



HUMAN EVOLUTIONARY DEMOGRAPHY

EDITED BY
OSKAR BURGER, RONALD LEE AND REBECCA SEAR



<https://www.openbookpublishers.com>



©2024 Oskar Burger, Ronald Lee and Rebecca Sear

This work is licensed under a Creative Commons Attribution 4.0 International license (CC BY 4.0). This license allows you to share, copy, distribute and transmit the text; to adapt the text and to make commercial use of the text providing attribution is made to the authors (but not in any way that suggests that they endorse you or your use of the work). Attribution should include the following information:

Oskar Burger, Ron Lee and Rebecca Sear (eds), *Human Evolutionary Demography*. Cambridge, UK: Open Book Publishers, 2024, <https://doi.org/10.11647/OBP.0251>

In order to access detailed and updated information on the license, please visit <https://doi.org/10.11647/OBP.0251#copyright>

Further details about CC BY licenses are available at <https://creativecommons.org/licenses/by/4.0/>

All external links were active at the time of publication unless otherwise stated and have been archived via the Internet Archive Wayback Machine at <https://archive.org/web>.

Digital material and resources associated with this volume are available at <https://doi.org/10.11647/OBP.0251#resources>.

Unless otherwise stated in the caption, all figures are created by the author and licensed CC BY 4.0. Every effort has been made to identify and contact copyright holders and any omission or error will be corrected if notification is made to the publisher.

ISBN Paperback: 978-1-80064-170-9

ISBN Hardback: 978-1-80064-171-6

ISBN Digital (PDF): 978-1-80064-172-3

ISBN Digital (HTML): 978-1-80064-682-7

ISBN Digital (EPUB): 978-1-80064-173-0

DOI: 10.11647/OBP.0251

Cover image: Ryota Nagasaka. Street Photography, April 20, 2020, https://unsplash.com/photos/w_5TUm7Xa00

Cover design: Jeevanjot Kaur Nagpal

23. Bateman's Principles and the Study of Evolutionary Demography

Monique Borgerhoff Mulder

Over the last 40 years, investigators have been applying ideas from the body of theory known as sexual selection to the behaviour of humans, breaking exciting new interdisciplinary ground. The Darwin-Bateman Paradigm has been central to this endeavour, essentially the idea that males are more competitive over mates than are females, and that mating success affects reproductive success more strongly in males than in females. Less known among social scientists is the fact that biologists continue a vigorous debate over the validity of this paradigm. In this chapter I take social scientists into some of these issues, to see how and why the study of the operation of sexual selection on males and females has changed as a result of clearer theory and better methods. The simple takeaway message is that in many species gender roles are much less distinct than original investigations of the Darwin-Bateman paradigm might suggest. Applying some of the emerging insights to humans, we find a surprisingly limited general understanding about the extent and patterning of variability in reproductive success in either sex. Furthermore, success in the marriage or mating pool is associated with a range of reproductive outcomes, both positive and negative, for men and women. A new methodological approach is proposed for studying the effects of mating success on reproductive success which may help to sort through some of the extensive variation in our species. More generally, the chapter argues that an updated understanding of Bateman's work might serve to guide evolutionary demographers today, just as Bateman's original work steered research in the early days of sociobiology.

Introduction

In 1948 Angus Bateman published a paper of enduring influence on evolutionary biology in which he tested Charles Darwin's ideas on sexual selection (Bateman 1948). From his experiments on fruit flies, he observed that the variance in the number of offspring left by males was greater than that left by females, and that this was largely due to variance in the number of females with whom males sired offspring. From this he inferred differential eagerness and discrimination over mating among males and females, and that this difference results from the fact that males can produce millions of small relatively cheap sperm whereas females produce fewer, larger, and relatively more expensive eggs. These sex-specific behavioural patterns were referred to as "coy" and "promiscuous", for females and males respectively. Arnold (1994) has clarified that Bateman actually derived three principles from his experiments: males have greater variance in reproductive success than females (Principle 1), males have greater

variance in mating success than females (Principle 2), and reproductive success will increase with number of mates for males but not for females (Principle 3). The corollary of a stronger “Bateman gradient” (the regression of reproductive success on mating success) for males than females was that sexual selection will typically act more strongly on males than on females.

After several decades of relative obscurity these ideas were picked up by and Robert Trivers (1972) and Michael Wade and Stevan Arnold (1980), albeit focusing on rather different driving forces of sexual selection — Wade and Arnold on anisogamy (differences in the size and cost of sperm and egg, i.e. prezygotic investment) and Trivers more generally on sex differences in parental investment (pre and post zygotic). Bateman’s three principles emerged as cornerstones to the study of sexual selection, structuring analyses of sex differences, the evolution of mating systems and the patterning of parental care. Indeed, as of October 2017 2018 Bateman’s paper has been cited 3508 times, and enshrined as the Darwin-Bateman Paradigm (Dewsbury 2005; Parker & Birkhead 2013).

Over the years Bateman’s ideas have undergone considerable challenge and re-examination (e.g., Hrdy 1986; Gowaty 1997; Klug et al. 2010), with critiques cantering on empirical, experimental, and theoretical considerations. Yet the basic intuitive logic of the paradigm survives this critique (Jones 2009; Krakauer et al. 2011; Parker & Birkhead 2013; Anthes et al. 2017; Henshaw et al. 2018). Furthermore much comparative evidence from the animal kingdom, including humans, supports the three principles (e.g., Janicke et al. 2016). That said, these critiques have significantly amplified and refined our understanding of the sex roles and mating strategies, and the conflicts between males and females more generally (Jones 2009; Anthes et al. 2017; Henshaw et al. 2018).

The objective of this chapter is to provide an update on the contemporary significance of Bateman’s principles for human demography. Social scientists typically view biological approaches to gender and reproduction as deterministic, and with good reason (Wood & Eagly 2012). This is because evolutionary social scientists’ expectations regarding sexual selection (recently reviewed in Puts 2016), and their heavy reliance on (presumed inherent) differences in parental investment between the sexes, often evoke stereotypic fixed gender roles (Borgerhoff Mulder 2010). This seriously mischaracterizes the diversity and patterning of gender differences in the ethnographic record (Eagly & Wood 1999). There is plenty of evidence that, for example, the division of labour is highly variable between societies (Bird 1999), that (like our non-human ancestors, Hrdy 1986; Hrdy 1997) women exhibit highly variable roles with respect to mate choice (Scelza 2013), and that this variability can be explained in part by socioecological factors as predicted by evolutionary models. Adult sex ratio, for example, influences attitudes towards promiscuity (Schacht & Borgerhoff Mulder 2015) and the patterning of violence (Schacht et al. 2014). Indeed we may not be quite the sexually-selected “peacock” some studies have suggested (as argued by Stewart-Williams & Thomas 2013).

Here I review the central role that Bateman’s principles played in launching human sociobiology and evolutionary psychology as empirical fields of investigation [2]. I then examine the critiques of the paradigm, highlighting those of most relevance for human studies [3], before returning to current understandings of Bateman’s principles in human demography, bringing attention to the new challenges that emerge and some possible ways forward [4]. I end with remarks on future horizons and intersections with societal values [5]. The second section is primarily of historical interest, and serves largely as an introduction to early human sociobiology

and evolutionary psychology for those unfamiliar with these fields. The third section is more technical, providing an update on how debates over Bateman's work, in both experimental and theoretical literature within evolutionary biology, are opening up new questions with regard to the study of multiple mating, sexual selection, the measures thereof, and the inferences that can be drawn. This will be of most interest to human evolutionary demographers who want to follow developments within the nonhuman literature, whereas Section 4 explores the implications therein for our empirical work as human evolutionary demographers, and draws further links to the standard demographic literature, identifying future directions. The final section examines, briefly, how changes in the study of sexual selection reflect changing social mores.

Bateman, Sociobiology and Evolutionary Psychology

Bateman's three principles, particularly through their influence on Trivers' (1972) characterization of the relationship between parental investment and sexual selection, were central to the founding of human sociobiology (Alexander 1974; Chagnon & Irons 1979) and evolutionary psychology (Symons 1979).

In the early days of applying evolutionary theory to human social behaviour the focus appears, at least in retrospect, to have been on demonstrating continuities between humans and other mammals, and indeed other animals more generally. Such continuities were justified on the basis of the shared evolutionary history of humans and nonhuman primates (e.g., Lovejoy 1981). However, the fields of human sociobiology and evolutionary psychology really took off with demonstrations that theory developed to explain variability in behaviour among birds, mammals, fish and insects could shed light on human patterns of sexual dimorphism (Alexander et al. 1979), mating systems (Dickemann 1979), and sex-biased parental investment (Hartung 1982). In other words, evolutionary scientists began to employ arguments for analogy (that behavioural similarities might arise from convergent evolution in the face of similar social or ecological challenges), as well as arguments for homology (similarities arise from common ancestry).

Initial interest focused on a low-hanging fruit — the greater variation in male than female reproductive success. In many small scale societies, including those with prescriptively monogamous marriage like the Pitcairn Islanders (Brown & Hotra 1988) and those living in complex states (Betzig 1986; Betzig 2012), men showed greater reproductive variability than women. Furthermore polygyny was not only widespread (Flinn & Low 1986), but patterned within populations according to the “polygyny threshold model” (Orians 1969); effectively following the prediction that polygyny will be more pronounced where men vary greatly in the resources they hold and women (or their families) select men according to their resources (Borgerhoff Mulder 1990). Such data were interpreted as strong evidence that human behaviour was a product of natural selection insofar as its variability within and between societies could be explained by theory developed for non-humans.

Researchers were also motivated to investigate the causes of differential reproductive success among men, noting that success in the reproductive sphere often correlates with success in the cultural, social or economic sphere (Irons 1979). For example, men with exceptional hunting skills (Kaplan & Hill 1985), or the ability to make efficient (or adaptive) marital decisions under specific ecological conditions (e.g., brothers sharing a wife in environments with limited

arable land, Crook & Crook 1988) show higher reproductive success than men without these traits. Even traits like the propensity to murder (Chagnon 1988) or rape (Thornhill & Thornhill 1983) might, under certain circumstances, be seen as adaptive strategy (insofar as the trait is associated with enhanced male fitness), although many such claims were controversial (Smith et al. 2001). Ambitiously, Irons (1979) suggested that success in the reproductive sphere might not only map onto, but also shape, emic definitions of success across different cultures.

Because of their interest in evolutionary processes investigators focused on variability in reproductive success (or fitness) and its determinants, often relying (explicitly or not) on Bongaarts' (1976) intermediate determinants of fertility — such as child survival (Sear et al. 2002), birth intervals (Blurton Jones 1986) or length of the lifespan (Perls et al. 1998; Penn & Smith 2007). This effective rapprochement to the discipline of demography (*sensu strictu*) was exemplified in papers identifying the principles of ecological (Low et al. 1992) or evolutionary (Low et al. 2002) demography that increasingly drew the interest (and collaboration) of more conventional demographers.

In retrospect, while foundational to the fields of sociobiology and evolutionary psychology, much of this work now appears quite coarse. Work was primarily correlational, with little attention to the development or transmission of traits. More specific critiques emerged: for example, Hrdy (1986; 1997) pointed repeatedly to the absence of attention to female strategies and counterstrategies against male control (see Borgerhoff Mulder & Rauch 2009; Scelza 2013), and Smith et al. (2001) drew attention to the tendency to deploy overly simplistic adaptationist logic. Interestingly, the view that women had little autonomy in pre-demographic populations has some cogency for demographers (Folbre 1983; Campbell et al. 2013). Furthermore the assumption that sex roles are universally structured by Bateman's principles has led to greatly exaggerated inferences regarding sex differences within the field of evolutionary psychology (as explored by Stewart-Williams & Thomas 2013). Yet, despite these problems, a body of theoretically-motivated empirical and interdisciplinary analyses was emerging, prompted by the hypothesis that the lower investing sex (men) follows very different reproductive strategies than the heavier investing sex (women).

Challenges to, and the Current Status of, Bateman's Principles

Within the sexual selection literature critiques have crystalized as a result of experimental, technical and theoretical advances. Problems have become apparent in the design of (and hence inferences from) Bateman's original experiments (most recently reviewed in Tang-Martínez 2016). At the same time new techniques have allowed for accurate determination of paternity (Birkhead 2000), and theoreticians have expressed concerns with the assumption of a deterministic relationship between anisogamy and post-zygotic parental investment (and sex roles) (Kokko & Jennions 2012). Each of these developments has challenged the idea that females necessarily benefit less than do males from multiple mating, and have prompted a much broader exploration of the theoretical significance of Bateman's gradients for the operation of sexual selection (Sutherland 1985; Klug et al. 2012; Parker & Birkhead 2013). The following section draws on the literature within evolutionary biology, and provides a more technical update on how these debates over Bateman's work are opening up new questions with regard to the study of multiple mating, the measures thereof, and the inferences to be drawn.

The procedural and statistical errors in Bateman's work have been much reviewed (e.g., Tang-Martínez 2012). Flaws have been identified in assessing paternity (Gowaty et al. 2012). Statistically, an overestimate of subjects with zero mates and an underestimate of subjects with more than one mate results in systematically-biased estimates of offspring number for males and females (Snyder & Gowaty 2007; Gowaty et al. 2012; see also Collet et al. 2014). Furthermore, not only Bateman, but those who cited the paper, chose to overlook the results of experiments labelled as "Series 1 to 4", emphasizing only the later "Series 5 and 6". In the earlier series females not only mate multiply but appear to benefit in terms of fitness therefrom. Indeed, if all the data are combined Bateman's third principle does not hold (Snyder & Gowaty 2007). Such successive simplifications of complex data sets can lead to the emergence of paradigms, which in themselves can act as further blinders to perceiving alternative patterning in the data (Tang-Martínez 2016). In this case, the Darwin-Bateman Paradigm has been formalized in textbooks, such as the early and highly influential text for human sociobiologists and evolutionary psychologists (Daly & Wilson 1978) and later texts (Buss 1999; Barrett et al. 2002). As a result, misrepresentations of male and female behaviour appeared in the literature that went far beyond what Bateman actually saw; in fact, Bateman's work was entirely non-behavioural.

Empirical findings that females can also benefit from multiple matings are now commonplace (Hauber & Lacey 2005; Simmons 2005; Clutton-Brock 2009; Gerlach et al. 2012). These findings do not of course mean that Bateman was wrong (Wade & Shuster 2005; Krakauer et al. 2011), nor that anisogamy (the initial sex differences in investment in reproduction) is irrelevant. Rather the debate that has arisen from trying to make sense of these "exceptions" has led to improvements in the modelling of sexual selection, specifically with respect to identifying causal priority in processes that are inherently complex and co-evolutionary (e.g., Jennions & Fromhage 2017). While the specifics of model dynamics need not concern us here, the pursuit of coherent and consistent models (McNamara et al. 2000; Kokko & Jennions 2008) and unbiased estimates of variance in reproductive success, variance in mating success, and the Bateman gradients (see Anthes et al. 2017 for a recent overview) are raising issues of direct relevance to the practice of evolutionary demography.

First, consider sex differences in the cost of reproduction. Sperm are of course cheaper to produce than eggs — this difference lies at the root of who is identified as male or female (anisogamy) (Kokko & Jennions 2012). While the literature is far too broad to cover here (for a good early review, see Wedell et al. 2002), the assumption that insemination is cheap is challenged in many systems, particularly insects, where seminal fluid, nuptial gifts, even body parts are contributed to females as part of male mating effort. For some species the critical sex differences in costs of reproduction that underlie Bateman's principles may have been overemphasized; and in some cases, they are reversed. Accordingly, males may not always be selected to mate indiscriminately, and male mate choice can be adaptive (Gowaty et al. 2002), and males have to face trade-offs between the number of females they inseminate and the quality of those females (e.g., Péliissié et al. 2014). As we discuss in the next section, this raises questions about how much reproduction can successful men get away with.

A second issue to consider is the accumulating evidence that females are neither necessarily coy nor discriminating over mating multiple times, and that this can contribute to considerable reproductive inequality among females. This is particularly in evidence in cooperatively breeding animals (Hauber & Lacey 2005), and again the literature is enormous

(Clutton-Brock & Huchard 2013). With the advent of molecular methods of determining paternity, fieldworkers found (first in many birds and now across taxa) that females engage in copulations with multiple mates regardless of the “social” mating system. Hypotheses for the adaptive value of this behaviour proliferated (Jennions & Petrie 2000), leading to active interest in polyandrous mating, dubbed (in the title of the opening chapter in a Themed Issue in *Philosophical Transactions of the Royal Society*) a “revolution” in our understanding of female reproductive strategies (Parker & Birkhead 2013). Accordingly, biologists’ attention is now turning towards understanding both the causes of this variability among females, as well as the role of female competition (often overlooked in the literature, Stockley & Bro-Jørgensen 2011). Such competition has also been neglected within the human evolutionary demographic literature, as discussed in the next section.

A third development was the dedication of much empirical effort to both quantify Bateman gradients for each sex and, probably more importantly, scrutinize the legitimacy of inferences drawn regarding Bateman’s third principle, the sex difference in slope of reproductive success on mating success. With respect to this latter goal there is now plenty of evidence that females benefit, and sometimes benefit proportionately more so than do males, from multiple mating (Hauber & Lacey 2005; Simmons 2005; Clutton-Brock 2009; Gerlach et al. 2012). This is the case even in the fruit fly family (Gowaty et al. 2002; Taylor et al. 2008) where Bateman did his work. Notably these “exceptions” occur not only in so-called sex-role reversed species (e.g., Jones et al. 2000) where (by definition) males provide more parental care than females and where such patterning might indeed be expected.

This initially unexpected patterning to Bateman gradients has led investigators to dig deeper into the mechanisms that mediate mating success and reproductive success (Tang-Martínez 2016; see also Henshaw et al. 2018). In some species the advantage to females from multiple mating appears to accrue through higher fecundity, in others improved offspring survival, and yet others longer lifespans (the role of genes and material benefits in contributing to these associations are as yet often unknown). Possible causes (or correlates) of these patterns are the costs of mating, the extent of paternal provisioning, and whether paternal provisioning exceeds maternal provisioning.

Species also differ in whether female reproductive success increases only when females mate with multiple males as opposed to mating repeatedly with one male. In observational studies we typically only know how often males and females mate, whereas in experimental studies (or studies where paternity is assigned through genetic markers) we may know only the number of sires of a female’s offspring. With all of the evidence on how females can cryptically select (post copulation) which male fertilizes her ova (as in sperm competition, for example, Eberhard 1996; Birkhead 1998; Gasparini & Evans 2018), a male’s observed mating success does not necessarily proxy for the numbers of offspring he sires. Conversely where sires are determined through genetic analysis, as in Bateman’s experiments, investigators have no idea how many males a female mated with, only how many males have sired her offspring (Dewsbury 2005). In the nonhuman literature multiple mating by females can positively affect a female’s reproductive success through various mechanisms — the nutrients in semen, the provision of nuptial gifts, additional care from extra pair mates, or backup partners if the current one dies. But it is also clear that multiple mating can have negative outcomes for health and lifespan, as reviewed both long ago (Snowdon 1997) and more recently (Tang-Martínez 2016). How these patterns

intersect with number of sires and/or number of matings is as yet unclear, a question that has potentially important implications for evolutionary human demography as discussed below.

The final points to emerge from this recent interest in Bateman's gradients are methodological, but important with respect to the drawing of accurate inferences from empirical studies of the relationship between mating success and reproductive success (Anthes et al. 2017). First, arithmetically it is necessarily easier to detect a larger number of sires when females produce a large number of eggs, so statistical associations are problematic and need to be corrected (Gagnon et al. 2012). Second, the causality may go the other way (Collet et al. 2014). If highly fecund females attract the attention of extra-pair males on account of their fecundity, the high fertility of multiple mating females will be a consequence of their reproductive performance rather than a cause (Ketterson et al. 1998; Gerlach et al. 2012). And third, a trait such as body size (associated with egg production in many species) could cause both greater mating success and greater fertility, such that correlations between mating and reproductive success may be partially spurious (Anthes et al. 2017).

Evolutionary biologists are increasingly recognizing these problems. Furthermore, in pursuit of the broader objective of differentiating the effects of sexual selection (big individuals get more mates) from those of natural selection (big individuals produce more, and larger, offspring), biologists are now starting to decompose the distinct components of mating success (Jones 2009; Péliissié et al. 2014; Janicke et al. 2015), and the paths whereby mating success affects reproductive success (e.g., Henshaw et al. 2018), issues picked up in the next section.

Bateman and Contemporary Evolutionary Demography

What does the current status of the Darwin-Bateman Paradigm mean for our understanding of human reproductive strategies, and evolutionary demography more generally? I address key points arising from the assessment above with some examples from studies in evolutionary demography and life history. This in no way substitutes for a full review of the relevant literatures, although I make references to standard demographic literature where relevant; further, I rely heavily on studies with which I have been associated. The goal is to highlight lacunae in our current understanding of human reproductive strategies, and to explore how a modern understanding of Bateman's work might serve to guide us again, as it did in the early days of sociobiology.

Variance in the Reproductive Success of Men and Women

Undoubtedly, many results from the earlier sociobiological studies (Section 2) hold. Men typically have greater variance in reproductive success than do women. In addition it is clear that there are strong associations between measures of culturally valued traits (*sensu* Irons 1979) and the reproductive success of men (and to some extent women), not only in traditional (pre-demographic) societies (Smith 2004; Nettle & Pollet 2008) but also in industrial populations (Stulp et al. 2016). These associations proxy as estimates for selection coefficients of single generation individual reproductive success on cultural success, and are of similar magnitude to selection coefficients estimated for nonhumans (as reviewed in Nettle & Pollet 2008). Further indications of significant variance in male reproductive success comes from genetic data from distinct patrilineages; these studies reveal high rates of some Y-chromosomal lineages going extinct with others expanding markedly (Zerjal 2003; Balaesque et al. 2015). Recent studies improve

methodologically on earlier work on sex differences in variance in reproductive success and, where possible, use data less prone to bias (towards or against the culturally successfully), for example church records of births and deaths (Courtiol et al. 2012). With such materials for eighteenth-/nineteenth-century Finns, sex difference in variance in reproductive success can be apportioned quantitatively to men's higher variance in early survival, in ever-marrying, in their number of marriages and the fertility of their wives.

Before moving on to women, it bears noting that there is little precise understanding of what limits variability in male reproductive success. Consistent with the polygyny threshold model (Orians 1969), reproductive inequality among men should increase with increasing wealth inequality, but it doesn't (Ross et al. 2018). Physiologically there are few relevant constraints so the answer to this question turns more on social norms and trade-offs. While there are likely to be societal benefits from men coming to some amicable agreement over the partitioning of reproduction (e.g., Alexander 1979; Hawkes et al. 1995; Henrich et al. 2012), the precise means whereby this happens are unclear. Of course paternal provisioning and complementary biparental care play a big role in structuring the trade-offs that shape men's reproductive strategy (Kaplan 1996; Kaplan et al. 2009; Hooper et al. 2014), but how exactly these check acute competition among males is still unclear. What might account for the relatively (compared to non-humans, see below) muted male variance? There may be aspects of male provisioning that are not infinitely divisible among wives, mates and offspring that render the marrying of many wives fitness-depleting (Fortunato & Archetti 2009). Or perhaps the explanation lies in the particular structure of wealth inequality. Ross et al (2018) show how when wealth is not only very unequally distributed but skewed towards the very few men who own the lion's share of the wealth, there are simply too few men to pass the polygyny threshold holding too higher percentage of the wealth, serving to reduce both polygyny and male reproductive variance (see also Oh et al. Under review). Or maybe the effects of social censor (effectively punishment) of deviant males who break the norms of sexual behaviour are sufficient (as Smith et al. 2001 proposed in their critique of evolutionary arguments concerning rape); even then, however, the origin of these values regarding morality and justice need explanation, as they are clearly not universal.

Let us turn now to the general expectation from the Darwin-Bateman Paradigm that women will exhibit less variability in reproductive success than men. As reviewed above, there are both theoretical and empirical grounds for scrutinizing the underlying assumptions and evidence associated with this idea. Looking specifically at humans, Brown et al (2009) catalogue how variation in women's reproductive success may have been seriously underestimated. One problem is poor data on extramarital births, although this is a problem for birth histories of both males and females, (and more so for males if children typically reside with their biological mothers than their biological fathers). A second problem arises from the almost universalistic assumption regarding the critical importance to women of paternal care in their offspring, namely that their reproductive success is highly contingent on male care. While biparental care is undoubtedly a central adaptation within human evolution (Kaplan & Lancaster 2003), this does not mean that under specific circumstances women cannot show as great a variance in reproductive success than men, nor that they cannot find provisioning elsewhere (Hrdy 2005; Kramer & Ellison 2010). Indeed among the Pimbwe farmers, fishers and hunters of Tanzania there is no significant variance in mating or reproductive success between men and women

(Borgerhoff Mulder 2009; Borgerhoff Mulder & Ross 2019). Furthermore men must also be concerned with the survival of their children and the paternity of their next child, and this can lead to somewhat counter-intuitive predictions (*vis à vis* the Darwin–Bateman Paradigm) regarding what is, or is not, in both men's and women's fitness interests (Moya et al. 2016). However perhaps the most serious problem noted by Brown et al. (2009), arises from the labels that we typically use for marriage systems — monogamy, serial monogamy and polygyny. Notably serial monogamy proxies for serial monogyny but not serial monandry. As such, even though polyandrous marriage as an institution is rare, our reliance on formal labels makes women who mate and/or marry multiply appear to be much less numerous than they are (see also Starkweather & Hames 2012). In short, because humans are so variable in how they organize both their production and reproduction, and the labels for marriage systems are somewhat male-biased, we suspect that human populations are unlikely to conform uniformly to Bateman's first (and second) principles as initially expected.

To address this lack of systematic data with which to compare variance in reproductive success between men and women, and how such sex differences might differ from those of non-human social mammals, Ross et al. (In revision) analysed reproductive records from 97 small scale societies. We find that humans in these populations show significantly lower sex differences in reproductive inequality than non-human mammals. More intriguingly for the argument here, however, the difference between humans and non-human mammals (and particularly non-human primates), primarily reflects increased reproductive inequality among women rather than decreased reproductive variance among men.

This result suggest that much more attention should be directed in evolutionary demography to the factors responsible for variation among women, and the patterning of competition among women (for an overview see Fisher et al. 2013), possibly within the theoretical framework of cooperative breeding (Cant et al. 2009; Hill & Hurtado 2009; Lahdenpera et al. 2012; Mace & Alvergne 2012). Cooperative breeding promotes reproductive competition within families over the use of communally held resources (both material resources and access to helpers). Some have suggested that humans evolved as cooperative breeders, on the grounds that in many societies families/households consist of multiple adults, and reproductive-aged adults often help to provision or care for children at cost to their own reproduction. Intriguingly many issues here align with discussions among demographers over the definition of a household (Randall et al. 2011) and the cleavages therein with respect to intergenerational transmission (Quisumbing & Maluccio 2003) and illegitimacy (Koster 2018).

What We (Don't) Know about Bateman's Third Principle in Humans

Perhaps because of the lack of interest in variance in reproductive success among women, there are few published Bateman gradients for humans.¹ Moorad (2011) focuses on a colonizing population with polygyny and relatively high fertility (nineteenth-century Utah), and Jokela et al. (2010), Käär et al. (1998) and Courtiol et al. (2012) on socially monogamous populations where multiple mating basically derives from divorce or widowhood (twentieth-century US

¹ This does not mean that such information would be unavailable after a systematic literature review, insofar as fertility can additionally be inferred from parity distributions. Notably, however, data on childbearing across multiple unions for males and females are rarely available in national censuses (Guzzo 2014).

citizens, eighteenth-/nineteenth-century Sami herders, and eighteenth-/nineteenth-century Finns respectively). In each case only men clearly benefitted from mating with different partners, whether through simultaneous (polygyny) or successive marriages (see, for more evidence on outcomes associated with second marriages, Forsberg & Tullberg 1995; Leonetti et al. 2007). Less conventional sex differences in the effects of mating success and reproductive success are found in the Pimbwe (Borgerhoff Mulder 2009) and the Hadza hunter-gatherers of Tanzania (Blurton Jones 2016), as discussed below.

Rather than simply counting partners to determine how mating strategies affect fitness, others have focused on the mechanisms whereby individuals can acquire multiple mates — through extra-marital affairs (including informal polyandry and partible paternity) as well as through multiple and/or serial marriages (or partnerships) with divorce. These issues (recently reviewed by Scelza 2013) are examined first, insofar as they can impact associations between partner number and reproductive success, before proposing a new way of unpacking the Bateman gradient.

Extrapair matings can potentially increase men's reproductive success (as long recognized by evolutionary social scientists, Perusse 1993; see also von Rueden et al. 2011, who show that high status men can simultaneously increase marital reproductive success as well as achieve more extramarital relationships). Women too can increase their reproductive success through extramarital affairs, as shown for the southern African agropastoral Himba (Scelza 2012), although in all these kinds of studies the bias of differential discovery risk, as noted above (Gerlach et al. 2012), remains to be addressed. Of relevance here are studies of the effects of informal polyandry on women's fitness. While formal polyandry is rare, systems in which women have sexual partnerships with multiple men who bear some economic responsibility for the children they have sired ("informal polyandry" Starkweather & Hames 2012) are much more common (and likely underreported). Furthermore, there are some societies (notably in Amazonia) with so-called "partible paternity" (a belief that a woman's multiple lovers contribute biologically to her pregnancy); here children "fathered" by more than one man show enhanced survival rates, perhaps because of additional provisioning or some other safety net afforded children with multiple fathers (Hill & Hurtado 1996; Beckerman et al. 1998). However, there is as yet little understanding of the full range of fitness costs and benefits of such informal polyandry systems (Walker et al. 2010; Scelza & Prall 2017), and more generally of whether or not the provisions of multiple fathers should be viewed as substitutes or complements.

Turning to more formally recognized unions, divorce and remarriage for men is generally associated with greater reproductive success; indeed successive marriage is the primary factor contributing to the persistent finding (reviewed above) that men have higher variance in reproductive success than do women (e.g., Jokela et al. 2010). In part this is because, after a divorce or widowing, men are more likely to remarry than women (as seen consistently, for example, across historical populations, Dupaquier et al. 1981), in part because of a tendency to marry second wives much younger than themselves (e.g., Starks & Blackie 2000), and in part because of longer reproductive lifespans. Nevertheless in many studies reverse causality, or confounding factors, may be at play — is there anything special about men who do go on to second marriages; for example, in the Bantu population with whom I work, men with three or more marriages tend to have fewer surviving children, perhaps because they are unable to keep partners for any length of time (Borgerhoff Mulder 2009). Furthermore, remarriage does not

necessarily bring a man fitness advantages — gains in fertility with new mates must be offset against any reduced survival of existing children, particularly if his divorced wife remarries (Daly & Wilson 1998) or if her resources become stretched. Using estimates of some of these parameters across a number of small scale societies (e.g., Sear & Mace 2008) Winking and Gurven (2011) nevertheless show that men's benefits from remarriage commonly exceed the costs. So why don't men divorce more often, or more generally why don't men's reproductive interests conflict more starkly with those of women? Clearly the trade-offs will depend on many ecologically- and socially-induced factors such as the certainty of paternity in first and second marriages, the availability of unattached women, and the substitutability of paternal care, including the response of women to the withdrawal of their partners' support. These are all classic issues studied by behavioural ecologists interested in mating systems (Clutton-Brock 1991; Borgerhoff Mulder 1992; Moya et al. 2016) that would benefit from more systematic demographic analysis.

As regards the effects of divorce and remarriage on women, the situation is less clear. Generally demographers, especially those who conduct studies in western industrial contexts, find that widowed or divorced women who remarry have lower overall fertility than those whose first marriages are still intact (Cohen & Sweet 1974), although some women do make up for first marriage fertility deficits with their second marriage (Thornton 1978). Lower overall fertility among women who have had multiple marriages may be quite general insofar as childless women (or those with low fertility) are more likely to seek divorce/be divorced than women in more reproductively productive marriage — indeed across many cultures childlessness promotes divorce (Betzig 1989). Reviews of the divorce literature typically focus on the factors precipitating divorce in western countries, and on the much contested outcomes for children of divorced parents, with little to no investigation of the impact on (or associations with) reproduction (Amato 2010).

Even with the emergence of studies focusing on multiple-partner fertility (MPF, the production of children with more than one partner, see Guzzo 2014) estimating the effects of multiple partners on fertility have proven to be a “surprisingly difficult task” (:72). This results not only from the high data requirements for identifying MPF, the widely variable estimates resulting from different sampling and definitional procedures, and the strong sample selective forces at play. For example, although MPF individuals tend to have half a child more than those who reproduce with only one partner (although the children generally have poorer wellbeing and mental health outcomes). This higher fertility is partially attributable to the low education levels, early age at first birth, and deprived socioeconomic circumstances of MPF parents, effects not yet clearly untangled; furthermore, new relationships can, under some circumstances, precipitate new pregnancies to cement the relationship. Alternatively, where MPF is associated with lower fertility, this might reflect substantive causative factors, such as reduced support from kin (Harknett & Knab 2007) who are less inclined to invest in households with unrelated children. Lowered fertility among MPF individuals could also result from selective bias, such as infertility and/or marital discord, as well as the time lost to reproduction between marriages or partnerships. The complexity of these relationships is revealed in Lappegård and Rønsen's (2013) analysis showing that MPF among Norwegian women is most common in both the lowest and the highest socioeconomic strata — the former on account of high marital dissolution, the latter perhaps because of greater attractiveness of MPF to women with economic autonomy.

Clearly such nuanced studies of MPF, and indeed of the quality of partnership relationship (as reviewed in Balbo et al. 2013) can shed much needed mechanistic light on Bateman gradients for men and women.

In the evolutionary demographic literature, there are some scattered reports of women benefitting reproductively from multiple marriages. In a study of rural Bolivian women, those with three sequential marital partners have more children than woman with only one spouse (an anecdotal observation in Snopkowski 2016), which could result from remarrying wealthier men (as with US unmarried mothers, Bzostek et al. 2012). Similarly Indian Khasi women in second marriages show shorter interbirth intervals than women in first marriages (Leonetti et al. 2007), and Pimbwe women who marry three or more times show higher fertility and reproductive success by the time they reach menopause (Borgerhoff Mulder 2009). Causality, as Gerlach et al. (2012) note in their analysis of Bateman gradients, is of course again a problem here, insofar as self-selection (or the non-random assortment of individuals into different (here) marital statuses) can bias analyses; for example highly fecund and/or hard working women may attract the attention of new potential spouses, such that their high fertility drives their mating success. Furthermore it is quite plausible that other phenotypic traits, such as health, might affect both a woman's ability to re-partner multiple times and her production of surviving offspring, thereby creating a spurious correlation between mating success and reproductive success, as reviewed in Anthes et al (2017).

In sum, it is plausible, but in no way demonstrated, that multiple marriage or mating could be an adaptive mating strategy for women if the future fitness gains with different partners are greater than the future fitness with a current partner. A key parameter to consider here is availability of preferable outside options to the divorcing woman, which must be weighed against a host of social and ecological parameters which might include: the costs of lost paternal (assuming the children follow the mother) investment to child survival and subsequent success, the extent to which stepfathers exert negative effects on child outcomes, and, more generally, the strength of the social support network to which a woman has access and with whom her children might reside. Indeed, the varying significance of paternal investment may account for the association between high reproductive rates of extramarital sex and limited heritable wealth transmitted through the male line (Gaulin & Schlegel 1980). Again, systematic analyses, as larger comparative data sets become available, would pay off, especially if they pay attention to differentiating the factors precipitating marital dissolution and successful remarriage, how these might differ between the sexes (e.g., Snopkowski 2016), and what the specific mechanisms for differential fertility contingent on partner number might be (e.g., Lappegård & Rønsen 2013).

Finally, it is worth pointing out that demographers have been dealing with these issues for many years. At a symposium on marriage and remarriage in 1979 they debated the extent to which the negative effects of divorce and widowhood on overall fertility rates were compensated by remarriage (Dupaquier et al. 1981). This problem was deemed "insoluble" (:4) by Ashley Coale, and indeed ensuing chapters in the conference proceedings demonstrate the outcome is highly contingent on custom, religion, the division of labour, and property inheritance. Furthermore, it is eminently clear that the autonomy women enjoy with respect to their sexual behaviour is strongly influenced by laws that preferentially punish women's adultery over that of men, by genital mutilation, and by intimate partner violence, rendering the measure

of mating success a complex phenomenon. For all these reasons demographers would surely agree with evolutionary biologists that the Bateman's third principle not only needs careful measurement, but is unlikely to hold in all populations, and needs further unpacking with increasingly sophisticated statistical methods.

Unpacking Bateman

Why might Bateman's third principle hold in some populations but not others, and more interestingly why? To answer this question, we need to agree on what we mean by the term mating success. As reviewed above, evolutionary biologists studying sexual selection still disagree over how best to measure mating success. For those of us studying humans, this problem seems, *prima facie*, more straightforward. Demographers and ethnographers have for many years relied primarily on simply counting marriages, although increasingly investigators use more culturally appropriate arrangements, as Guzzo (2014) reviews historically for the USA and as anthropologists determine for their particular field contexts (e.g., Borgerhoff Mulder 2009; Scelza 2012). Leaving aside "known unknowns", such the issue of misreported or unknown paternities (which could presumably be integrated into a Bayesian uncertainty coefficient on the basis of population level estimates, Anderson 2006), should we simply be counting the number of partners/spouses? Or would we benefit from a decomposition of some of the elements of mating success?

Nicholas Blurton Jones (2016) decided counting spouses was not the best way to go forward. In his analysis of Bateman gradients in Hadza foragers of Tanzania, he chose the proportion of adult lifespan spent married as the best proxy of mating success, irrespective of the number of individuals partnered. He finds that Hadza men who spend much of their adult life married have the highest reproductive success whereas there is no systematic relationship for women between their success (in keeping children alive, the outcome measure is not directly comparable) and the proportion of their lifetime spent married.

In my review (Borgerhoff Mulder 2017) I queried why the amount of time spent married was the best measure of successful mating. It seemed to me there was more to mating success than keeping a spouse. I suggested that (from a female's point of view) "...if husbands are important and I am stuck with a bad one, best to ditch him and skip to another, even if it costs me a little time" (:126, and of course precisely the same argument can be made from a man's perspective). In other words, I questioned whether the percent of adult lifespan married is, on its own, a good proxy for mating success. There is undoubtedly some intuitive sense to Blurton Jones' decision — the ability to retain mates is important, especially if they are high quality and if constant biparental care from biological parents is important to child outcomes. Furthermore, he is correct to recognize that the effect of mate number on reproductive success is neither the only, nor indeed necessarily the most interesting, dimension on which the two sexes differ (a point now well recognized in sexual selection theory, as reviewed above). But is amount of time spent married really the best operationalization of mating success?

Motivated by this question, and the more general struggle demographers face in drawing inferences about the effects of divorce and remarriage/partnering on fertility (on account of causality and potential spurious correlations), a priority for evolutionary anthropologists now is to unpack the Bateman gradient.

Accordingly, we (Borgerhoff Mulder & Ross 2019) decided to reanalyse an updated and larger sample from the Pimbwe, a rural Bantu population of fishers, foragers and farmers living in western Tanzania. Rather than differentiating extrapair matings from divorce/remarriage (difficult insofar as the first so often leads to the second), and premarital sex from first marriages (again challenging without exact dates of relationship formation and/or pregnancies) we took a simpler (and more catholic) course, one also more suited to future comparative studies. We decided to develop models within which we could distinguish the effect of the number of different individuals with whom he/she had been married (or partnered) from number of years a focal individual has been married or partnered (as well as from the timing of the partnership, and partner quality, not discussed further here). To do this we use local concepts of “marriage” based on co-residence or shared parenthood. In many respects our “number of different individuals” parallels the new wave in conventional demography focusing on multiple-partner fertility (reviewed above), although we also include marriages/partnerships that are childless insofar as these entail effort towards mating success. In this way we can start unpacking the concept of mating success.

We show first that while men and women both benefit from the number of years they are married, men benefit more than do women. This is consistent with the Bateman’s third principle, and likely reflects the existence of some polygyny in this population, as well as longer male reproductive lifespans. Second, and contrary to Bateman’s third principle, women benefit whereas men suffer reproductively from increasing their number of mates, holding constant the effective time-frame over which they have been married. In this way we reveal distinct, sex-specific pathways (with respect to “mating success”) through which reproductive success can be optimized. In short, we propose a model for analysing the effects of the number of years an individual is partnered, the number of distinct partners, as well as the timing and quality of these partnerships. This decomposition of mating success into its various components may prove useful in structuring future comparative analyses of Bateman’s third principle in a more systematic way, as in the non-human studies reviewed above. Furthermore, it will be particularly valuable as more individual-level trait (such as economic status and education) are incorporated into the model as weights affecting fertility both directly and through marriage.

Future Horizons

In reviewing the status of Bateman’s contributions to human demography I have identified where the amplification and refinement of his ideas reveal lacunae in our knowledge as evolutionary demographers. Particularly puzzling is why men don’t have greater variability in reproductive success, especially in small-scale societies with little rival familial wealth to distribute among multiple offspring. Despite polygyny and serial monogamy, human males fall at the low end of variance in male fitness among mammals. I also noted the unusually high (again from a mammalian perspective) reproductive inequality among women. Finally, I pointed to the need for a better understanding of both the patterning of the Bateman gradients, and the social and ecological factors responsible for this variability.

With respect to the Bateman gradient, I proposed an unpacking of the concept of mating success, for two reasons. First, it is becoming increasingly clear from the debates over the Darwin-Bateman Paradigm that sexual selection is a hugely complex process, requiring highly dynamic modelling of a large number of traits (both fixed and context dependent) that are changing in

both evolutionary and ecological time. Even in nonhumans, where experimentation is possible, there is as yet very limited understanding of how genetic architecture, environmental dynamics and social interactions affect the continuous evolution of sexually selected traits (Kuijper et al. 2012). Second, there have been some puzzling discrepancies within human evolutionary demography with respect to how mating success is measured — number of spouses or number of years in marriage (Blurton Jones 2016; Borgerhoff Mulder 2017). Examining the distinct effects of each (spousal years and number of different spouses) may prove helpful in parsing out various dimensions of sex differences in reproductive strategy across different human populations. As an increasing number of studies with individual level data become available from multi-sited field research (Lawson et al. 2015), large national surveys (Snopkowski & Sear 2013) and compilations of individual studies (Borgerhoff Mulder et al. 2009) such simplifications may provide a useful first step for understanding sex differences in reproductive strategy as captured by the Bateman gradient.

Evolutionary social scientists' study of the Bateman gradient, perhaps unsurprisingly, focus primarily on marriage and its effects on men's fitness. Most researchers hail from western cultures where, until relatively recently, marriage was believed to play a large role in structuring reproduction, and where divorce typically promotes marriages of older men to younger women (Starks & Blackie 2000); as noted by Guzzo (2014), the conceptual tools of demographers reflect, presumably with some lag, actual behaviour on the ground. Indeed, as Nicholas Blurton Jones has pointed out (pers. comm.), it is largely researchers with longitudinal data from societies very different from our own (Borgerhoff Mulder 2009; Winking & Gurven 2011; Scelza 2012; Blurton Jones 2016) who recognize the stark economic and social trade-offs for men *and women* in sticking with one partner as opposed to engaging in the often dangerous pursuit of new partners, although again this is of course changing.

Darwin and Bateman's arguments reflected contemporary cultural values regarding women. Darwin was influenced by Victorian standards of his day (Hrdy 1997; Dewsbury 2005) and maybe Bateman was aware of the concerted campaign to get women out of the labour force and into the home following their active engagement in industrial production and other war-related activities (Tarrant 2006). Current discussions of the Darwin-Bateman paradigm are increasingly taking place in a very different world, one where not only sex roles but sexual identities are far less binary than ever imagined in the past; as such, posing sexual selection within a more gender-neutral framework is appealing (Gowaty & Hubbell 2005). We have clearly moved far from the Darwin-Bateman Paradigm view of sex roles as heavily bifurcated between choosy females versus indiscriminate and competitive males, with respect to theory development, empirical understanding of the animal kingdom, and our conceptualizations of gender in human society. We understand now that not only are sex roles highly flexible, but that they can be difficult to assign on the basis of single traits, as indicated in recent debates over the foundational role of anisogamy (Schärer et al. 2012; Ah-King & Ahnesjö 2013; Kokko et al. 2013); in fact there are some species without anisogamy, where only "mating types" can be identified. As such, there are plenty of new avenues for exchanging ideas between the natural and social sciences yet to explore. Although the purpose of this chapter has been to open up new questions for thinking about sexual selection within evolutionary demography, there are equally intriguing strands to follow with respect to how our current social concerns shape our science.

Acknowledgements

I could not have written this chapter without the work of my collaborators Cody Ross and Paul Hooper. I have also benefitted from the comments of Brooke Scelza, Kristin Snopkowski and Rebecca Sear and Alessandra Cassar, from communications with Nick Blurton Jones, and from colleagues at the Centre for Ecology and Conservation at the University of Exeter – Penryn.

References²

- Ah-King M, Ahnesjö I. 2013. 'The "sex role" concept: an overview and evaluation'. *Evolutionary biology*, 40.4: pp. 461–70. <https://doi.org/10.1007/s11692-013-9226-7>
- Alexander RD. 1974. 'The evolution of social behavior'. *Annual review of ecology and systematics*, 5.1: pp. 325–83. <https://doi.org/10.1146/annurev.es.05.110174.001545>
- Alexander RD. 1979. *Darwinism and human affairs*. University of Washington Press, Seattle.
- Alexander RD, Hoogland JL, Howard RD, Noonan KM, Sherman PW. 1979. 'Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans'. Pp. 402–35 in Chagnon NA, and Irons W, editors. *Evolutionary Biology and Human Social Behavior: An anthropological perspective*. Duxbury, North Scituate, Mass.
- Amato PR. 2010. 'Research on divorce: Continuing trends and new developments'. *Journal of Marriage and Family*, 72.3: pp. 650–66. <https://doi.org/10.1111/j.1741-3737.2010.00723.x>
- Anderson KG. 2006. 'How well does paternity confidence match actual paternity? Results from worldwide nonpaternity rates'. *Current Anthropology*, 47. 3: pp. 511–18. <https://doi.org/10.1086/504167>
- Anthes N, Häderer IK, Michiels NK, Janicke T. 2017. 'Measuring and interpreting sexual selection metrics: evaluation and guidelines'. *Methods in Ecology and Evolution*, 8.8: pp. 918–31. <https://doi.org/10.1111/2041-210x.12707>
- Arnold SJ. 1994. 'Bateman's principles and the measurement of sexual selection in plants and animals'. *American Naturalist*, 144: pp. S126–S149. <https://doi.org/10.1086/285656>
- Balaresque P, Poulet N, Cussat-Blanc S, Gerard P, Quintana-Murci L, Heyer E, Jobling MA. 2015. 'Y-chromosome descent clusters and male differential reproductive success: young lineage expansions dominate Asian pastoral nomadic populations'. *European Journal of Human Genetics*, 23.10: pp. 1413–22. <https://doi.org/10.1038/ejhg.2014.285>
- Balbo N, Billari FC, Mills M. 2013. 'Fertility in advanced societies: A review of research'. *European Journal of Population/Revue européenne de Démographie*, 29.1: pp. 1–38. <https://doi.org/10.1007/s10680-012-9277-y>
- Barrett L, Dunbar RIM, Lycett J 2002. *Human evolutionary psychology*. Palgrave, Basingstoke, UK.
- Bateman AJ. 1948. 'Intrasexual selection in *Drosophila*'. *Heredity*, 2.3: pp. 349–68. <https://doi.org/10.1038/hdy.1948.21>
- Beckerman S, Lizarralde R, Ballew C, Schroeder S, Fingelton C, Garrison A, Smith H. 1998. 'The Bari partible paternity project: Preliminary results'. *Current Anthropology*, 39.1: pp. 164–67. <https://doi.org/10.1086/204706>
- Betzig L. 1989. 'Causes of Conjugal Dissolution: A Cross-cultural study'. *Current Anthropology*, 30.5: pp. 654–76. <https://doi.org/10.1086/203798>
- Betzig L. 2012. 'Means, variances and ranges in reproductive success: Comparative evidence'. *Evolution and Human Behavior*, 33.4: pp. 309–17. <https://doi.org/10.1016/j.evolhumbehav.2011.10.008>

2 Note this chapter has been posted on the Open Science Framework website since 06/01/2020, after it was accepted for publication, so the references will reflect when the chapter was written and not the OBP publication date.

- Betzig LL 1986. *Despotism and differential reproduction: A Darwinian view of history*. Aldine de Gruyter, Hawthorne, NY.
- Bird R. 1999. 'Cooperation and conflict: The behavioural ecology of the sexual division of labor'. *Evolutionary Anthropology*, 8.2: pp. 65–75. [https://doi.org/10.1002/\(sici\)1520-6505\(1999\)8:2%3C65::aid-evan5%3E3.0.co;2-3](https://doi.org/10.1002/(sici)1520-6505(1999)8:2%3C65::aid-evan5%3E3.0.co;2-3)
- Birkhead T. 1998. 'Cryptic female choice: criteria for establishing female sperm choice'. *Evolution*, 52.4: pp. 1212–18. <https://doi.org/10.2307/2411251>
- Birkhead TR. 2000. *Promiscuity*. Harvard University Press, Cambridge, MA.
- Blurton Jones N. 1986. 'Bushman birth spacing: A test for optimal interbirth intervals'. *Ethology and Sociobiology*, 7.2: pp. 91–105. [https://doi.org/10.1016/0162-3095\(86\)90002-6](https://doi.org/10.1016/0162-3095(86)90002-6)
- Blurton Jones N 2016. *Demography and Evolutionary Ecology of Hadza Hunter-Gatherers*. Cambridge University Press, Cambridge.
- Bongaarts J. 1976. 'Intermediate fertility variables and marital fertility rates'. *Population Studies*, 30.2: pp. 227–41. <https://doi.org/10.2307/2173606>
- Borgerhoff Mulder M. 1990. 'Kipsigis women's preferences for wealthy men: Evidence for female choice in mammals'. *Behavioural ecology and Sociobiology*, 27.4: pp. 255–64. <https://doi.org/10.1007/bf00164897>
- Borgerhoff Mulder M. 1992. 'Reproductive decisions'. Pp. 339–74 in Smith EA, and Winterhalder B, editors. *Evolutionary ecology and human behavior*. Aldine de Gruyter, New York.
- Borgerhoff Mulder M. 2009. 'Serial monogamy as polygyny or polyandry? Marriage in the Tanzanian Pimbwe'. *Human Nature*, 20.2: pp. 130–50. <https://doi.org/10.1007/s12110-009-9060-x>
- Borgerhoff Mulder M. 2010. 'The unusual women of Mpimbwe: why sex differences in humans are not universal'. Pp. 85–106. *Mind the Gap*. Springer.
- Borgerhoff Mulder M. 2017. 'Review of Demography and Evolutionary Ecology of Hadza Hunter-Gatherers by Nicholas Blurton Jones'. *Human Nature*, 28.1: pp. 117–27. <https://doi.org/10.1007/s12110-016-9280-9>
- Borgerhoff Mulder M, et al. 2009. 'Intergenerational wealth transmission and the dynamics of inequality in small-scale societies'. *Science*, 326.5953: pp. 682–88. <https://doi.org/10.1126/science.1178336>
- Borgerhoff Mulder M, Rauch KL. 2009. 'Sexual conflict in humans: Variations and Solutions'. *Evolutionary Anthropology*, 18.5: pp. 201–14. <https://doi.org/10.1002/evan.20226>
- Borgerhoff Mulder M, Ross CT. 2019. 'Unpacking Mating Success and Testing Bateman's Principles in a Human Population'. *Proceedings of Royal Society B*. 286.1908: p. 20191516. <https://doi.org/10.1098/rspb.2019.1516>
- Brown DE, Hotra D. 1988. 'Are prescriptively monogamous societies effectively monogamous'. Pp. 153–59 in Betzig L, Borgerhoff Mulder M, and Turke PW, editors. *Human reproductive behaviour: a Darwinian perspective*. Cambridge University Press, Cambridge.
- Brown GR, Laland KN, Borgerhoff Mulder M. 2009. 'Bateman's principles and human sex roles'. *Trends in Ecology & Evolution*, 24.6: pp. 297–304. <https://doi.org/10.1016/j.tree.2009.02.005>
- Buss DM 1999. *Evolutionary psychology: the new science of the mind*. Allyn and Bacon, Boston.
- Bzostek SH, McLanahan SS, Carlson MJ. 2012. 'Mothers' Repartnering after a Nonmarital Birth'. *Social Forces*, 90.3: pp. 817–41. <https://doi.org/10.1093/sf/sos005>
- Campbell MM, Prata N, Potts M. 2013. 'The impact of freedom on fertility decline'. *J Fam Plann Reprod Health Care*, 39.1: pp. 44–50. <https://doi.org/10.1136/jfprhc-2012-100405>
- Cant MA, Johnstone RA, Russell AF. 2009. 'Reproductive conflict and the evolution of menopause' in Hager R, and Jones CB, editors. *Reproductive skew in vertebrates: Proximate and ultimate causes*. Cambridge University Press, Cambridge.
- Chagnon N. 1988. 'Life histories, blood revenge, and warfare in a tribal population'. *Science*, 239.4843: pp. 985–39. <https://doi.org/10.1126/science.239.4843.985>

- Chagnon NA, Irons W 1979. *Evolutionary biology and human social behavior: an anthropological perspective*. Duxbury Press, North Scituate, Mass.
- Clutton-Brock T 1991. *The evolution of parental care*. Princeton University Press, Princeton.
- Clutton-Brock T. 2009. 'Sexual selection in females'. *Animal Behaviour*, 77.1: pp. 3–11. <https://doi.org/10.1016/j.anbehav.2008.08.026>
- Clutton-Brock TH, Huchard E. 2013. 'Social competition and selection in males and females'. *Philosophical Transactions of the Royal Society B*, 368:20130074. <https://doi.org/10.1098/rstb.2013.0074>
- Cohen SB, Sweet JA. 1974. 'The Impact of Marital Disruption and Remarriage on Fertility'. *Journal of Marriage and Family*, 36.1: pp. 87–96. <https://doi.org/10.2307/350998>
- Collet JM, Dean RF, Worley K, Richardson DS, Pizzari T. 2014. 'The measure and significance of Bateman's principles'. *Proceedings of the Royal Society B: Biological Sciences*, 281.1782: p. 20132973. <https://doi.org/10.1098/rspb.2013.2973>
- Courtioi A, Pettay JE, Jokela M, Rotkirch A, Lummaa V. 2012. 'Natural and sexual selection in a historical polygynous population'. *Proceedings of the National Academy of Science*, 109.21: pp. 8044–49. <https://doi.org/10.1073/pnas.1118174109>
- Crook JH, Crook SJ. 1988. 'Tibetan polyandry: Problems of adaptation and fitness'. Pp. 97–114 in Betzig L, Borgerhoff Mulder M, and Turke P, editors. *Human reproductive behavior: A Darwinian perspective*. Cambridge University press, Cambridge.
- Daly M, Wilson M 1978. *Sex, Evolution, and Behavior*. Duxbury Press, North Scituate.
- Daly M, Wilson M 1998. *The Truth about Cinderella*. Weidenfeld & Nicolson, London.
- Dewsbury DA. 2005. 'The Darwin-Bateman paradigm in historical context'. *Integrative and Comparative Biology*, 45.5: pp. 831–37. <https://doi.org/10.1093/icb/45.5.831>
- Dickemann M. 1979. 'The ecology of mating systems in hypergynous dowry systems'. *Social Science Information*. 18.2: pp. 163–95. <https://doi.org/10.1177/053901847901800201>
- Dupaquier J, Helin E, Laslett P, Livi-Bacci M, Sogner S, editors. 1981. *Marriage and REmarriage in Populations of the Past*. Academic Press, London.
- Eagly AH, Wood W. 1999. 'The origins of sex differences in human behavior – Evolved dispositions versus social roles'. *American Psychologist*, 54.6: pp. 408–23. <https://doi.org/10.1037/0003-066x.54.6.408>
- Eberhard WG 1996. *Female control: sexual selection by cryptic female choice*. Princeton University Press, Princeton, NJ.
- Fisher ML, Garcia JR, Chang RS 2013. *Evolution's empress: Darwinian perspectives on the nature of women*. Oxford University Press.
- Flinn MV, Low BS. 1986. 'Resource distribution, social competition, and mating patterns in human societies'. Pp. 217–43 in Rubenstein DI, and Wrangham RW, editors. *Ecological aspects of social evolution: birds and mammals*. Princeton University Press, Princeton, N.J.
- Folbre N. 1983. 'Of patriarchy born: The political economy of fertility decisions'. *Feminist Studies*, 9.2: pp. 261–84. <https://doi.org/10.2307/3177490>
- Forsberg AJL, Tullberg BS. 1995. 'The relationship between cumulative number of cohabiting partners and number of children for men and women in modern Sweden'. *Ethology and Sociobiology*, 16.3: pp. 221–32. [https://doi.org/10.1016/0162-3095\(95\)00003-4](https://doi.org/10.1016/0162-3095(95)00003-4)
- Fortunato L, Archetti M. 2009. 'Evolution of monogamous marriage by maximization of inclusive fitness'. *Evolutionary Biology*, 23.1: pp. 149–56. <https://doi.org/10.1111/j.1420-9101.2009.01884.x>
- Gagnon M-C, Duchesne P, Turgeon J. 2012. 'Sexual conflict in *Gerris gillettei* (Insecta: Hemiptera): influence of effective mating rate and morphology on reproductive success'. *Canadian journal of zoology*, 90.11: pp. 1297–1306. <https://doi.org/10.1139/z2012-098>

- Gasparini C, Evans JP. 2018. 'Female control over multiple matings increases the opportunity for postcopulatory sexual selection'. *Proceedings of the Royal Society B: Biological Sciences*, 285:1888: p. 20181505. <https://doi.org/10.1098/rspb.2018.1505>
- Gaulin SJC, Schlegel A. 1980. 'Paternal confidence and paternal investment: a cross cultural test of a sociobiological hypothesis'. *Ethology and Sociobiology*, 1.4: pp. 301–09. [https://doi.org/10.1016/0162-3095\(80\)90015-1](https://doi.org/10.1016/0162-3095(80)90015-1)
- Gerlach N, McGlothlin J, Parker P, Ketterson E. 2012. 'Reinterpreting Bateman gradients: multiple mating and selection in both sexes of a songbird species'. *Behavioural ecology*, 23.5: pp. 1078–88. <https://doi.org/10.1093/beheco/ars077>
- Gowaty P, Steinichen R, Anderson WW. 2002. 'Mutual interest between the sexes and reproductive success in *Drosophila pseudoobscura*'. *Evolution*, 56.12: pp. 2537–40. [https://doi.org/10.1554/0014-3820\(2002\)056\[2537:mibtsa\]2.0.co;2](https://doi.org/10.1554/0014-3820(2002)056[2537:mibtsa]2.0.co;2)
- Gowaty PA. 1997. 'Sexual dialectics, sexual selection, and variation in reproductive behavior'. Pp. 351–84 in Gowaty PA, editor. *Feminism and evolutionary biology*. Chapman and Hall, New York.
- Gowaty PA, Hubbell SP. 2005. 'Chance, time allocation, and the evolution of adaptively flexible sex role behavior'. *Integrative and Comparative Biology*, 45.5: pp. 931–44. <https://doi.org/10.1093/icb/45.5.931>
- Gowaty PA, Kim Y-K, Anderson WW. 2012. 'No evidence of sexual selection in a repetition of Bateman's classic study of *Drosophila melanogaster*'. *Proceedings of the National Academy of Sciences*, 109.29: pp. 11740–11745. <https://doi.org/10.1073/pnas.1207851109>
- Guzzo KB. 2014. 'New partners, more kids: Multiple-partner fertility in the United States'. *The ANNALS of the American Academy of Political and Social Science*, 654.1: pp. 66–86. <https://doi.org/10.1177/0002716214525571>
- Harknett K, Knab J. 2007. 'More kin, less support'. *Journal of Marriage and Family*, 69.1: pp. 237–53. <https://doi.org/10.1111/j.1741-3737.2006.00356.x>
- Hartung J. 1982. 'Polygyny and the inheritance of wealth'. *Current Anthropology*, 23.3: pp. 1–12. <https://doi.org/10.1086/202775>
- Hauber ME, Lacey EA. 2005. 'Bateman's principle in cooperatively breeding vertebrates: the effects of non-breeding alloparents on variability in female and male reproductive success'. *Integrative and Comparative Biology* 45.5: pp. 903–14. <https://doi.org/10.1093/icb/45.5.903>
- Hawkes K, Rogers AR, Charnov EL. 1995. 'The Males Dilemma – Increased Offspring Production Is More Paternity to Steal'. *Evolutionary Ecology*, 9.6: pp. 662–77. <https://doi.org/10.1007/bf01237661>
- Henrich J, Boyd R, Richerson PJ. 2012. 'The puzzle of monogamous marriage'. *Philosophical Transactions of the Royal Society (B)*, 367.1589: pp. 657–69. <https://doi.org/10.1098/rstb.2011.0290>
- Henshaw JM, Jennions MD, Kruuk LE. 2018. 'How to quantify (the response to) sexual selection on traits'. *Evolution*, 72.9: pp. 1904–17. <https://doi.org/10.1111/evo.13554>
- Hill K, Hurtado AM 1996. *Aché life history: the ecology and demography of a foraging people*. Aldine de Gruyter, New York.
- Hill K, Hurtado AM. 2009. 'Cooperative breeding in South American hunter-gatherers'. *Proceedings of Royal Society B*. 276.1674: pp. 3863–70. <https://doi.org/10.1098/rspb.2009.1061>
- Hooper PL, Gurven M, Kaplan H. 2014. 'Social and economic underpinnings of human biodemography', in Weinstein M, and MA. L, editors. *Sociality, Hierarchy, Health: Comparative Biodemography*. National Academies Press.
- Hrdy S. 1997. 'Raising Darwin's consciousness: female sexuality and the prehuman origins of patriarchy'. *Human Nature*, 8.1: pp. 1–49. <https://doi.org/10.1007/s12110-997-1003-9>
- Hrdy SB. 1986. 'Empathy, polyandry, and the myth of the coy female'. Pp. 119–46 in Bleier R, editor. *Feminist approaches to science*. Pergamon Press, New York.

- Hrdy SB. 2005. 'Cooperative breeders with an ace in the hole'. Pp. 295–317 in Volland E, Chasiotis A, and Schiefenhoewel W, editors. *Grandmotherhood: the evolutionary significance of the second half of female life*. Rutgers University Press, New Brunswick.
- Irons W. 1979. 'Cultural and biological success'. Pp. 252–72 in Chagnon NA, and Irons W, editors. *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*. Duxbury Press, North Scituate.
- Janicke T, David P, Chapuis E. 2015. 'Environment-dependent sexual selection: Bateman's parameters under varying levels of food availability'. *The American Naturalist*, 185.6: pp. 756–68. <https://doi.org/10.1086/681128>
- Janicke T, Häderer IK, Lajeunesse MJ, Anthes N. 2016. 'Darwinian sex roles confirmed across the animal kingdom'. *Science Advances*, 2.2. <https://doi.org/10.1126/sciadv.1500983>
- Jennions MD, Fromhage L. 2017. 'Not all sex ratios are equal: the Fisher condition, parental care and sexual selection'. *Phil. Trans. R. Soc. B*, 372.1729: p. 20160312. <https://doi.org/10.1098/rstb.2016.0312>
- Jennions MD, Petrie M. 2000. 'Why do females mate multiply?' *Biological Reviews of the Cambridge Philosophical Society*, 75.1: pp. 21–64. <https://doi.org/10.1017/s0006323199005423>
- Jokela M, Rotkirch A, Rickard I, Pettay J, Lummaa V. 2010. 'Serial monogamy and reproductive success in a contemporary human population'. *Behavioural ecology*, 10: pp. 906–12.
- Jones AG. 2009. 'On the Opportunity for Sexual Selection, the Bateman Gradient and the Maximum Intensity of Sexual Selection'. *Evolution*, 63.7: pp. 1673–84. <https://doi.org/10.1111/j.1558-5646.2009.00664.x>
- Jones AG, Rosenqvist G, Berglund A, S.J. A, J.C. A. 2000. 'The Bateman gradient and the cause of sexual selection in a sex-role-reversed pipefish'. *Proc. R. Soc. B*, 267.1444: pp. 677–80. <https://doi.org/10.1098/rspb.2000.1055>
- Käär P, Jokela J, Merilä J, Helle T, Kojola I. 1998. 'Sexual conflict and remarriage in preindustrial human populations: Causes and fitness consequences'. *Evolution and Human Behavior*, 19.3: pp. 139–51. [https://doi.org/10.1016/s1090-5138\(98\)00007-5](https://doi.org/10.1016/s1090-5138(98)00007-5)
- Kaplan H. 1996. 'A theory of fertility and parental investment in traditional and modern human societies'. *Yearbook of Physical Anthropology*, 101.S23: pp. 91–135. [https://doi.org/10.1002/\(SICI\)1096-8644\(1996\)23+%3C91::AID-AJPA4%3E3.0.CO;2-C](https://doi.org/10.1002/(SICI)1096-8644(1996)23+%3C91::AID-AJPA4%3E3.0.CO;2-C)
- Kaplan H, Hill K. 1985. 'Hunting ability and reproductive success among male Ache foragers: preliminary results'. *Current anthropology*, 26.1: pp. 131–33. <https://doi.org/10.1086/203235>
- Kaplan HS, Hooper PL, Gurven M. 2009. 'The evolutionary and ecological roots of human social organization'. *Phil. Trans. R. Soc Lond. B*, 364.1533: pp. 3289–99. <https://doi.org/10.1098/rstb.2009.0115>
- Kaplan HS, Lancaster JB. 2003. 'An evolutionary and ecological analysis of human fertility, mating patterns, and parental investment'. Pp. 170–223 in Wachter KW, and Bulatao RA, editors. *Offspring: Human Fertility Behavior in Biodemographic Perspective*. National Academies Press, Washington DC.
- Ketterson ED, Parker PG, Raouf SA, Nolan Jr V, Ziegenfus C, Chandler CR. 1998. 'The relative impact of extra-pair fertilizations on variation in male and female reproductive success in dark-eyed juncos (*Junco hyemalis*)'. *Ornithological Monographs*, 49: pp. 81–101. <https://doi.org/10.2307/40166719>
- Klug H, Alonsi SH, Bonsall MB. 2012. 'Theoretical Foundations of Parental Care' in Royle NJ, Smiseth PT, and Kölliker M, editors. *The Evolution of Parental Care*. Oxford University Press, Oxford.
- Klug H, Heuschele J, Jennions MD, Kokko H. 2010. 'The mismeasurement of sexual selection'. *Journal of Evolutionary Biology*, 23.3: pp. 447–62. <https://doi.org/10.1111/j.1420-9101.2009.01921.x>
- Kokko H, Booksmythe I, Jennions MD. 2013. 'Causality and sex roles: prejudice against patterns? A reply to Ah-King'. *Trends in ecology & evolution*. 28.1: pp. 2–4. <https://doi.org/10.1016/j.tree.2012.08.008>
- Kokko H, Jennions MD. 2008. 'Parental investment, sexual selection and sex ratios'. *Journal of Evolutionary Biology*, 21.4: pp. 919–48. <https://doi.org/10.1111/j.1420-9101.2008.01540.x>
- Kokko H, Jennions MD. 2012. 'Sex Differences in Parental Care' in Royle N, Smiseth PT, and Kölliker M, editors. *The Evolution of Parental Care*. Oxford University Press, Oxford.

- Koster J. 2018. 'Family ties: the multilevel effects of households and kinship on the networks of individuals'. *R. Soc. Open Sci.*, 5.4: p. 172159. <https://doi.org/10.1098/rsos.172159>
- Krakauer AH, Webster MS, Duvall EH, Jones AG, Shuster SM. 2011. 'The opportunity for sexual selection: Not mismeasured, just misunderstood'. *Journal of Evolutionary Biology* 24.9: pp. 2064–71. <https://doi.org/10.1111/j.1420-9101.2011.02317.x>
- Kramer KL, Ellison PT. 2010. 'Pooled Energy Budgets: Resituating Human Energy Allocation Trade-offs'. *Evolutionary Anthropology*, 19.4: pp. 136–47. <https://doi.org/10.1002/evan.20265>
- Kuijper B, Pen I, Weissing FJ. 2012. 'A guide to sexual selection theory'. *Annual Review of Ecology, Evolution, and Systematics*, 43.1: pp. 287–311. <https://doi.org/10.1146/annurev-ecolsys-110411-160245>
- Lahdenpera M, Gillespie DOS, Lummaa V, Russell AF. 2012. 'Severe intergenerational reproductive conflict and the evolution of menopause'. *Ecology Letters*, 15.11: pp. 1283–90. <https://doi.org/10.1111/j.1461-0248.2012.01851.x>
- Lappegård T, Rønsen M. 2013. 'Socioeconomic differences in multipartner fertility among Norwegian men'. *Demography*, 50.3: pp. 1135–53. <https://doi.org/10.1007/s13524-012-0165-1>
- Lawson DW, James S, Ngadaya E, Ngowi B, Mfinanga SGM, Hartwig K, Borgerhoff Mulder M. 2015. 'No evidence that polygynous marriage is a harmful cultural practice in northern Tanzania'. *Proceedings of the National Academies of Sciences*, 112.45: pp. 13827–13832. <https://doi.org/10.1073/pnas.1507151112>
- Leonetti DL, Nath DC, Hemam NS. 2007. 'In-law conflict: Women's reproductive lives and the roles of their mothers and husbands among the matrilineal Khasi'. *Current Anthropology*, 48.6: pp. 861–90. <https://doi.org/10.1086/520976>
- Lovejoy CO. 1981. 'The Origins of Man'. *Science*, 211.4480: pp. 341–50. <https://doi.org/10.1126/science.211.4480.341>
- Low BS, Clarke AL, Lockridge KA. 1992. 'Toward an Ecological Demography'. *Population and Development Review*, 18.1: pp. 1–31. <https://doi.org/10.2307/1971857>
- Low BS, Simon CP, Anderson KG. 2002. 'An evolutionary ecological perspective on demographic transitions: modeling multiple currencies'. *American Journal of Human Biology*, 14.2: pp. 149–67. <https://doi.org/10.1002/ajhb.10043>
- Mace R, Alvergne A. 2012. 'Female reproductive competition within families in rural Gambia'. *Proceedings of the Royal Society of London B*, 279.1736: pp. 2219–27. <https://doi.org/10.1098/rspb.2011.2424>
- McNamara JM, Székely T, Webb JN, Houston AI. 2000. 'A dynamic game-theoretic model of parental care'. *Journal of Theoretical Biology*, 205.4: pp. 605–23. <https://doi.org/10.1006/jtbi.2000.2093>
- Moorad JA, Promislow DEL, Smith KR, Wade MJ. 2011. 'Mating system change reduces the strength of sexual selection in an American frontier population of the 19th century'. *Evolution and Human Behavior*, 32.2: pp. 147–55. <https://doi.org/10.1016/j.evolhumbehav.2010.10.004>
- Moya C, Snopkowski K, Sear R. 2016. 'What do men want? Re-examining whether men benefit from higher fertility than is optimal for women'. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371.1692: p. 20150149. <https://doi.org/10.1098/rstb.2015.0149>
- Nettle D, Pollet TV. 2008. 'Natural selection on male wealth in humans'. *American Naturalist*, 172.5: pp. 658–66. <https://doi.org/10.1086/591690>
- Oh S-Y, Bowles S, Borgerhoff Mulder M, Ross CT. Under review. *The Decline of Polygyny: An Interpretation*.
- Orians GH. 1969. 'On the evolution of mating systems in birds and mammals'. *American Naturalist*, 103.934: pp. 589–603. <https://doi.org/10.1086/282628>
- Parker GA, Birkhead TR. 2013. 'Polyandry: The history of a revolution'. *Philosophical Transactions of the Royal Society B*, 368.1613 p. 20120335. <https://doi.org/10.1098/rstb.2012.0335>
- Pélessié B, Jarne P, Sarda V, David P. 2014. 'Disentangling precopulatory and postcopulatory sexual selection in polyandrous species'. *Evolution*, 68.5: pp. 1320–31. <https://doi.org/10.1111/evo.12353>

- Penn DJ, Smith KR. 2007. 'Differential fitness costs of reproduction between the sexes'. *Proceedings of the National Academy of Sciences*, 104.2: pp. 553–58. <https://doi.org/10.1073/pnas.06093011103>
- Perls TT, Bubrick E, Wager CG, Vijg J, Kruglyak L. 1998. 'Siblings of centenarians live longer'. *Lancet*, 351.9115: pp. 1560–60. [https://doi.org/10.1016/s0140-6736\(05\)61126-9](https://doi.org/10.1016/s0140-6736(05)61126-9)
- Perusse D. 1993. 'Cultural and reproductive success in industrial societies: Testing relationship at the proximate and ultimate levels'. *Behavioral and Brain Sciences*, 16.2: pp. 267–322. <https://doi.org/10.1017/s0140525x00029939>
- Puts D. 2016. 'Human sexual selection'. *Current Opinion in Psychology*, 7: pp. 28–32. <https://doi.org/10.1016/j.copsyc.2015.07.011>
- Quisumbing AR, Maluccio JA. 2003. 'Resources at marriage and intrahousehold allocation: Evidence from Bangladesh, Ethiopia, Indonesia, and South Africa'. *Oxford Bulletin of Economics and Statistics*, 65.3: pp. 283–328. <https://doi.org/10.1111/1468-0084.t01-1-00052>
- Randall S, Coast E, Leone T. 2011. 'Cultural constructions of the concept of household in sample surveys'. *Population studies*, 65.2: pp. 217–29. <https://doi.org/10.1080/00324728.2011.576768>
- Ross CT, Borgerhoff Mulder M. 'In revision. Humans have small sex differences in reproductive skew compared to non-human mammals'. *Proceeding of the National Academies of Sciences*.
- Ross CT, et al. 2018. 'Greater wealth inequality, less polygyny: rethinking the polygyny threshold model'. *Journal of The Royal Society Interface*, 15.144. <https://doi.org/10.1098/rsif.2018.0035>
- Scelza BA. 2012. 'Female choice and extra-pair paternity in a traditional human population'. *Biology Letters*, 7.6: pp. 889–91. <https://doi.org/10.1098/rsbl.2011.0478>
- Scelza BA. 2013. 'Choosy But Not Chaste: Multiple Mating in Human Females'. *Evolutionary Anthropology*, 22.5: pp. 259–69. <https://doi.org/10.1002/evan.21373>
- Scelza BA, Prall SP. 2017. 'Partner preferences in the context of concurrency: What Himba want in formal and informal partners'. *Evolution and Human Behavior*, 39.2: pp. 212–19. <https://doi.org/10.1016/j.evolhumbehav.2017.12.005>
- Schacht R, Borgerhoff Mulder M. 2015. 'Sex ratio effects on reproductive strategies in humans'. *R. Soc. Open Sci*, 2.1: p. 140402. <https://doi.org/10.1098/rsos.140402>
- Schacht R, Rauch K, Borgerhoff Mulder M. 2014. 'Too Many Men? The Violence Problem'. *Trends in Ecology and Evolution*, 29.4: pp. 214–22. <https://doi.org/10.1016/j.tree.2014.02.001>
- Schärer L, Rowe L, Arnqvist G. 2012. 'Anisogamy, chance and the evolution of sex roles'. *Trends in Ecology & Evolution*, 27.5: pp. 260–64. <https://doi.org/10.1016/j.tree.2011.12.006>
- Sear R, Mace R. 2008. 'Who keeps children alive? A review of the effects of kin on child survival'. *Evolution and Human Behavior*, 29.1:1-18. <https://doi.org/10.1016/j.evolhumbehav.2007.10.001>
- Sear R, Steele F, McGregro IA, Mace R. 2002. 'The effects of kin on child mortality in rural Gambia'. *Demography*, 39.1: pp. 43–63. <https://doi.org/10.1353/dem.2002.0010>
- Simmons LW. 2005. 'The evolution of polyandry: sperm competition, sperma selection, and offspring viability'. *Annual Reviews of Ecology, Evolution and Systematics*, 36.1: pp. 125–46. <https://doi.org/10.1146/annurev.ecolsys.36.102403.112501>
- Smith EA. 2004. 'Why do good hunters have higher reproductive success?' *Human Nature*, 15.4: pp. 343–64. <https://doi.org/10.1007/s12110-004-1013-9>
- Smith EA, Borgerhoff Mulder M, Hill K. 2001. 'Controversies in the evolutionary social sciences: a guide for the perplexed'. *Trends in Ecology & Evolution*, 16.3: pp. 128–35. [https://doi.org/10.1016/s0169-5347\(00\)02077-2](https://doi.org/10.1016/s0169-5347(00)02077-2)
- Snopkowski K. 2016. 'Marital Dissolution and Child Educational Outcomes in San Borja, Bolivia'. *Human Nature*, 27.4: pp. 395–421. <https://doi.org/10.1007/s12110-016-9265-8>
- Snopkowski K, Sear R. 2013. 'Kin influences on fertility in Thailand: Effects and mechanisms'. *Evolution and Human Behavior*, 34.2: pp. 130–38. <https://doi.org/10.1016/j.evolhumbehav.2012.11.004>

- Snowdon CS. 1997. 'The "nature" of sex differences: Myths of male and female'. Pp. 276–93 in Gowaty PA, editor. *Feminism and evolutionary biology: Boundaries, intersections, and frontiers*. Chapman & Hall, New York.
- Snyder BF, Gowaty PA. 2007. 'A reappraisal of Bateman's classic study of intrasexual selection'. *Evolution*, 61.11: pp. 2457–68. <https://doi.org/10.1111/j.1558-5646.2007.00212.x>
- Starks PT, Blackie CA. 2000. 'The relationship between serial monogamy and rape in the United States (1960-1995)'. *Proceedings of the Royal Society Biological Sciences Series B*, 267.1449: pp. 1259–63. <https://doi.org/10.1098/rspb.2000.1136>
- Starkweather KE, Hames R. 2012. 'A survey of non-classical polyandry'. *Human Nature*, 23.2: pp. 149–72. <https://doi.org/10.1007/s12110-012-9144-x>
- Stewart-Williams S, Thomas AG. 2013. 'The ape that thought it was a peacock: Does evolutionary psychology exaggerate human sex differences'. *Psychological Inquiry*, 24.3: pp. 137–68. <https://doi.org/10.1080/1047840x.2013.804899>
- Stockley P, Bro-Jørgensen J. 2011. 'Female competition and its evolutionary consequences in mammals'. *Biological Reviews*, 86.2: pp. 341–66. <https://doi.org/10.1111/j.1469-185x.2010.00149.x>
- Stulp G, Sear R, Schaffnit SB, Mills MC, Barrett L. 2016. 'The Reproductive Ecology of Industrial Societies, Part II'. *Human Nature*, 27.4: pp. 445–70. <https://doi.org/10.1007/s12110-016-9272-9>
- Sutherland WJ. 1985. 'Chance can produce a sex difference in variance in mating success and account for Bateman's data'. *Animal Behavior*, 33.4: pp. 1349–52. [https://doi.org/10.1016/s0003-3472\(85\)80197-4](https://doi.org/10.1016/s0003-3472(85)80197-4)
- Symons D 1979. *The evolution of human sexuality*. Oxford University Press, New York.
- Tang-Martinez Z. 2012. 'Repetition of Bateman challenges the paradigm'. *Proceedings of the National Academy of Sciences*, 109.29: pp. 11476–11477. <https://doi.org/10.1073/pnas.1209394109>
- Tang-Martinez Z. 2016. 'Rethinking Bateman's Principles: Challenging Persistent Myths of Sexually Reluctant Females and Promiscuous Males'. *The Journal of Sex Research*, 53.4–5: pp. 532–59. <https://doi.org/10.1080/0224499.2016.1150938>
- Tarrant S. 2006. *When sex became gender*. Routledge, New York.
- Taylor ML, Wigmore C, Hodgson DJ, Wedell N, Hosken DJ. 2008. 'Multiple mating increases female fitness in *Drosophila simulans*'. *Animal Behaviour*, 76.3: pp. 963–70. <https://doi.org/10.1016/j.anbehav.2008.05.015>
- Thornhill R, Thornhill NW. 1983. 'Human Rape: An Evolutionary Analysis'. *Ethology and Sociobiology*, 4.3: pp. 137–73. [https://doi.org/10.1016/0162-3095\(83\)90027-4](https://doi.org/10.1016/0162-3095(83)90027-4)
- Thornton A. 1978. 'Marital dissolution, remarriage, and childbearing'. *Demography*, 15.3: pp. 361–80. <https://doi.org/10.2307/2060656>
- Trivers R. 1972. 'Parental investment and sexual selection'. Pp. 139–79 in Campbell B, editor. *Sexual Selection and the Descent of Man 1871–1971*. Aldine Press, New York.
- von Rueden C, Gurven M, Kaplan H. 2011. 'Why do men seek status? Fitness payoffs to dominance and prestige'. *Proceedings of the Royal Society of London B*, 278.1715: pp. 2223–32. <https://doi.org/10.1098/rspb.2010.2145>
- Wade M, J., Arnold SJ. 1980. 'The intensity of sexual selection in relation to male sexual behavior, female choice and sperm precedence'. *Animal Behavior*, 28.2: pp. 446–61. [https://doi.org/10.1016/s0003-3472\(80\)80052-2](https://doi.org/10.1016/s0003-3472(80)80052-2)
- Wade MJ, Shuster SM. 2005. 'Don't throw Bateman out with the bathwater'. *Integrative and Comparative Biology*, 45.5: pp. 945–51. <https://doi.org/10.1093/icb/45.5.945>
- Walker RS, Flinn MV, Hill KR. 2010. 'Evolutionary history of partible paternity in lowland South America'. *Proceedings of the National Academy of Sciences*, 107.45: pp. 19195–19200. <https://doi.org/10.1073/pnas.1002598107>
- Wedell N, Gage MJG, Parker GA. 2002. 'Sperm competition, male prudence and sperm-limited females'. *Trends in Ecology & Evolution*, 17.7: pp. 313–20. [https://doi.org/10.1016/s0169-5347\(02\)02533-8](https://doi.org/10.1016/s0169-5347(02)02533-8)

- Winking J, Gurven M. 2011. 'The total cost of father desertion'. *American Journal of Human Biology*, 23.6: pp. 755–63. <https://doi.org/10.1002/ajhb.21207>
- Wood W, Eagly AH. 2012. 'Biosocial Construction of Sex Differences and Similarities in Behavior'. *Advances in experimental social psychology*, 46: pp. 55–123. <https://doi.org/10.1016/b978-0-12-394281-4.00002-7>
- Zerjal T. 2003. 'The Genetic Legacy of the Mongols'. *The American Journal of Human Genetics*, 72.3: pp. 717–21. <https://doi.org/10.1086/367774>