bateman’s ideas quickly captured the interest of evolutionary minded anthropologists and psychologists, first through inclusion in Wilson’s *Sociobiology* (Wilson 1975) and the subsequently growing focus on evolutionary causation of behaviour, and then later through the prominent early work of evolutionary psychologists focused on human mating behaviour (e.g. Buss 1989). For example, in their seminal work on sex differences in mating strategies, Buss and Schmitt (1993) argue, in line with Trivers, that obligatory parental investment differences are a fundamental evolutionary driver in human male preferences for promiscuous (short-term) mating. In this context, they also contend that the broad preferences of males for multiple partners, in the context of polygamy, similarly evolved as a function of the same sex differentials. Since then, evolutionary psychologists have gathered a substantial amount of evidence for consistent sex-differences in reproductive strategies, sometimes labelled the males compete-females choose (MCFC) model, across geographies (e.g. Chang et al. 2011; Souza, Conroy-Beam, and Buss 2016) and methodologies (e.g. Conroy-Beam et al. 2015; Thomas et al. 2020), broadly along the lines of Trivers’ original sex-specific predictions. In this manner, sexual selection theory-derived work on evolved human mating strategies continues as a fruitful (one may be tempted to say “fertile”) field of ongoing research (Buss and Schmitt 2019; Mogilski 2021), albeit an often contentious one (Stewart-Williams and Thomas 2013; Eagly and Wood 1999; Zentner and Mitura 2012). In an adjacent but separate line of research, Bateman’s principles have been directly put to the empirical test with human populations (reviewed in Betzig 2012). The sex differences in variance of reproductive success in this context are often associated with the cultural practice of polygyny, which allows for large differentials in reproductive success among males via varying number of partners (Low 1988). There are significant difficulties in compiling data on reproductive success in humans, for example because paternity is particularly challenging to discern in the absence of comprehensive genetic testing - nevertheless anthropologists, demographers, and occasionally historians have collected a wealth of cross-cultural data on reproductive success by sex (Betzig 2012; Brown, Laland, and Mulder 2009). On the matter of Bateman’s principles, Brown, Laland, and Mulder (2009) report that while there is some good evidence that reproductive success is more variable in males than females overall across multiple datasets, seemingly affirming Bateman’s first principle, this difference is neither universal nor constant. For example, in data on the Meriam people of Australia, variance of reproductive success in women is twice as high as that in men, running directly counter to Bateman’s first principle (Smith, Bird, and Bird 2003). Similarly, Brown, Laland, and Mulder (2009) contend that, contrary to a widely-held assumption among evolutionary-minded behavioural scientists, the widespread practice of polygyny does not necessarily indicate greater variation in mating success (Bateman’s second principle) among males than females, a criticism to which I will return in the next section. Overall, the Darwin-Bateman paradigm has certainly been a dominant and driving theoretical narrative in the evolutionary investigation of human sex roles across both evolutionary psychological and behavioural ecological approaches, and, as I will explore in later sections, sits at the base of many evolutionary approaches to human marriage systems as well.

Recent critiques and a new sexual selection paradigms. But recent advances across multiple disciplines have cast reasonable doubt on the clear applicability of Bateman’s principles to humans, or at least

imply that the coy female-ardent male dichotomy requires substantial additional nuance. These critiques generally span three categories - theoretical advancements in parental investment and sexual selection theory, empirical critiques of Bateman and Triver’s original work, and methodological difficulties in applying Bateman’s principles to humans specifically. I will discuss each in turn.

First off, the factors influencing strength and direction of sexual selection have been subject to recent theoretical revisions. H. Kokko and Jennions (2008) question two key features of Trivers’ reasoning on sex role divergence, which they describe as the “female” and “male” argument, respectively. The female argument relates to the poorly substantiated claim that pre-zygotic investment (anisogamy) necessarily leads to post-zygotic parental care. Fundamentally, however, this association does not strictly hold, as past investment in offspring should be irrelevant, in principle, to decisions regarding to future care - the cost of anisogamy is unrecoverable, and evolution should favour the care decision with the highest future payoff (Dawkins and Carlisle 1976). It is not immediately obvious why female’s future payoff from parental care should be higher than male’s, and whether past investment reduces the cost or increases the benefits of future care is uncertain (H. Kokko and Jennions 2008). The “male argument” relates to the idea that if effort or time are limited resource, and intra-sexual competition for mates is higher in males than in females, this necessarily leads to more investment in competition in males at the cost of parental care. However, Fromhage, Elgar, and Schneider (2005) have suggested that strong male-male competition may actually favour monogamous mating (as the mate search cost in this scenario may be very high). Overall, it is clearly worth considering under what circumstances the marginal benefit of care may outstrip the marginal benefit of competition, thus favouring male parental care (H. Kokko and Jennions 2008). Overall, H. Kokko and Jennions (2008) question the straightforward relationship between anisogamy and choosiness/promiscuity expounded on by Trivers. In a related piece of work, theoretical modelling indicates that rather than anisogamy alone, sex-specific mortality cost of caring, sex-specific mortality cost of mate searching, mate encounter rate, variation in mate quality, and the operational sex ratio (which will be discussed in greater detail in the next section) all seem to be important parameters in determining the strength and direction of sexual selection, and the associated choosiness it engenders (Kokko and Monaghan 2001). Notably, anisogamy may well factor into some of these elements, but the exact mechanisms by which it does requires a nuanced understanding of all implicated parameters. Thus, broadly, these models seek to extend and refine rather than replace existing models of sexual selection and parental investment. A more forceful variation of this critique, which discounts the causal role of anisogamy entirely, is advanced by some evolutionary biologists who argue that the use of “sex roles” in this line of research is inherently problematic (given their non-continuous nature and variability across taxa), and dismiss inherent sex differences in favour of environmental and/or stochastic effects which lead to flexible “sex-typical” (in the intraspecific sense) behaviours (Gowaty and Hubbell 2009; Ah-King 2013). For reference, Ah-King and Ahnesjö (2013) offer a useful review of this perspective (but see H. Kokko, Booksmythe, and Jennions 2013), a detailed discussion of which would, however, exceed the scope of this introduction.

Outside of these theoretical refinements, there have been specific empirical challenges to Bateman’s principles, both via reexamination of his original experiments and their conceptual replication across taxa (see Tang-Martínez 2016 for a review). Multiple scholars have extensively criticised Bateman’s experimental design and procedure (Dewsbury 2005; Tang-Martínez and Ryder 2005), with specific criticisms spanning selective use of data (Tang-Martínez and Ryder 2005), choice of species and sample size (Hoquet 2020), statistical technique and inference (Sutherland 1985; Snyder and Gowaty 2007), and systematic mismeasurement of fitness variance (Gowaty, Kim, and Anderson 2012). Of particular note here is a full-scale replication of Bateman’s experiments which revealed flaws in Bateman’s measurement of both mating and reproductive success, both of which are crucial to the formulation of his principles (Gowaty, Kim, and Anderson 2012, 2013). A more conceptual challenge to the Darwin-Bateman paradigm is the repeated evidence of multiple female matings and polyandry across multiple taxa including primates (e.g. Newcomer, Zeh, and Zeh 1999; Drea 2005; Lewis, Cratsley, and Rooney 2004). In line with these observations, empirical work has also demonstrated that females may benefit from polyandry, counter to some of Bateman’s conclusions (Slatyer et al. 2012; but see Akçay and Roughgarden 2007). Additionally, the overarching finding that sexual selection may strongly target females, and that male mate choice can play a significant evolutionary role is now largely uncontroversial among evolutionary biologists, even those who advocate for the usefulness and general validity of Bateman’s principles (T. Clutton-Brock 2009; T. H. Clutton-Brock and Huchard 2013;

Janicke et al. 2016). The issue remains, however, that much of this nuance is often lost in discussions of Bateman’s principles outside of evolutionary biology [e.g. the evolutionary psychology approaches discussed above; Moniq Borgerhoff Mulder (2021)]. Overall, all this empirical criticism tends to coalesce into one suggestion; that it is perhaps more fruitful to examine Bateman’s principle on a species-by-species basis, rather than applying it, in indiscriminate fashion, to the entirety of biology (Tang-Martínez 2016).

Fortunately, evolutionary anthropologists are afforded to do just that. But even among humans specifically, application of Bateman’s principles runs into some challenges. One would be remiss not to mention the contribution that Sarah Blaffer Hrdy has made in challenging the application of static, Bateman-derived sex roles in human and non-human primates (Hrdy 1981). In line with aforementioned empirical challenges, Hrdy (1986) discusses at length evidence for polyandrous mating in primates, including barbary macaques, baboons and langurs, and challenges the uncritical extension of Bateman’s results. Clearly, Bateman’s principles within human populations, too, are subject to a range of interacting factors discussed in the theoretical approaches above, which render unitary mating strategies in humans counter-intuitive - as exemplified by the diversity of human mating systems codified via different marriage norms and practices (**fortunato2018?**). However in this context, prevalence of culturally sanctioned polygyny (see Murdock 1967), has been interpreted as evidence for the general validity of Bateman-derived sex roles in humans, as polygyny seems to be testament to male promiscuity and directly lead to higher variance of male reproductive success (Bateman’s second principle) by unequally distributes mating opportunities among men (Schmitt 2005). Multiple researchers have cautioned against the use of this unsophisticated analogy (Brown, Laland, and Mulder 2009; Monique Borgerhoff Mulder 2009; Smiler 2011). For one, Murdock (1967) ’s ethnographic data, often the primary citation regarding the cross-cultural prevalence of polygyny, itself shows that while polygynous marriage is often allowed, it is comparatively rare - that is to say, even in polygynous societies many males are monogamous. Conversely, both monogamous and polygynous societies may be marked by “serial monogamy” (i.e. remarriage or re-partnering), which further dissolves the relationship between marriage systems and actual mating patterns (**fortunato2018?**), and leads to the emergence of female mating behaviour favouring multiple partners (Monique Borgerhoff Mulder 2009). It is unclear whether the coy female-ardent male dichotomy clearly derives from these patterns (Brown, Laland, and Mulder 2009). These difficulties are also exacerbated by the fact that “promiscuity” is a somewhat ill-defined concept that can either refer for the number of partners (mate-number promiscuity) or the number of matings (mating-number promiscuity; see Shuster and Wade 2003). The operating definition is clearly relevant in the context of mating and marriage systems as only mate-number promiscuity is necessarily indicative of polygamous mating.

It is worth noting that these critiques ought not to be interpreted as entirely invalidating Bateman’s contributions or his eponymous principles per se (see Morimoto 2020), and that it would be counterproductive to simply dismiss an entire body of well-evidenced associated research (Wade and Shuster 2005; Janicke et al. 2016). But they do draw attention to the fact that, in their applications to humans in particular, Bateman’s principles have both been fuelled by, and have fuelled, out-dated preconception about traditional sex roles and behaviours (Knight 2002) - that is to say, normative *a priori* assumptions about how females and males *ought to* behave. Arguably, such imposition of social stereotypes on biological principles and vice versa impedes epistemological efforts in both science and society, which neither are likely to benefit from. Instead, a research approach based on the careful re-examination of the Darwin-Bateman paradigm allows to amplify and extend our understanding of the evolution of sex roles and mating strategies in a way that an over-reliance on Trivers’ arguments would simply not allow for. Part of the purpose of this dissertation is to use recent theoretical advances in sexual selection theory to refine our understanding of the evolution of human mating and marriage systems. One key factor identified in the operation of sexual selection is the sex-ratio - which I shall now turn to.

2. Sex-ratio theory: principles and applications

Basic tenets of sex ratio theory. The causes, consequences, and evolution of sex-ratio patterns across biological species has been a point of contention throughout the history evolutionary thought. Darwin (1981) himself wrote, after unsuccessfully grappling with it, that “the whole problem is so intricate it is safer to leave its solution for the future” (find exact page). Only over half a century later, after seminal works by Düsing

(1884) and Fisher (1930), did biological science follow suit in formulating such a solution. Most notable in this context remains Fisher’s key mathematical treatment of the topic, eponymously named Fisher’s principle (or the Fisher condition), which explains why, evolutionarily, the sex-ratio at birth (BSR) converges toward an even 1:1 split. It is worth noting at this point that the Fisher’s theory of sex-ratio and sex allocation is a null-model (that is to say, it makes a number assumptions that many species may be expected to deviate from; see West 2009). Nevertheless Fisher’s explanation makes a simple and elegant observation: In sexually reproducing species, offspring generally have one father and one mother – the overall reproductive success of the male and female population within those species is, therefore, equal. If one sex is rarer (that is to say, if the sex ratio is uneven), their average (or per capita) reproductive success increases relative to the more frequent sex. Their higher average reproductive success makes them, evolutionarily, more attractive and effective offspring. Consequently, parental genes which lead to overproduction of the rarer sex are likely to start contributing more to the gene pool as their offspring will have higher average reproductive success – until, that is, they aren’t the rarer sex anymore (and therefore lose their reproductive advantage). The equilibrium in which neither sex has a higher average reproductive success is a ratio of 1:1. That equilibrium is the Fisher condition. This does not run contrary to Bateman’s principles, as these are concerned with sex differences in *variance*, rather than average reproductive success.

Fisher’s theory is a useful starting point for examining sex ratios, but it comes with a number of corollaries. First off, it usually specifically refers to the sex ratio at birth (BSR), elsewhere referred to as the secondary sex ratio (Graffelman and Hoekstra 2000; but see Fromhage and Jennions 2016). But the ratio of males to females tends to vary throughout an organisms lifecycle, and meaningful differences in the sex ratio is often seen at conception (CSR), at birth and in adulthood (ASR; also primary, secondary, and tertiary sex ratio, respectively, after Székely, Weissing, and Komdeur 2014). Additionally, some researchers have advocated for the use of an intermediate “sex ratio at (sexual) maturation” (MSR), a concept closely related to, but temporally preceding, the ASR (Fromhage and Jennions 2016). This is because, unlike the ASR, the MSR is not subject to bias resulting from, for example, sex-specific mortality or lifespan differentials (and thus allows for more straightforward application of the Fisher condition; see M. D. Jennions and Fromhage 2017). Finally, while measures like the MSR and ASR count all living individuals at a given point in time, they might be misleading when it comes to mating markets because not all adults are going to be mate-searching at any given point in time. Instead, there is an operational sex ratio (OSR) which only includes sexually receptive individuals and dynamically responds to individuals entering and leaving the mating market (e.g. to care for their offspring, to enter monogamous pair bonds). In a nice continuation of the sexual selection work detailed above, the OSR was identified shortly after Trivers as an additional determinant of sex role divergence, with the argument that whichever sex the OSR is biased toward would experience higher intrasexual competition for mates and, by extension, stronger sexual selection, which leads to even more competition via a positive feedback loop (Emlen and Oring 1977; Kvarnemo and Ahnesjö 1996). Emlen and Oring (1977) in particular related the OSR directly to mate monopolisability, arguing that, for example, a male-biased OSR is an indication of *male* ability to monopolise mates (e.g. through polygyny). The empirical record offers no clear endorsement of such a relationship (Ims 1988; Weir, Grant, and Hutchings 2011), and theoreticians have moved away from the OSR as a strong predictor of sexual selection and mate monopolisation (Klug et al. 2010; Shuster 2009). After all, there does not seem to be a strong *a priori* reason to believe that adding more members of the mate-limited sex offers more opportunity for mate monopolisation - if anything, it appears as if it would be harder to defend mates in that case. Given these conceptual difficulties, and the fact that measuring the OSR itself is problematic (T. Clutton-Brock 2017), any work that aims to understand the evolution of mating system must look beyond biased OSRs alone to explain variation in mating behaviours (see Kokko and Monaghan 2001; H. Kokko and Jennions 2003).

Instead of the OSR alone, recent work has highlighted the role of the ASR in determining reproductive strategies (Schacht et al. 2017; Kappeler 2017). Of course, the ASR and OSR are related - a biased ASR may well lead to a biased OSR, especially at the start of a given mating period (M. Jennions et al. 2017). But the ASR is also directly determined by factors that only indirectly affect the OSR, like sex- or activity-specific mortality costs, and there are scenarios in which a sex might be in the majority in one but in the minority in the other (H. Kokko and Jennions 2008). In fact, the ASR is determined by a wide range of demographic and ecological factors, which can be investigated in evolutionary models in which these factors are explicitly considered (Székely, Weissing, and Komdeur 2014). Importantly, the OSR is simultaneously

cause *and* consequence of mating systems, whereas the ASR is largely an external cause (unless reproductive decisions alter mortality risk - in any case, the strong impact of demographic processes on ASR is bound to weaken that reverse causality). Models which have advocated for the importance of the ASR in the evolution of mating systems and parental care (e.g. H. Kokko and Jennions 2008) have found support from empirical work which highlights that male-biased ASRs can indeed be predictive of higher male parental care and monogamy, or even polyandry, across species (Liker, Freckleton, and Székely 2013), or even within species via phenotypic plasticity (Karlsson, Eroukhmanoff, and Svensson 2010). In any case

3. Explanations for marriage patterns in humans

Polygyny threshold model

Harem defense polygyny

Market forces / sex-ratio dependent polygyny

Rival wealth-induced monogamy

Cultural group selection

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