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MALE HETEROGENEITY AND FEMALE CHOICE IN HUMAN MATING: MAXIMISING WOMEN'S FERTILITY IN OFFSETTING STRESS, AGE, AND UNWANTED ATTENTION, WHILE FACILITATING EXTRA-PAIR CONCEPTION (PART ONE)

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ABSTRACT

Women's mate choice, given profoundly differential male genetic quality (specifically genomic integrity), is heavily skewed towards topmost-ranked males, producing polygyny with residual monogamy and bachelordom. Polygyny is ancestral, as in gorilla harems (apparently homologous with human female cliques): originally predation-avoidance grouping, male-interposed to obviate female-female stress depressing fertility to sub-replacement (Dunbar). Pair-bonding ensures successive highest-possible-quality offspring while offsetting age-related fertility decline, and dissuading low-mate-value social-sexual approach, thereby actually facilitating access by (or to) high-mate-value males for extra-pair conception. It's a female fertility platform and springboard for its enhancement. Failure properly to incorporate male heterogeneity and female discernment explains a longstanding theoretical impasse, with infanticide prevention a default mistaken hypothesis attempting to account for monogamy's chimerical opportunity costs.

Keywords: male heterogeneity, female choice, monogamy, polygyny, pair-bond, genomic integrity



THE CENTRALITY OF DIFFERENTIAL MALE MATE VALUE

That the human mating system cannot be understood without making central male heterogeneity and female choice was the conclusion in a key review (Human Origins and the Transition from Promiscuity to Pair-Bonding) by Gavrilets (2012), as reiterated by Rooker & Gavrilets (2016). This should have come as no surprise, and was no new insight. It's a commonplace if not universal perception that men (as for males generally across species) are seen to vary considerably, indeed enormously as mate prospects. Complementing this, women (as for females generally across species) are seen to be very particular in their choosing. With variation, if more limited, also among women, then males and females pair up according to their equivalent albeit very differently based mate values—the perception by those of the opposite sex of an individual's overall worth as a sexual partner (the sum of traits likely to confer fitness in terms of reproductive output). Men and women mate *assortatively*, that is, according to their similar level of attractiveness. Profound differential male mate value, keen female discernment and consequent assortative mating would be expected to be at the core of any and every hypothesis of the basis and evolution of the human mating system (and of pair-bondingevolved neuro-hormonally cemented enduring attachment-or simply pair-living, across primates, mammals, and species in general). Yet this has not been considered properly, if at all. One if not the only exception is the 2013 paper by the present author, which here receives major update, development and different presentation.

With Gavrilets' corrective unheeded, there is an absence of competing cogent hypotheses to test, and trying to decide between existing ones unsurprisingly has not been fruitful. There continues to be a widely acknowledged impasse in understanding of pair-living/-bonded (monogamous) species generically, not just regarding humans specifically. Reviewers agree on the current impossibility of coming to robust conclusions, though often cite low data quality and inappropriate comparisons (perhaps scapegoating methodological for unrecognised root conceptual problems). Most recently, Fernandez-Duque, Huck, Van Belle & Di Fiore (2020) in examining comparison studies of the evolution of monogamy have "serious doubts" about all of them, given data so poor as to be "distressing". Lambert, Sabol & Solomon (2018) conclude there is no best model, and Kvarnemo (2018) finds overall monogamy is "still surprisingly poorly understood", with no single overriding explanation, instead being more taxon-specific (pertaining to a particular group of individuals; for example, populations of the same species in



different ecological niches, sub-species, a genus or family of species, etc). Klug (2018) sees no way forward but pluralism plus different explanations of origin as distinct from maintenance (an impasse familiar from the study of the origin of sex and the sexes, indicating a likely similar failure to see the wood for the trees).

Without considering male heterogeneity, female choice and the resulting assortative mating, paired-off men and women may be seen and studied simply as interchangeable binary units entirely independent of each other and of others within the local population not paired up, despite all individuals being part-and-parcel of what is a mating system: a whole-group phenomenon. The resulting misconstrued hypotheses generate equivocal data, prompting their over-complex elaboration, and the risk that what seemingly key factors emerge may be artefactual. However, the failure here is likely not merely an unfortunate constraint of scientific inquiry through a need for parsimony and circumspection. A driver, at least in part, appears to be the denial of the reality of hierarchy in a fundamental misrepresentation of the nature of male heterogeneity. Instead of comprehending hierarchy as the foundational facet of human male sociality it is—as it is for animal species generically—there is the notion that hierarchy is an historical, social construct. Inasmuch as this isn't simply inappropriate ideological intrusion into science, it both stems from and creates the false notion that forager / hunter-gatherer societies are egalitarian, in that males do not display markedly differential possession of or access to resources. But this is because there is little or no facility to do so in such societies, so rank hardly could be distinguished on that basis (and hierarchy usually would not be expected to be overt if it is settled and thereby much less salient). Resource-holding is merely indicative of rank in male hierarchy, which functions not to allocate resources but sexual access (Moxon, 2009). Accordingly, trying to use resource-competition scenarios to assess the ranking of individuals fails: the rank order appears resource- and situation-specific (Lanctot & Best, 2000). Resourceholding cannot constitute rank, otherwise males in species where there is no resource-holding to indicate rank could not display the clear and stable ranking they do. For ranking to be meaningful—stable and transitive (such that alpha being dominant to beta, and beta dominant to gamma, then gamma is sub-dominant to alpha)—it has to be resource-neutral, as it were. Either the summation of a male's intrinsic qualities or some major aspect of them (which would be embodied and revealed in ramification across the whole genome through *genic capture*, the mutual influence of most if not all genes, such that each and every one has huge ramification in



expression across the whole genome). Belief in an ancestral non-hierarchical sociality precludes accepting that any sort of inherent distinctions in quality have profound social salience; not least that anything concerning hierarchy could be invoked in mating system aetiology.

Gavrilets' 2012 paper remains the key recent one in the field in that not only is it a rare actual test of several rival models of the evolution of the human mating system, but there is the addition, across all of them, of the parameters of male heterogeneity and female choice. His results lead Gavrilets to conclude that no hypothesis is feasible without them, as they "point to the crucial importance of female choice and emphasize the need for incorporating between-individual variation". Whether this means existing hypotheses nevertheless identify factors that are necessary but not sufficient, or that male heterogeneity plus female choice *in themselves*, in their ramification, may be the only main factors required, Gavrilets does not venture. The task herein is to develop this as an hypothesis, along with any necessary qualifications.

The problem with the whole body of research, reiterated in 2016 (Rooker & Gavrilets), is echoed (looking across primates generally) by Huck, Di Fiore & Fernandez-Duque (2020), who urge incorporating into models "competition and variance in reproductive success across a population"—that is, taking into consideration all individuals in the reproductive group, including non-reproducers. Kvarnemo (2018), in discovering, contrary to what is commonly expected, substantial sexual selection under long-term mutual monogamy, stresses that "mate quality is obviously more important than mate numbers, which in turn affects the need for premating mate choice". Unfortunately, rather than by modelling, hypotheses continue to be examined usually only by phylogenetic analysis, an examination of the evolutionary history of the diversification of species. Though usefully delineating the change in possibly relevant factors, often this does not allow either their separation or to establish causal direction. It tends to miss discovering the need for missing parameters, and hence why theorising has managed to continue without being obliged to incorporate male heterogeneity and female choice.

Surprisingly, having outlined what at the very least is a necessary major corrective, Gavrilets himself fails to apply it properly to his own comparative modelling, restricting interpretation of male heterogeneity to fighting ability (determining the minority of males who could, supposedly, *monopolise* multiple females) and of female choice to only the services males may provide, and not in terms of intrinsic quality of males. Without such self-hobbling,



Gavrilets' conclusions likely would be doubly underscored. Albeit along the right lines, the outline of a cogent aetiology is obstructed by largely ignoring foundational biological principle.

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MATING DEALS WITH THE CORE PROBLEM OF MAINTAINING GENOMIC INTEGRITY

The foundational biological principle that is the missing underpinning of hypothesis is this: the core problem faced by all biological entities of the relentless accumulation of gene replication error, necessitating repeated *purging*, the elimination of defective genes by natural and/or sexual selection, either through reducing the reproductive output of individual carriers, or consigning them to reproductive or actual oblivion. Given that the female as the gestating sex is always the *limiting factor* of reproduction, in effect purging has to be quarantined on the male half of the lineage, leaving the female to reproduce unhindered. Hence the male functions as the *genetic filter*, to use Atmar's (1991) label for the process, or *mutational cleanser*, to use West-Eberhard's (2005). As Martinossi-Allibert, Rueffler, Arnqvist & Berger (2019) put it: "sexual selection in males has the potential to purge deleterious alleles from the population while leaving females, who experience weaker selection, spared of the demographic cost of adaptation". Consequently, selection acts far more on the male than on the female, as is now extremely well evidenced and modelled (for citations and a mini review see Moxon, 2019, pp. 42-43).

Several mechanisms have evolved to express pointedly the male genome and to expose it to natural and especially sexual selection, resulting in males to some degree failing to reproduce if to reproduce at all, in proportion to the extent to which they carry deleterious genetic material (for an outline, see Moxon, 2012; 2016, pp. 16-25). It is not just that the male is obliged to take on this function, but that this functional distinction between the sexes appears to be their origin (Moxon, 2019), with sex itself having evolved to deal with mutational load (not to produce variation, as has long been mistakenly thought), as also concluded most recently by MacPherson, Scot & Gras (2021) and Zadorin & Rivoire (2021).

Male heterogeneity here is genetic quality in the special sense of *genomic integrity*, the maintenance of good inter-functionality of the whole of an individual's complement of genetic material (both coding and non-coding, regulatory genes), rather than the default notion in biology of the quality distinguishing males being *good genes*, the possession of the genes or

genetic variants most obviously conferring incremental competitive advantage; for example, height. A *good genes* understanding is notwithstanding equivocal meta-analytic findings (Prokopet al., 2012) suggesting males instead may be attractive to females in ways unrelated to fitness (the *sexy sons* notion of benefit to females in greater reproductive output of their own in turn attractive male offspring), plus methodological issues and questions about interpretation (Achorn & Rosenthal, 2020). The evidence and modelling fall short in looking for fitness *gains* when instead it's an *absence of fitness decline* that should be sought, in keeping with simply managing to *stand still* in what is a *red queen* scenario—thus dubbed from the Alice in Wonderland character obliged to keep moving simply to stand still. Rather than *good genes* per se, "female mating biases align with *the avoidance of bad genes*" (Dugand, Kennington & Tomkins, 2018). See also Velando, Torres & Alonso-Alvarez (2008).

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The principal mechanism here is the assortment of males to rank according to their relative lack of deleterious genetic material. The resulting dominance (and/or prestige) hierarchy, as already pointed out, is shown to function to allocate sexual access (not resources per se) (Moxon, 2009). The principal mode of allocation is the intrinsic part females play in correspondingly keying into the male hierarchy as the mate-choosers. Given how crucial a function is purging deleterious genetic material, together with the low overall reproductive output of the female making it important that each conception counts, then it would be expected that all females vie for the male with the very topmost *genomic integrity*—that is, the most-highly-purged male genome. Thus, male heterogeneity, given the imperative of purging, is greatly amplified in being very heavily skewed in its translation into male mate value.

Note that if it were quality per se, then it would be additive, and all that would be needed of a male would be for him to be *good enough*. All individuals above a certain threshold thereby might be considered interchangeable. But distinctions between purged male genomes are not in absolute but relative terms. It's because constantly emerging genetic defects are potentially lethal, even as a single mutation, and likely to be synergistic across the whole genome, leading to depressed performance across-the-board, that the fight against them is a *red queen* phenomenon. Having to run just to avoid slipping backwards, as it were: chasing and closing, though never quite catching. Winning an endless series of battles in a war that never can be won requires constant greatest effort, utilising whichever is the currently top performing individual



as the template for all. The chosen male *can never be too good*. He needs to be *as good as it's possible to be*, with no female settling for less than the highest-possible genetic quality (*genomic integrity*) male obtainable in the circumstances. Hence an evolved enormous skew in the perception of male mate value towards the apex of an ordinal series. Male hierarchy potentially is a *winner takes all* scenario in terms of reproduction, assuming it were practically possible for the *alpha* to sire all offspring in the local group. This reproductive skew would be reinforced by the differential reproductive suppression of males that appears to be inextricable with ranking (Moxon, 2009), increasing in degree with descent down the male hierarchy, compounding falling male mate value in terms of *genomic integrity*. The impact of lower status on male stress physiology, in turn depressing male reproductive physiology and motivation (and the converse re higher status), has been well studied, and can be either direct behavioural reproductive suppression by high-rankers or its anticipation by low-rankers in order that it's obviated in evolved self-suppression mechanism.

With the female functioning as the *conduit* to the next generation of the *filtered / mutationally cleansed* male genome, then males as well as females have a basis of mate choice through opposite-sex heterogeneity. Female differential ability to act as the *conduit* is summed up in *fertility*. However, this is a quite particular and at the same time common quality, unlike the general but pre-eminent one looked for in the male, and concerns a narrow set of restricted parameters manifest in correspondingly narrow and restricted indicators, so here quality *is* according to a threshold model. There is no imperative to be *as good as it's possible to be;* just *good enough*. There is, then, far less scope for variation in mate value among females than among males. In any case, the great bulk of the variation among human females is simply age (see below): females not very long after their fertility-peak more or less cease to be under consideration as part of the mating pool. Most tellingly, females are subject to far less stringent mate-choosing than are males, given the minimal cost and great reproductive benefit to males of mating (compared to the huge costs to females): males, given the opportunity, focus on gaining sexual partners in number more than—or at the same time as—just one of notable high fertility. It is easy to see, then, why the female is considered the *choosing* sex.

The different basis of mate choice according to sex is illustrated by findings regarding MHC (the Major Histocompatibility Complex), the key factor in immune response. Hanne,



Simmons & Rhodes (2009) find that a woman seeks a man with a strong MHC indicating immuno-competence, whereas a man seeks a woman who possesses MHC that merely contrasts with his own. The genetic complement under selection here clearly is that of the male, with the female's mate choice being in terms of a particularly well-functioning important aspect of the male requiring, as far as is possible, a perfectly non-compromised genetic basis. By contrast, the male's mate choice is in terms just of adding some hybrid vigour to assist in transmitting his filtered genome through to the next generation.

THE NEED FOR PAIR-BONDING AND SAME-PARTNERED SUCCESSIVE CONCEPTION

With the prodigious sexual capacity of the male, promiscuity at first glance would seem potentially to suffice as a mating system. The most-highly-purged male could be selected by all the females in the local reproductive group or wider mating pool. However, this would entail low regularity of sex (if not also compatibility issues, both physical and/or physiological), on average substantially delaying time taken to conceive if to conceive at all, including even with the most fertile females. Output/efficiency presumably would be greatly improved by the most-highlypurged male focusing on a number of very-high-fertility females over time, as in pair-living/bonding, thereby ensuring iterated sex on a regular basis, and, therefore, conception and in minimal time. This presumably is the proximal function of pair-bonding. The number of these females would need to be restricted—likewise the extent of sex outside pair-bonding—so as not to reintroduce the problem of the male's mating effort being spread too thinly.

The principal benefit of pair-bonding, however, would be if it is *long-term*. Conception then would be *repeated*, leading to another benefit stemming from male heterogeneity. Offspring not only would continue to be assuredly produced and at minimal intervals, but all would be the most highly purged possible, as all would be sired by the same, most-highly-purged male. The alternative of only short-term pair-bonding, merely sufficient to ensure conception (or, as has been suggested, long enough to support the female during lactation), would be no different to promiscuity. It would risk the quality of offspring progressively decreasing with iterated assortative mating.

The quality (genomic integrity) of males subsequently secured in serial short-term pairbonding would correspond to the age-related declining fertility of the female herself. Not only is there deterioration of stored ova (leading to quickly rising rates of implantation failure), but also



progressive shortening of the potential reproductive lifespan (Conroy-Beam & Buss, 2019). A sharp early diminution in a female's sexual attractiveness occurs with a first pregnancy, and then the impact of childbirth, as indicated by low waist-to-hip ratio and BMI (Lassek & Gaulin, 2018), or, more accurately, shallow waist depth and small circumference (Rilling et al., 2009). It is not fertility that is indicated but being nulligravid (that is, not currently and never having been pregnant). The female signals not only her current immediate availability for reproduction, but that she has her full reproductive life ahead of her (that is, none of its being already in the past); assuredly starting at her fertile peak. This enables a female to secure for a pair-bond partner a male with the greatest genomic integrity consonant with her other fertility indicators. Pairbonding in effect projects forward in time female peak fertility, if at or circa the female age of peak fertility (and, therefore, attractiveness to males) the female looks for the male with the greatest genomic integrity she can find who is willing to pair-bond with her. There will never be a more auspicious time to do this, and the pair-bond effectively time-capsules her mate choice, which she could not do in reproducing promiscuously, as the genomic integrity of each successive father for her children is likely progressively to diminish in line with her own rapidly declining mate value. In other words, with pair-bonding the female in effect can cheat time.

Pair-bonding in the human case does appear to be of sufficient duration to effect repeat conception, albeit its estimation is extremely difficult, as discussed in Moxon (2013), with extremely inconsistent and very poorly comparable measures. Not least, data on marriage and even cohabitation is missing any period of initial informal pair-bonding, including the portion of this within those pair-bonds that later become marriages or cohabitations. The human pair-bond typically is about five years, according to Sefcek, Brumbach, Vasquez & Miller (2006), which is greater than inter-birth intervals in hunter-gatherer societies (those presumed closest to ancestral populations) of three to four years (Kaplan, Lancaster & Hurtado, 2000) or 3.65 years (Robson, van Schaik & Hawkes, 2006). Note that pair-bond duration would not have to be decisively longer than the inter-birth interval but merely comparable for pair-bonding to be adaptive in respect of repeat conception, as generally in the evolutionary creation of an adaptation even merely statistical biasing of behaviour usually suffices. Furthermore, pair-bonding would fulfil the putative function by merely providing a platform for other, usual modes of affiliation and attachment to augment and perhaps then supersede it. Such affiliation and attachment could have served to reduce in the first place the requirement for a lengthy period of

pair-bonding per se.

Most often cited or used as a basis for estimation is Fisher's four years (Fisher, 1989, 1994), which by other measure is a substantial under-estimate, being the modal average of the time from marriage to divorce. First, it's only a subset of all marriages, and a severely systematically biased one at that, as all those that did not end in divorce are excluded. Second, ignored is all of the period of pair-bonding prior to its formalisation even as cohabitation. Third, all of the very high proportion of marriages that are very lengthy are missed out in not using the median or mean as the measure. Note, though, the inter-birth interval data is also lacking, as it does not include the period from the inception of pair-bonding to conception. Taking the median rather than the mode, even for divorcing couples the duration of the average marriage almost doubles to seven years, and far longer than that for the whole set. Fisher's rationale for taking the modal peak is that in being what is typical rather than merely average we may detect the underlying natural extent of pair-bonding. Yet divorce itself in not being typical of marriage may represent less an absence of other affiliative and attachment processes *piggy-backing* the pair-bond than extrinsic factors precipitating pair-bond termination. If the latter pertain only to a contemporary and not an ancestral context, they would not be part of the milieu in which pair-bonding became adaptive. Consequently, pair-bonding that was highly adaptive ancestrally may be weaker in contemporary scenarios, reducing average duration to below what it may have been when originally evolved, providing other than a full picture today, clouding its function.

A key aspect and revealing feature of pair-bond duration is that it's U-shaped: typically, either long (if not very long) or very short. Fisher's data misses both these poles, neither of which can be considered atypical. Of those pair-bonds that dissolve, there is a very heavy skew toward this being very early in the relationship, as routinely commented on in the relationships-advice literature and journalism. Data for both developed-world and hunter-gatherer societies bear this out. Furthermore, specifically marriage data greatly understates relationship breakdown overall. In the USA, of unmarried couples, 70% break up within their first year (Rosenfeld, Thomas & Falcon, 2018). In the case of marriages, given the hurdle of the formalisation of the relationship causing lead times for dissolution, it's necessary to measure failure within the first year other than just by the divorce rate. Then it is found that over a fifth—amounting to half or more of all those marriages that end in failure—if not already dissolved were well on the way to that

to 2% of couples had

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outcome (Leonard & Roberts, 1998): 1% to 2% of couples had already completed divorce, 5% had permanently separated, and a further 14% had separated for a period at some point (heralding their demise). Additionally, much of the divorce rate in the second year should be attributed to the first, given that's when proceedings began or when the instability in the relationship had already made one or both parties minded to initiate them. Regarding hunter-gatherers, Blurton-Jones, Marlowe, Hawkes & O'Connel (2000), in studying across four quite different populations, note the great number of marriages breaking up before children are born is owing to their failure in fecundability, the probability of a female conceiving in a given period of time. Partners wait only so long to test the concrete fertility of the pairing before baling out. Similar is found with pastoralists. Du & Mace (2019) conclude: "The production of offspring, regardless of their survivorship, also had a positive effect on marriage duration, as did trial marriage, a time period before formal marriage". So, it's not producing children per se but confirmation of the potential to do so that is at issue. Trial marriage is commonplace. Pair-bonding generally appears indeed to be on trial until reproductive output is assured by conception, so it may be that in an important sense this is when bonding properly begins or fully completes. So, Fisher could well be right to exclude both extremes of duration: *long* because it's not pair-bonding per se sustaining the relationship; short because in important senses it's pre-bonding. Matching or exceeding the inter-birth interval might, then, be a good measure of pair-bond duration to evidence the putative function of ensuring at least one successive conception. The data clearly supports this.

POLYGYNY-MONOGAMY-BACHERLORDOM

The logic of the most rudimentary polygamy—polygyny, that is (one male multiply paired with females)—with the male of the greatest *genomic integrity* being the only male females choose for pair-bonding, affords much less opportunity for most females to mate with him than would be the case promiscuously, driving fierce female competition. Females would do better to vie for a parallel pair-bond with not just one but a number (albeit a very limited number) of top-ranking males (the very topmost plus a tiny few of the next highest-ranking males). Hence a number of polygynous males. A trade-off of a degree of diminished (compared to the *alpha*) male *genomic integrity* against reliability of long-term regular sex in pair-bonding, then can lead to assortative mating to encompass a larger portion of the male hierarchy. Males ranking high-to-middling additionally could also pair off polygynously, though each may attract fewer females



with decreasing rank. Given the very strong skew in mate value, this would quickly fall from a multiple to just one. Polygyny becomes monogyny (just one female per male; in other words, monogamy), leaving a surfeit of mateless males—*zerogamy*, as now popularly labelled. However fine-scaled is this assortment, as it proceeds the relative *genomic integrity* of males would decrease at least roughly in step with the corresponding lesser ability of the female partner to transmit the male's genes into the next generation. In this way, whatever the degree of male *genomic integrity*, it is not compromised by any less inter-generational transmissibility than it warrants, and vice-versa, overall producing high (if not the highest possible) reproductive output (quantity x quality) and efficiency of the local reproductive group or mating pool.

Note that the females are never selecting some interchangeable *also-ran* male. Those females mating with males who don't have the mate value to warrant multiple pairings, and therefore mate monogamously, still will have chosen a male with a degree of *genomic integrity* greater than that possessed by still lower-ranked males (and certainly more than that of the low*est*-rankers). The supply of females will have run out before not just many but (ancestrally, at least, as evidenced below) *most* males get any opportunity to assort with them, owing to so many females having paired off multiply with just the one male—or even eschewing monogamy with well-below-average-ranked males, preferring instead intermittent consortship or promiscuity with males of higher rank. This is why it is so mistaken to view a basis of assortment as merely varied, idiosyncratic or arbitrary, as is implied by and the hidden assumption of usual hypotheses. The real possibility of complete matelessness would drive males to settle for partnering merely monogamously. Indeed, partner scarcity is proposed as the basis of monogamy (Schacht & Bell, 2016).

It is held that monogamy is difficult to explain because the male sustains something of the order of a fivefold opportunity cost of not having multiple pair-bond partners as in polygyny (for example, Dunbar, 2018), but although this can be argued in the case of *obligate* monogamy, it is not applicable to monogamy as a residue of polygyny. Polygyny is not a potential alternative for males who struggle to gain even a single partner. Far from monogamy entailing opportunity cost, it is a clear benefit to non-polygynous males because otherwise not only will they be *zerogamous* but they won't be able to acquire a sexual partner outside of a pair-bond either. They will not be able to reproduce *at all*, because a male finding himself in the lower realms of assortative



mating—in monogamy *clearing*, as it were—will have even less (much less) chance of mating promiscuously. Unlike men, women require substantially more attractive partners for extra-pair (no-strings) sex than for pair-bonding (Szepsenwol, Mikulincer & Birnbaum, 2013), just as do females in other species (eg, Cochaset al., 2006; Kempenaerset al.,1992). Again, male heterogeneity enters as crucial to reveal what is going on.

A very different picture emerges here to that envisaged in modelling by Gavrilets, who recognises only the very top-ranking males as pairing up through any intrinsic quality—and only their fighting ability, which may recruit only a subset of the full range of genetic quality demonstrating *genomic integrity*—and this by imposition, not female choice. All other males are considered to possess little if any, or effectively zero mate value, and therefore in effect are interchangeable. Not until some of them realise they can adopt an alternative mate acquisition mode of offering to provide services beyond mating itself, such as provisioning. Only then and not before, in Gavrilets' modelling, does female choice emerge as a factor in mating systems. Clearly, this is a highly restricted model not reflecting biological reality.

The polygyny-monogyny-zerogyny mix arising from the simple logic of male-female assortment according to differential intrinsic mate value is an accurate characterisation of the human mating system, which is not monogamy. Monogamous species are obligately so. Polygyny and monogamy (and bachelordom) are inextricably linked, with polygyny central and monogamy (and bachelordom) in its shadow, notwithstanding that not only is there monogamy in all societies, but polygyny never accounts for more than a minority of pair-bonds. The very severe skew in male mate value produced by the imperative of purging means it can only be a small minority of males who are polygynous. So it is that in half of the societies thus categorized, less than five percent of men take on more than one wife (Labuda, Lefebvre, Nadeau & Roy-Gagnon, 2010). A large preponderance of societies (85%) in the anthropological record allowed polygyny (White et al., 1988). As well as polygyny being formally sanctioned in most societies, it occurs overtly in all societies in the guise of serial monogamy (Schacht & Kramer, 2019), as well as covertly in the de facto polygyny of *mistress-keeping*. Suda (2007) in a paper on contemporary and traditional African practice, titled Formal monogamy and informal polygyny in parallel, outlines that "although much of the ethnographic literature indicates that heterosexual monogamy remains the statistical marriage norm, polygyny was nevertheless empirically widespread in traditional Africa and is increasingly being reinvented, often clandestinely ..." (p. 56). That polygyny is the human norm is the conclusion, in a book-length review of the topic, by Baresh (2016), who sees "the underlying prevalence of polygamy as the default setting for human intimacy" (p. 2).

A particular form of polygyny in the anthropological literature is concubinage (here with a more restrictive meaning than non-marital co-habitation), also known as polycoity, which might be considered a hybrid of monogamy and polygyny in that there is a primary pair-bond plus one or more secondary, substantially lesser ones. Actually, this is the usual nature of polygyny. Chika & Nneka (2014), for example, point out: "The husband in most cases showers much love on the most favoured wife" (p. 23). Almost always there is a preferred wife over all others, whether an always-favoured or the newest (youngest), with the latter case being usual (eg,Gwirayi, 2016), which in effect is serial monogamy. Essien puts it emphatically: "The hierarchy of wives is indisputable and the inferiority of the secondary wives is beyond any argument". This distinction underlines that polygyny is not some collective bonding with one male but parallel monogamy. Distinguishing between polygyny and monogamy gets harder the more they are investigated.

THE FEMALE AS THE CHOOSER

The full extent of the heavy reproductive skew towards males with the most *genomic integrity* would be revealed by adding to the within-pair reproductive output of polygynous males that which is through *extra*-pair conception. This is the reproductive output from clandestine polygyny plus any sex outside of any pair-bonding (*casual* sex, as it were). The latter would be very largely if not exclusively with polygynous males, in that (as afore-mentioned) human females require partners of substantially higher mate value for extra-pair sex than for pair-bonding (Szepsenwol, Mikulincer & Birnbaum, 2013).

Extra-pair paternity is now shown to be extraordinarily high in populations most closely resembling ancestral ones: foragers or pastoralists. Among African pastoralists, Scelza et al. (2020) find extra-pair paternity to be 48%. A natural base rate of extra-pair paternity (*non-paternity*) had thus far been hidden. Macintyre & Sooman (1991) discuss the impossibility of verifying the usually cited 10%—medical students are told it's 10-15%, which is in line with the worldwide median of 10% arrived at by Baker & Bellis (1995)—because known or suspected cases would self-select out of sampling to avoid discovery by the presumed father, leaving all measures



inherently gross under-estimates. Nevertheless, a series of unpublished studies of English samples put the rate at 30% (20-30% according to a likewise unpublished Liverpool survey). Research hitherto anyway has been restricted to European or European-descent populations, and therefore to (long-)developed societies, that profoundly contrast with the traditional agrarian, let alone those that might more resemble ancestral populations. It might be expected that the former feature factors depressing *non-paternity* and/or its discovery that were not present until recently.

The new data from pastoralists on extra-pair paternity indicates monogamy may function in part or mainly as back-up to supply an already high level of male *genomic integrity*, for if there has not occurred extra-pair conception with a male of *genomic integrity* substantially greater still. The latter is not unlikely to occur given the heightened sexual motivation of females at ovulation, which, in temporarily reducing, relatively, the salience of anything but sex, reduces concern for pair-bond maintenance, allowing the risk-taking required in extra-pair sex. It has been thought that during their brief fertile phase around ovulation women switch from being attracted to their pair-bond partner to extra-pair males (for example, Larson, Pillsworth, & Haselton, 2012). However, regular failure to replicate has been reported, most recently by Thomas, Armstrong, Stewart-Williams & Jones (2021), Stern, Kordsmeyer & Penke (2021), and van Stein, Strauß & Brenk-Franz (2019)—who nevertheless confirm heightened sexual motivation—or that only a modest or slight effect is evident (Marcinkowska et al., 2020). A new review (Jones, Hahn & DeBruine, 2019) finds largely null results even in old studies. All indicate a faulty interpretation has been at play. Rather than a preference for extrapair males over the pair-bond partner, it's surely conditional on differential mate value. In the absence of an extra-pair male of substantially greater genomic integrity than the pair-bond partner, the female simply will have heightened sexual interest in her pair-bond partner. A general attraction to potential extra-pair males would not make sense. What has been dubbed the dual mating strategy or (good genes) ovulatory shift hypothesis is an artefact again of failing to incorporate male heterogeneity, instead to assume that the female, rather than looking for genetic quality (genomic integrity) in any and every male sexual partner, seeks different or additional qualities in a long-term partner: investment of some kind, usually assumed to be provisioning of offspring. But this requires evidence, which is absent, indeed countered (see





below). Women instead seek *genomic integrity* in *all* male partners, but substantially more so in specifically extra-pair partners because of the risk of pair-bond dissolution, and thereby the loss of a genome with high *genomic integrity* by which to conceive a subsequent series of offspring—which she won't be able to replace with anything like an equivalent male given her own steeply falling mate value. The extra-pair partner is available only for one conception, unless he too becomes a pair-bond partner of the female.

Furthermore, women have an aversion to sex during the infertile (luteal) phase, presumably because sex poses a substantial risk of implantation failure should an ovum be fertilised (Steiner, Pritchard, Young & Herring, 2014). Hence, it would seem, an evolved implantation-failure avoidance mechanism in pre-menstrual syndrome (Moxon, 2020). Added together, these phenomena are likely severely to depress the frequency of sex, which is the ageold principal complaint men have about marriage. Albeit minimal sex usually suffices to maintain a pair-bond (given the very well-known phenomenon in psychology experiment of reinforcement regimes that although infrequent nonetheless are effective, especially if they are unpredictable), this female overall strategy risks partner defection. Should a woman detect lesser investment in the pair-bond by her partner than by herself—in other words, a strong possibility of her pair-bond male defecting-she increases the regularity of sex with him, though only in the luteal (non-fertile) phase of her cycle (Grebe, Gangestad, Garver-Apgar & Thornhill, 2013), thereby continuing to facilitate (albeit not to preference) extra-pair sex during the fertile phase. It's a measure of the imperative to further boost fertility overall that even when the pair-bond is under threat the heightened sexual motivation at ovulation is not directed specifically towards the pair-bond partner.

All entails a large degree of female partner-choice, whether proceptive (taking the sexual initiative) or through selective acquiescence. Given the various difficulties attending engaging in extra-pair sex and potential costly implications, it is inconceivable that it could occur on this scale without females being not only fully complicit but actively the choosing sex. With so much at stake in extra-pair sex, women surely are the arbiters, whether or not they are the main initiators.





The centrality of female choice to add to that of male heterogeneity is shown in polygyny not being some male imposition as often supposed: "Many women in Africa choose polygynous over monogamous marriages even in the absence of pressure from relatives" (Anderson, 2000). There are even benefits in terms of childcare. Anderson finds other adult females acting as alloparents, taking on parental duties despite not being parents of the offspring themselves. Female kin and co-wives provide the resources that contribute to the reproductive success of women married polygynously. There are benefits from polygyny not just for first but also for subsequent wives (Uggla, Gurmu & Gibson, 2018), contradicting assumptions that women in polygynous marriages are just *making the best of a bad job*. There is not only no evidence that polygynous marriage is a harmful cultural practice, claim Lawson et al. (2015), but any costs of sharing a husband are offset by greater wealth of polygynous households, consistent (the author himself notes) with models of polygyny based on female choice. So even on an inappropriate economic analysis ignoring the centrality of intrinsic male heterogeneity, polygyny is not disadvantageous but beneficial to women.

That women are the choosers, not men, is very clear whether in polygyny or monogamy. Corresponding to male advertisement of quality so as to prompt female choice, the female choosing the particular male is basic in evolutionary theory and long ago confirmed in the case of humans. Cross-cultural verbal interaction research by Stephens (1963) showed that notwithstanding men being the sexual initiators, women are the choosers; or, as Moore (1985) put it, the controllers of mate choice (including initiation). This extends to arranged marriage (the dominant form of match-making across Africa, the Middle East and Asia, and all but ubiquitous across the world prior to industrialisation), which was and is invariably orchestrated by women: either family members (aunt, elder sister, sister-in-law, or possibly an older matriarch) and/or an outsider female matchmaker. It's the cross-cultural norm today and throughout history (for a brief review, see Moxon, 2017, p146).

[This concludes part one of this paper, which demonstrates the centrality of male heterogeneity and female choice to the human mating system. Part two (in the second issue of NMS 2021) examines its phylogeny: a gorilla-like ancestry, and the homology of gorilla female subgroups with the human female clique; this from a pre-adaptation to polygyny of an interceding male to prevent female fertility collapse through the stress caused by fractious female sub-groups.



The male bodyguard function is outlined, and how this has been misconstrued as mate-guarding. Supposed infanticide prevention is revealed to be a red herring. Male service to the female is amply evidenced as an overall principle, congruent with the hypothesis of the human mating system as a ramification of male heterogeneity and female choice.]

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