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 TWO)

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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

PREAMBLE

Part one of this paper (published in New Male Studies: An International Journal, Issue 10.1) demonstrates the centrality of male heterogeneity and female choice to the human mating system. Part two examines its phylogeny: a gorilla-like ancestry, and the homology of gorilla female sub-groups 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.

OUR MATING SYSTEM'S GORILLA-LIKE ANCESTRY

Polygyny is known to have been central to human mating ancestrally. DNA analysis reveals only 40% of men were ever fathers (Wilder, Mobasher & Hammer, 2004), fitting with data of worldwide Y-chromosome diversity indicating only a few men may have contributed a large fraction of the Y-chromosome pool at every generation until only recently (Dupanloup et al., 2003). Some evidence points to this change being in the era of early modern humans, circa 150,000 years ago (Walker, Flinn & Ellsworth, 2011). Note this would occur simply from a large increase in local populations, given no reason to suppose the sharp reproductive skew towards an apex of only a very few males would change. The tendency to *winner takes all* suggests that the residue of monogamy and bachelordom has grown without a commensurate proliferation of polygyny.

Also indicating that polygyny is human-ancestral are the oft-cited long-known results from standard comparison of sex dimorphism in body size and other parameters across the family tree of hominid species. From these it has been proposed that the human mating system was never chimpanzee- but gorilla-like: long-term pair-bonds of one male with multiple females (Nakahashi & Horiuchi, 2012; Geary & Bailey, 2011). An evolutionary transition from this to the human mating system is discounted by Chapais (2008) in his assertion that separate *harems* would be unlikely to fuse to form the human sociality of multiple males and multiple females all together, and that instead this is more directly our ancestral state—like the hamadryas baboon today. But this is to ignore a lot of research, notably in the 1990s, reporting large gorilla groupings of multiple one-male-+-multi-female sub-groups (see the book covering three decades of this research, by Robbins, Sicotte & Stewart, 2001). Gorillas evidently exhibit group fission-fusion of modules of a single male and his *harem*. This is analogous, likely homologous with human family grouping, and confirmed in gorilla-human comparative work (Morrison, 2019) demonstrating “common underlying multi-level social structure and the considerable similarities in inter-group territorial dynamics”; findings that “strongly emphasise the importance of gorillas as a model system for human social evolution”. Chapais therefore seems right that a multi-male-+-multi-female sociality is ancestral: it’s simply that he didn’t realise that this is what we have in the gorilla.

Reinforcing this is another window on the extinct ape common ancestor provided by the orangutan, in that this species is now shown to be gorilla-like *and* more human-like than is the chimpanzee. The orangutan in comparison to all other apes has evolved only very slowly (Locke et al., 2011), whereas human evolution comparatively in major respects has been effectively reversed by neoteny (Franchini & Pollard, 2017). Thus is explained the uncanny morphological and other human-orangutan similarity, whereas there is notable human-chimpanzee *dis*similarity (Grehan & Schwartz, 2009). The molecular evidence has been held not to support this, but is not relevant in being in respect only of coding genes, when “most genomic changes that distinguish humans from their primate relatives are in non-coding sequences with regulatory functions” (Ligrone, 2019), especially in the so-called Human Accelerated Region (HAR), and not least those regulating neoteny. Tang et al. (2020) demonstrate that some human features indeed may be explained by neoteny, notably in the brain, with infant human brain growth being a mere third the rate of that of chimpanzees. It’s likely, then, that the orangutan’s mating system much more closely resembles those of species in the human phylogeny than does the chimpanzee’s, which appears to be a profound divergence. The upshot is that there is no utility and instead only hindrance and false trails in looking to the chimpanzee for our ancestral mating system. The orangutan, despite its semi-solitary living, is, like the gorilla, polygynous. It’s dubbed *short-term* polygynous, though this is rather inaccurate given that the sexually exclusive consortships of up to seven months reported by Utami et al. (2002) are a continuation of long-term affiliations formed in adolescence, which also revive between child-rearing (Grehan, 2006). Apparently, there *is* long-term pair-living/bonding in the orangutan, or there would be but for periodic separation owing to necessary dispersal to ensure sufficient food resources. Any dissimilarity to the gorilla pattern is through the orangutan’s relatively recent evolution to largely solitary living; the result of a major environmental change producing food scarcity, according to Harrison & Chivers (2007): “the orang-utan's present-day mating system most likely evolved from a gorilla-like base, with one dominant male guarding a harem of females”.

THE HOMOLOGOUS HUMAN FEMALE CLIQUE

A gorilla-human seeming homology pertaining to mating system is the gorilla *harem* and the human female *clique*. The latter typically numbers four to six, or an average size of 5.11 members (Kwon & Lease, 2007); the former, a maximum of five individuals—the limit, across primate species, of the number of females per polygynous male (Pawlowski, Lowen & Dunbar, 1998). The workings and nature of the *clique* as the key form of girl, adolescent, and indeed adult human female sociality has been entirely neglected in the scientific literature in favour of consideration only of supposed unisexual sociality, despite it being abundantly clear that male sociality is entirely different, with male (but not female) sociality essentially group-based as opposed to dyadic (David-Barrett et al., 2015), and the female (but not the male) social dynamic being exclusion (Benenson et al., 2013). Presumably, this neglect is through fear of usual censure and career derailment of being considered in some way to negatively portray women. Insights instead come from parenting literature—most notably by Wiseman (2016), but also several other authors—finding its way into scholarship as teacher resources (Harley & MacNeil, 2017) and via *Psychology Today* (Powell-Lunder, 2013).

As Powell-Lunder stresses, girls in general belong to a *queen bee*-led small coterie; that is, a *clique*. Not just those who are the most popular (who are merely the most conspicuous and suitable as protagonists in famous films such as *Mean Girls*). Furthermore, Powell-Lunder elaborates, the *cliques* to which most girls belong are still fiercer environments than those of the *populars*, because of the fear that exclusion from this less exclusive social milieu may leave nowhere else to go. *Clique* members adopt the various well-documented (Wiseman, 2016) unranked roles, in an ethos of fierce avoidance of one-upmanship, with just one of them at any one time a potential replacement in being the *deputy* of the *queen bee*, who appears, therefore, not an *alpha* at the apex of a hierarchy but *first among equals*. The hallmark of *clique* sociality is of course the extremely well-known intense *policing* of membership, under the fierce control of the *queen bee* (unless and until she is deposed by her *deputy*). Also, the firm exclusion of all others, the difficulty in gaining membership, and the constant prospect of losing it. The imperative appears to be an all-encompassing desire to achieve and maintain *clique* membership by serving the *queen bee* and taking great care not to be seen to challenge her (on pain of expulsion), yet inhabiting or creating a springboard position from which to be the usurper should there be an opportunity (with sufficiently good prospects of success).

From a comparative, evolutionary perspective, the human female *clique* looks like a proto- (though possibly only facultative, or even vestigial) *co-operative breeding* unit, with a (potential) sole breeding female controlling a group of fellow females she reproductively suppresses so they can be utilised (through channelling their reproductive motivation) as alloparents. It may be that in the *deputy* there is a reserve breeding female or a subsidiary as a result of only partial reproductive suppression. Perhaps the rest of the females, though reproductively suppressed more than is the *deputy*, nevertheless are not fully so, and may then breed to a limited degree or in some circumstances. If not obligate, this could be facultative *co-operative breeding* triggered by local severe ecological stress, as an adaptation to head off the possibility of local extinction, by restricting reproduction, possibly to the extent of a 100% skew to the one most fertile female in the sub-group. In her being paired with one of the males with the least deleterious genetic complement, and the use of locally very limited resources (including the parenting efforts of other reproductive-age females) being reserved exclusively for their use, then there would be a good chance that the one most reproductively fit couple of each sub-group could manage to produce a next generation. Such a *best shot* likely would outdo the alternative of too many pairs attempting to breed, as this would place them in mutual competition over temporarily impossibly limited resources. It may be that in extremis only one pre-eminent sub-group—therefore, just one couple—gets to reproduce from out of the entire group (collection of sub-groups). This would account for the character of the one *popular* clique of the most highly fertile females.

The stresses attending human females together in a breeding unit are evident in the experiences of co-wives in polygyny. According to Essien (2018), “co-wife conflict especially in the early years of marriage is pervasive, and often marked by outbursts of verbal or physical violence”. “Ongoing and contentious rivalry” and “a recurrent motif of strident co-wife hostility” is how Jankowiak, Sudakov & Wilreker (2005) put it: "… we found women' s sexual desire and reproductive interests paramount factors in promoting co-wife conflict (that is a) deep-seated resentment". Oppong, Monebenimp & Nzefa (2019) discuss the "emotional suppression" felt by co-wives. The chronic stress experienced by co-wives is so severe that a principal theme of the findings by Tabi, Doster & Cheney (2010) is infertility, with it prompting co-wives to welcome additional wives so as to avoid divorce. The co-wives' predicament in their contradictory social dynamic is neatly summed up in the title of Madhavan's (2002) paper, *Best of friends and worst of enemies: competition and collaboration in polygyny*. Female *clique* dynamics in a nutshell.

THE MALE *BODYGUARD* TO FEND OFF *FEMALE* AGGRESSION

The human-clique-homologous gorilla pattern of small female sub-groups interpolated by males is now understood (Dunbar, 2020) originally to be an adaptation to reduce stress on females from females in other sub-groups, which could not be addressed by group fission given that large overall grouping itself is an adaptation—to avoid predation. Failing to deal with female intra-sexual stress would directly reduce female fertility to sub-replacement, leading to local extinction. Dunbar writes:

> *"One possible mechanism would be the impact that social stress has on the mammalian female menstrual system (and hence fecundity), the endocrinology of which is now well understood (Abbott 1984; Abbott et al. 1984; Gordon et al. 1992; McNeilly et al. 1994; McNeilly 2001a,b; von Borrel et al. 2007; Chatterjee & Chatterjee 2009; Son et al. 2012; Iwasa et al. 2017; see also Wasser & Barash 1983; Huchard & Cowlishaw 2011)".*

Human females are no different in stress causing reproductive suppression (Wasser & Isenberg, 1986). Interpolating males to reduce female-female aggression would be a *pre-adaptation* to subsequent pair-bonding. Likewise appears to be *concealed ovulation*, which also functions to reduce female-female aggression, according to Krems et al. (2021), who, in testing a *male investment* model of concealed ovulation against one of *female rivalry*, find clear support for the latter and none for the former. The evidence here is that females evolved *concealed ovulation* because cues to ovulation trigger aggression from other females trying to boost their own mating opportunities by reducing those of others.

It has long been known that low level agonistic interactions between female gorillas increase dramatically in frequency with the number of females, and *not* with group size (males and females both) per se (Watts, 1985). A strong parallel is evident in the closely-related primates, baboons. Within-group female coalitions attack and thereby reproductively suppress their female victims, who experience more cycles before conception and longer inter-birth intervals (Wasser & Starling, 1988), with female group size causing increased female-female competition that correspondingly elevates stress levels (Hill, Lycett & Dunbar, 2000). "Conflicts between neighbouring *harems* are usually initiated by one, occasionally two, females; if the conflict escalates, more females will become involved, until eventually the *harem* males are drawn into the dispute and force the separation of the two groups of females (Dunbar 1983b, 2018)" (Dunbar, 2020). The parallel appears to be very general indeed, and recognised some time ago by Gowaty (1996): "In fact, female-female aggression may be the most parsimonious explanation for socially monogamous males in many species" (p. 28).

Both sexes experience crowding stress from same-sex others, but whereas for male mammals this is from spatial proximity, for females it's caused simply by their total number (Brown & Grunberg, 1995). It's social dynamics per se. Splitting the group of course would merely reintroduce the very predation threat that increasing group size evolved to counter. A separation of females is required that is more complete than is the merely spatial. Interceding males, one per each female sub-group, would be an adaptive solution if this socially buffered the female sub-groups from each other, at the same time facilitating sufficient cohesion to create overall one coordinated large group to dissuade or deal with predators. As noted by Dunbar (2012): "It seems that in the large groups adult males act as bridges, or weak links, that help maintain the cohesion between clusters of females". This is strongly echoed in the afore-mentioned new work (Morrison, 2019) showing unexpected ape contiguity with human multi-level social structure and inter-group dynamics.

This interceding male Dunbar dubs the *bodyguard*, which is to borrow a term coined by Mesnick (1997) but which was on the understanding that deterrence was of *male* aggression. Dunbar himself formerly had considered the *bodyguard* to dissuade unwanted social-sexual advances from males, which had been proposed by Lumkin (1983), and as a possible basis of primate pair-bonding by Norscia & Borgognini-Tarli (2008). It was also the view of the present author in Moxon (2013), but there qualified to be specifically in respect of social-sexual advances from *low*-mate-value males, thereby actually facilitating the female pair-bond partner's accessibility to and by males of high mate value—that is, of a mate value substantially higher than that of the female's pair-bond partner. In other, colloquial words: clearing away the *riff-raff* leaves the deck clear for *hob-nobbing*. Indeed, this may be the principal benefit of *bodyguarding*, on top of and in the wake of the original function to reduce female-female stress. Low-mate-value males are unlikely anyway to present a threat to the female in terms of unwanted conception, given rank-appropriate behavioural self-inhibition by males, backed up by community sanction as well as that by the pair-bond male. Being of greater *genomic integrity* (in this scenario), the pair-bond male is likely to be physically and in other ways superior (more confident, belligerent, part of an effective coalition, etc), so would be anticipated to win any fight. In this way, *bodyguarding* appears to be routinely facultative.

Its workings in this respect are tapped into by Hoplock, Stinson & Joordens (2019) in finding that "highly-attractive men engage in mate-poaching behavior (proximity seeking) when a romantically-involved woman is accompanied by a less-attractive boyfriend, but not when she is alone or accompanied by a boyfriend who matches her attractiveness". Here, the redundancy and abandonment of *bodyguarding* in the scenario where it is not required by the female appears as if formalised, with high-mate-value males actually preferring the presence of the erstwhile *bodyguard* during extra-pair courting of women. Indeed, the tactic appears to be itself the very mode of courtship in attempts to poach pair-bonded females. High-mate-value males overtly usurp low-mate-value males with women partners they perceive may be in the market for extra-pair sex owing to substantial mate-value disparities. This is plainly what Moran, Kuhle, Wade & Seid (2017) discovered. And in this scenario, Fugère, Cousins & MacLaren (2015) find there is reciprocal behaviour from the female: more flirting, feeling less committed to the pair-bond and unconstrained by (what the authors term) *mate-guarding*.

BODYGUARDING HAS BEEN MISCONSTRUED AS MATE-GUARDING

Fugère, Cousins & MacLaren appear to misconstrue *bodyguarding* as instead *mate-guarding*, which is understandable in its being a far more familiar conceptualisation. A supposed defence of the female *not in the female's but the male guarder's own interests*: and of the female from *all* social-sexual approach (supposedly from high-mate-value as well as from low-mate-value male potential mate-poachers). It is a thus conceptualised defence that the aforementioned Lumkin (1983) suggested was usurped in the guarded female's interests to become defence specifically against *unwanted* male approaches: what is herein termed *bodyguarding*. *Mate-guarding* is a notion based on a chain of assumptions. The assumed male need to be assured of paternity, as a consequence of assumed male investment in offspring. Underlying all is the default assumption of male proprietorial control of the female, which appears to be inappropriate incursion of contemporary ideology—that only male interests ever are served. This notion has no scientific basis and is flatly contradicted by a diametrically opposite insight from biology: the fact that the female is the *limiting factor* in reproduction dictates that the female interest must be preferenced, as indeed it is.

The human mating system did not evolve from a need for male investment in offspring. Not only is evidence for paternal investment equivocal (for a very brief review, see Moxon, 2013, p27), but as is now well evidenced, modelled and very widely agreed, any paternal investment that may have evolved did so *in the wake of* the evolution of the human mating system, so cannot be the basis of it. This was the conclusion of an across-species (including human) key investigation by Brotherton & Komers (2003), and specifically regarding humans by Chapais (2008). Chapais (2011) concludes that human pair-bonding originated as “a pre-adaptation for the evolution of parental cooperation in the provisioning of progressively altricial (helpless) children”. Similarly outlining a primate phylogeny of pair-bonding, Geary & Bailey (2011) conclude that the emergence of a specifically human mating pattern merely coincided with increasing male provisioning. Opie et al. (2013) applied phylogenetic comparative methods widely to 230 different species, confirming an antecedent evolutionary pathway. Lukas & Clutton-Block (2013) also confirm this.

With the evidence overwhelming that male provisioning was not the basis of the human mating system, then the notion that its foundation is the need for the male to be assured of his paternity (in order to protect his investment) evaporates. There is no investment to protect. As it is the male’s investment that is taken to be the reason why males supposedly persist in trying to prevent the female partner from mating with other males, then such attempts would be pointless. The evidence indeed is that mate-guarding does not work—that is, what is presumed to be mate-guarding actually does not thus function. It fails so badly that by some measures extra-pair paternity is actually greater with mate-guarding, according to Kempenaers, Verheyen & Dhondt (1995), who conclude: “despite mate guarding, paternity seems to be largely under female control and unattractive males guarding their mate are making the best of a bad situation”. Little if any relationship exists between the strength of mate-guarding and paternity in avian species (Johnson & Burley, 1998), despite their seeming strict monogamy. Kokko & Morrell (2005) ask “if females regularly escape mate-guarding attempts, we face an enigma: why does mate-guarding evolve if it is so inefficient?“ The answer is because the male is not guarding his own interests but the female’s, as in bodyguarding. What has been taken to be mate-guarding of the male’s interests would appear in fact—as outlined above—to deter social-sexual advance only by males of lower mate-value (lesser genomic integrity)—that is, lower than that of her pair-bonded partner—who would not serve the female’s interests to accept, and surely she would not want. In marked contrast, higher mate-value (greater genomic integrity) suitors—that is, higher than that of her pair-bonded partner—would be in the female’s interests to accept, if the mate-value difference were significant enough to outweigh the risk to the endurance of the pair-bond. Again to reiterate: even if the male wished to try to prevent such mating, ultimately he would not be able to do so, as the adverse difference in ranking would be reflected in the suitor’s greater fighting ability or coalitional strength. Not that an agonistic encounter likely would occur: it would be obviated by the psychological and physiological mechanisms that have evolved in the service of hierarchy.

INFANTICIDE PREVENTION IS A *RED HERRING*

Not considered *bodyguarding*, though which might be thought a putative special form of it, is infanticide prevention: supposed male defence of a female to keep at bay other males who might kill unweaned offspring so as to prompt the female to end lactation and thereby resume cycling and fecundability. As a possible basis of the evolution of pair-living / -bonding it’s in major doubt even in principle. Supposedly to cut her losses in anticipation of infanticide in a *male takeover* scenario, a female may spontaneously abort a foetus (what is dubbed the *Bruce effect*), but again there is here a failure to take account of male heterogeneity. With the new male necessarily of a higher *genomic integrity* sufficient to have been able to effect takeover, the female gains in fertility, which quickly manifests in improved reproductive output in quality-x-quantity terms, given an immediate return to cycling, and then not just a replacement offspring in short order, but subsequent offspring of the same high *genomic integrity*. The imperative to maximise purging manifests again. Not only has the female not sustained any net cost, but has benefited. It is anyway frequently acknowledged how extraordinarily difficult it is to find evidence of the occurrence of infanticide, let alone of its prevention, in any species.

Infanticide prevention as the foundation of monogamy in humans and primates generally is championed most recently by Opie et al. (2019), but their phylogenetic analysis considers only a highly restricted set of other alternative key factors as hypotheses (just parental care and a distribution of females too thin for males practically to have harems, with neither of these incorporating male heterogeneity & female choice), so the analysis is set up as a forced choice where only infanticide prevention is likely to be supported. Fernandez-Duque, Huck, Van Belle & Di Fiore (2020) in reviewing competing hypotheses take particular issue with the infanticide prevention hypothesis, citing a phylogenetic analysis (Lukas & Clutton-Brock, 2013) completely at odds with Opie's earlier outline (Opie, Atkinson, Dunbar & Shultz, 2013)—which last has been the subject of rebuttals and counters to counter-rebuttals—going into considerable detail about poor methodology. Fernandez-Duque et al. explain that support for the infanticide prevention hypothesis (though here not alone among evolutionary explanations in sharing the same fault) is a case of the fallacy known as *affirming the consequent*. Making a poor case for its significance are unsatisfactory proxies of infanticide risk, that supposedly is addressable by the adaptation of pair-living/ -bonding. But the existence of the adaptation is itself the basis of inferring infanticide prevention is the problem the adaptation evolved to solve.

If infanticide were a significant problem for such as the gorilla, Dunbar (2020) points out, then fertility decline of females would be in line with increasing numbers of males, not exclusively through the increase in the number of females (as is found). Instead, infanticide in the wake of takeovers always remains a risk. If a *harem*'s male is deposed, there is no other male to defend against the usurping male if he chooses to be infanticidal. In the case of the *harem* male still being in place, there is no logical rationale for infanticide in the first place. There would be no benefit for another male to attempt to bring back into cycling a lactating *harem* female belonging to a *harem* still with its male, because the long delay between ending lactation and resuming cycling means the opportunity to capitalise on the initiative would be in the future, when the *harem* male would have to be challenged anew for the sexual access. Unless the male challenger has the wherewithal to take over the *harem*, then he's unlikely to achieve sexual access, and the female won't be co-operative in any case. This is to return to the situation in *bodyguarding*, where males of lower mate value than the pair-bonded (or *harem*) male are easily dissuaded from making socio-sexual advances, and indeed, would internalise this as self-inhibition. A male of substantially higher mate value than the pair-bond (or *harem*) male is a different proposition. His takeover would be part-and-parcel of the species' reproductive system, serving to increase reproductive output and efficiency, and the only individual who loses out is the deposed lower-mate-value male. A female *harem* member may suffer the immediate loss of a new-born through infanticide, but this is not a loss in even slightly wider perspective—just as in the spontaneous abortion scenario (above)—as it's a clear gain in the greater *genomic integrity* provided by the new *harem* male, which will be embodied in an immediate replacement offspring if one were to be lost to infanticide, and, more importantly, several subsequent offspring. Even if the harem male is replaced simply through his aging, this too is of significant benefit to the *harem* females in that the likelihood of gene replication error in the male's gametes will have increased dramatically. It's hard to see how the female would benefit in being protected from the threat of infanticide even if it were real.

Whether as social-sexual advance or attempting infanticide, the concern that lower-mate-value males may *gain the system*, as it were, is misplaced, as these are the very males not in a position to do so. By contrast, higher-mate-value males, who are of actual benefit to females, are not *gaining the system*, being very much a part of how the mating system works, which is to the benefit of females generally and only for a minority of males. The issue of infanticide-prevention and the scope for a male service to the female in this regard is a theoretical problem only—if that, in that the theory appears awry.

Another apparent misconception regarding infanticide prevention is that *concealed ovulation* serves this function. As already outlined, modelling now shows instead that it reduces female-female aggression (Krems et al., 2021). It has long been claimed that the most parsimonious conclusion about *concealed ovulation* is that it is not an adaptation at all: simply loss of function through the absence of selection pressure (Burt, 1992; Pawlowski, 1999). It is an untested presumption that *concealed ovulation* causes paternity uncertainty, sufficient that as a consequence a potentially infanticidal male sees a significant risk of unintentionally killing his own offspring.

Furthermore, strangely there has not been considered that *concealed ovulation* is of most utility to females in reducing the benefits and increasing the costs to lower-mate-value males in their social-sexual approaches in attempt to usurp pair-bonding. Together with what anyway are the difficulties for low-mate-value males in approaching a *bodyguarded* non-receptive female, the strategy of sneak mating attempts would not be worth the risks if it were made impossible to time them to when the female is fertile. In thus augmenting *bodyguarding* in keeping lower-mate-value males at bay, then again, as with the *bodyguard*, thereby is allowed mutual social-sexual approach of *higher*-mate-value males and pair-bond females. For a higher-mate-value extra-pair male, concealment of ovulation is not an issue. On the contrary, ovulation prompts female proceptive and receptive behaviour towards him, notwithstanding its not being *specifically* so: nevertheless it would be in this context—of extra-pair sex with a substantially higher-mate-value male being in the offing. There's another advantage. With the female allowing, indeed encouraging him to be close, he is in a position to detect subtle indications of impending ovulation (eg, Lobmaier et al., 2018) and sexual arousal (Wiseman & Shrira, 2020), that a *lower*-mate-value male, who, in not being allowed close and instead positively distanced, could not. He will never be in a position to increase the probability of conception to sufficiently offset the likely costs, to render a bid for a sneak mating worth the risk. Further disadvantaging lower-mate-value suitors may explain why human coitus itself is concealed. With the timing of sex a good indicator of likely heightened female sexual receptivity prompted by ovulation, its discovery by a lower-mate-value male would encourage his social-sexual approach in the immediate future so as still to be within the female's fertile window. *Not* concealing coitus would be provocative and potentially very destabilising, in line with the interpretation of new data by Yitzchak (2020) that hidden coitus serves to maintain cooperation with those within the group who are prevented from mating.

Placing infanticide prevention at the heart of the aetiology of the human mating system appears to be unwarranted inference, evoked as a default hypothesis through a false understanding that essentially humans are monogamous and that (as aforesaid) this has a seeming fivefold opportunity cost compared to polygyny, as might thus be considered *obligate* monogamy. In the human case, at least, with monogamy not being obligate, and simply a reduced form of polygyny for those males not able to secure multiple females, there is no opportunity cost to sustain. The misconception at root is through the failure to appreciate the centrality of male heterogeneity and female choice. Infanticide prevention is proffered for want of an alternative in the paucity of hypothesis generation that stems from mis-framing what is here at issue.

CONCLUSION

With pair-bonding to ensure repeat offspring of the greatest-possible *genomic integrity* (least mutationally compromised), featuring *bodyguarding* to dissuade low-mate-value male social-sexual approach, thereby actually facilitating approach by/to high-mate-value males for extra-pair sex; all while buffering against female age-related fertility decline, and built on a pre-adaptation of interposed males to reduce female-female stress … the overall picture of the basis of the human mating system is one of *service by the male to the female*. Yet neither provisioning (the erstwhile assumed mode of such service) nor infanticide-prevention (the still current oft-assumed mode) is its basis. Instead, it's the set of ramifications from keen female choice and profound heterogeneity of males, in turn from the imperative to purge relentlessly accumulating gene replication error.

Service by the male is investigated in a new review of the evolution of monogamy in a primate model by Dolotovskaya, Walker & Heymann (2020) by pitching against each other three categories of hypotheses: *male-services*, *resource-defence* and *mate-defence*—this last being *mate-guarding*. The authors conclude that "Our data is most consistent with the 'male-services' hypothesis for pair-bond maintenance, where a female contributes more to the proximity and affiliation maintenance while a male provides beneficial services". Note the authors are cautious in making their claims in respect of maintenance rather than origin per se, because they include care of infants, which they concede evolved *in the wake* of the evolution of pair-bonding. The principal *male services* they ascribe to protection from predation and territorial defence, though these are not from pair-bonding but are the platform on which it was possible. What remains may be simply the way male heterogeneity and female choice play out.

Male services, with the female the party keeping the pair together, chimes with the data on mate-retention tactics showing that most are women's or mostly used by women (for a brief outline and citations, see Moxon 2020, p10), and the research concerning the various other ways women in comparison to men reveal a far greater concern for and interest in their pair-bond (for an account, see Moxon 2016, pp.73-75). Of romantic attachment itself, males but not females are dismissive—in a near universal sex difference (Schmitt, 2003). All lines of evidence converge on a conclusion that human pair-living/-bonding is not at all the presumed proprietorial control by men of women. Indeed, it appears more the converse. Objectively, the human mating system is just that; a system, in which all individuals are engaged to play a part in what is a group-level phenomenon, with the goal of maximising overall reproductive output/efficiency. This is rather too obvious understanding to have been lacking—though still there are those hidebound by the outdated *group selection* debate, unaware of the now multiple complementary theoretical perspectives on how/why mutualism works. Appreciating the purging imperative driving the profound skew amplifying male heterogeneity, and even accepting that profound male heterogeneity exists, may be a different matter. Yet (the pre-adaptation of reducing female-female stress aside) a highly parsimonious hypothesis unfolds from the one premise of purging.

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Steve Moxon is an English independent (non-affiliated) cross-disciplinary researcher/writer of science review papers and books outlining original theory on the biological roots of human sociality, behaviour and psychology, with a special interest in the sexes—sex-difference/dichotomy. Regularly journal-published for the past decade, his topics include dominance hierarchy (and associated reproductive suppression), pair-bonding, partner violence, competitiveness, stress response mechanism, the origin of the sexual divide, and why culture is biology. Throughout is a necessary bottom-up approach, excluding all ideology: an avowed stance against 'PC' ('identity politics'), especially its core of feminism; all being non-, indeed anti-science. Steve also researches/writes about mythologies (ancient and contemporary), these being another window on understanding humanity; and is a songwriter, singer & guitarist. He resides in the Pennine hills north of Sheffield, Yorkshire, where he grew up, feels at home, and can walk or cycle through the stunning countryside of steep-sided wooded valleys and gritstone edges.

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