Human Pair-Bonding as a Service to the Female

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Though human pair-bonding generally is considered to be male proprietorial control and provisioning, the evidence does not support either of these assumptions. Not only is provisioning relatively lacking and of little impact, but in any case is antecedent to the evolution of human pair-bonding; and the male (in pair-bonding species generically) does not prevent the female partner from engaging in chosen extra-pair sex. In thus contradicting the standard biological model of male mate-guarding as preventing partner defection, its function instead appears to be to displace social/sexual access to the female by lower (but not by higher) mate-value males; thereby indirectly facilitating the female partner's extra-pair sex with males of her choice or acceptance (males of higher mate-value than the pair-bond partner). Furthermore, by producing successive offspring with the same male, the pair-bond in effect allows the female to project forwards in time her early peak in fertility (her own mate-value). [Reproducing instead through promiscuous sex would entail progressively lower fitness of offspring

NEW MALE STUDIES: AN INTERNATIONAL JOURNAL ~ ISSN 1839-7816 ~ VOL. 2, ISSUE 2, 2013 PP. 24-38

as the female's mate-value declines with age; and correspondingly the mate-value of each subsequent father.] Pair-bonding is, therefore, a service provided by the male to the female. The male's interests are served in that the offer of the service enables a degree of trade-off against deficiency in the male's own mate-value, to secure for regular sex a more fertile female than would be acquired otherwise. With pair-bonding primarily of benefit to the female, the requirement to mate-guard as hitherto understood, to prevent partner defection, is not performed by the male but by the female. This explains the findings of predominantly female 'control' within intimate-partnerships, and indirect measures showing women value and invest in the pair-bond more than do men.

Key Words: pair-bonding, mate-guarding, female 'control', mate-value

The facility to pair-bond is accepted as a human universal, with even its cultural manifestation in marriage ascribed a long evolutionary history [Walker et al 2011]. The sole recent challenge is a psychology / cultural-anthropology anti-biology polemic, *Sex at Dawn* [Ryan & Jetha 2010]; which was comprehensively refuted by evolutionary biology arguments in the riposte, *Sex at Dusk* [Saxon 2012], and the sole formal academic review [Ellsworth 2011]. Ryan & Jetha draw their conclusion that ancestrally humans were entirely promiscuous through defining the pair-bond as exclusive of any other sexual behaviour, obligatory, and of lifelong duration; when none of these criteria are reasonable. Pair-bonding can be polygynous or serially monogamous, and can persist despite extra-pair sex in various forms. There is no contradiction between a universal motivation to pair-bond and the failure of some or many individuals ever to do so — all too obviously, pair-bonding can be thwarted in so many ways that lifetime failure to form (or to sustain beyond the initial stages) a pair-bond is commonplace. And it would be difficult to make an adaptive case for an unconditional open-ended affiliation. The popularly held notion that the pair-bond is naturally of very long duration is through conflating pair-bonding with other forms of affiliation that may augment and/or replace pair-bonding to change the nature of the relationship – a usual development to which the parties to long-enduring marriages often readily attest. Ryan & Jetha do not acknowledge (even when repeatedly requested) [personal communications 2009, 2010] Fisher's cross-societal finding [Fisher 1989, 1994] that the facility to pair-bond indeed is universal, though with a short average duration of four years (based on the median age of separation after marriage). A short duration hardly calls into question the existence of pair-bonding, but it does inform the debate as to the basis of its being adaptive.

Theorising as to the basis of pair-bonding is summed up by Quinlan [Quinlan 2008] as two apparently conflicting theories of male mating competition and male provisioning of the female (henceforth 'male provisioning'), between which it is not possible to decide, with human pair-bonding appearing to have an ecologically varied complexity. The conflicting theories are two inter-related major assumptions usually made about the function of the pair-bond (generically across species, humans included): that it is male proprietorial control of the female's fertility, so as to provide paternity confidence; and that this serves to facilitate the resourcing of offspring. The latter would appear to entail the former, in that proprietorial control ensures the male's investment of provisioning is to his own genetic offspring and not to those of another male. Given the impasse Quinlan identifies, it would be instructive to examine the assumptions of male proprietorial control and provisioning to see if they are warranted. I will take them in turn.

The assumption of proprietorial control is contradicted by data from many ostensibly 'monogamous' species showing a high incidence of extra-pair paternity [eg Colombelli-Négrel et al 2009, Ležalová-Piálková 2010]. Humans are no exception: there is a substantial (albeit variably estimated) incidence of human extra-pair paternity, and most tellingly this applies even where it might least be expected, in a 'traditional', 'primitive' community [Scelza 2011]. Manson [Manson 1997] reviewed the literature on pair-bonding across species and found that the courtship element of pair-bonding is predictive of reproductive outcome, but that this is not true of the element of mate-guarding. A review of avian mating systems found little relationship between the strength of mate-guarding and paternity [Johnson & Burley 1998]. Kokko & Morrell [Kokko & Morrell 2005] ask the pertinent question: "if females regularly escape mate-guarding attempts, we face an enigma: why does mate guarding evolve if it is so inefficient?"

The most likely answer to this question is that the 'inefficiency' is apparent rather than real, owing to the actual nature of mate-guarding not being understood. A female appears to have little problem having sex with males *of her choosing*. It is with respect to female choice that mate-guarding seems 'inefficient'. Her choice will be from the pool of those males with a higher mate-value than that possessed by her pair-bonded partner, as is shown by women behaving in the very opposite way to men in *raising* their 'standards' re opposite-sex mate-value when looking for 'casual' sex [Szepsenwol, Mikulincer & Birnbaum 2013]. Female extra-pair choice for 'good genes' – that is, 'better' genes than those of the pair-bonded partner – appears indeed to be the basis of extra-pair sex [eg Cochas et al 2006, Kempenaers et al 1992]. With the consequences of sex for the female, there would be no value in extra-pair sex with any male of a lower mate-value than that of the pair-bonded partner.

If a male were to try to oppose the female partner's chosen extra-pair sex, then the cuckolding male, in being comparatively higher in mate-value, is likely to be the physically more powerful and/or more belligerent of the two, and/or to be a member of a stronger male coalition. Therefore, if the confrontation resolved to simple contest, most likely the male attempting to defend against cuckoldry would be defeated. The physiology and psychology concerning dominance hierarchy provide evolved mechanisms to avoid initiating or escalating conflict with higher- (but not lower-) ranking males, thus likely avoiding from the outset the possibility of an escalation. Yet given that the threat to paternity confidence is from higher, and not from lower mate-value males, then this would obviate the function of male mate-guarding as the basis of pair-bonding.

It would seem, therefore, that male mate-guarding – as understood to be proprietorial control to prevent the female from either initiating or accepting extra-pair sex with any other male – is something of a misnomer, as Kokko & Morrell realised; and presumably it must have a different function to that hitherto supposed. The only apparent – or at least the most obvious – alternative is that it serves not the interests of the male to avoid being cuckolded, but instead is a service to the female in preventing attempts at sexual access by males of *lower* mate-value (lower than that of her pair-bonded partner). This previously has been suggested [Norscia & Borgognini-Tarli 2008] as the basis of primate pair-bonding. Deterrence of unwanted suitors has been recognised [Lumpkin 1983], but assumed to be a development of male mate-guarding as usually understood, through its exploitation by females.

Lower mate-value males, in being sexually selected against by females and liable to face reproductive oblivion, are obliged to employ a riskier, long-odds approach to try to initiate courtship and obtain sex. Consequently, males in numbers are likely to try to gain access to females with relative mate-values too high for them to have an interest in mating. The problem this poses for females may be less the risk of unwanted, fitness-lowering sex (in the human case, given social prohibitions it's not likely that females require 'bodyguards' to prevent coerced mating; though it may be that some females could be cajoled into mating against their interests) than continual, persistent attention that would displace interest from the high mate-value males to whom the females are potentially sexually receptive, and effectively hinder the females' own initiatives to associate with such males.

In requiring a male to provide a mate-guarding service to deal with this problem, males of intermediate mate-value are in a position to exploit this need in conditionally offering the service only to those females whose mate-value (fertility) is higher than that of those females who would be willing to engage in sex promiscuously. Pair-bonding thus would emerge as an evolved mutual trade-off. The female obtains assistance to optimise sexual access to her (by not the 'wrong' and only the 'right' sort of males, as it were), thereby increasing her total fertility; whilst the male acquires for regular sex a more fertile female than he could otherwise procure 'casually'.

Turning to the other major assumption about the function of the pair-bond — that it facilitates male provisioning of offspring: this is the supposed basis of the need for paternity confidence. The male needs to be sure the offspring indeed are genetically his own, given that the male invests in offspring. This assumption is also contradicted by the evidence. There is comprehensive data that father-presence has little if any impact on child survival (because female relatives provide any childcare the mother could not provide herself, so there is no need to rely on the father); this being recently extensively reviewed [Sear & Mace 2008]. Studies in respect of child growth and morbidity show at best a weak, cross-culturally inconsistent impact of father-presence [Winking 2007]. As for the key material contribution of meat, the evidence is mixed. The well-known evidence from extant hunter-gatherer communities is that males share hunting proceeds to a large extent equitably across the group [eg Kaplan & Gurven 2005]. [Hunting usually yields nothing, but on occasion an abundance of very quickly perishable food, and consequently inasmuch as there is, in what is a cooperative venture, in any particular instance a successful individual hunter, this same individual is unlikely to be the successful one next time; so sharing incurs little cost whilst ensuring future cooperation.] Qualifying this are findings that men do in fact keep back meat for their own family [eg Hawkes et al 2001]. Most importantly, there is clear data showing that women in forager societies benefit nutritionally from a pair-bond partner during lactation, when their own ability to forage is most compromised, with men making up for this by contributing foods such as honey [Marlowe 2003]; this being shown to be the case across the various forms of 'traditional' society [Quinlan & Quinlan 2008].

That male provisioning during lactation is not apparent as any impact of father-presence is explained by male-provisioning post-dating the evolution of pair-bonding – across species generically [Brotherton & Komers 2003], and specifically regarding humans [Chapais 2008]. Chapais' is the most comprehensive recent exposition on the origins of human pair-bonding; the conclusion of which is that male mate-guarding is key (though Chapais' understanding is in male-proprietorial terms). Still more recently affirming this position [Chapais 2011], Chapais 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 conclude that the emergence of a specifically human mating pattern coincided with increasing male provisioning evolving out of a (polygynous) pair-bonding base [Geary & Bailey 2011].

In the light of male provisioning being itself facilitated by pair-bonding rather than the basis of it, a new interpretation is required of the important finding that although there is no correlation between male provisioning and child mortality, there *is* between male provisioning and average female total fertility [Marlowe 2001]. The relation here being only a correlation, it does not show the causal link as supposed. With pair-bonding being antecedent to male provisioning, then the increased female total fertility presumably is the result of the other contribution that males make of mate-guarding — as Chapais concludes. That increasing female total fertility is the function of pair-bonding is the conclusion in what is, other than Chapais', the most important recent review of the basis of pair-bonding, by Winking [Winking 2007]. The male's contribution – through (prior to Chapais' analysis), provisioning in Winking's view – allows the female to transfer effort from parenting to mating; though what form this takes is not discussed.

The female's increased mating effort could be either within or extra to the pair-bond, or both. It would seem to be both. From the consideration of mate-guarding above, then clearly the female has utility in the service provided by the male to displace social and sexual access by males of lower mate-value, and thereby in effect to facilitate her extra-pair sex with males of higher mate-value. But additionally, if when very young (at or near the peak of fertility shortly after puberty), through the fertility indicators of youth and beauty that at that time she possesses, a female can assortatively acquire a male partner of corresponding mate-value and secure him over a lengthy period; then she can have successive children with the same complement of 'good genes' at each successive conception. She can, in effect, *project forwards* in time her peak of fertility. Otherwise, the female would reproduce simply through promiscuous sex, and her offspring likely would have a progressively poorer male genetic complement as the mate-value of the men she is able to acquire falls with her advancing years (and the effects on her body of childbirth). Though over the course of the duration of the pair-bond, the female partner experiences a decline in mate-value with age, there is no corresponding fall in the mate-value of the male partner, because being in terms of 'good genes' as manifest in status (male dominance rank), male status if anything increases over time with cumulative outcomes of male intra-sexual competition. [Some males do of course 'flat-line' or actually fall in status, but this propensity usually will be evident beforehand in the mate-value criteria females scrutinise, leaving them of little interest to females.] The pair-bond thus can be considered in the light of the intersection of very different life-history trajectories in terms of mate-value according to sex. There is sex-differential – sex-dichotomous – mate-value trajectory. This major divergence over time of attractiveness according to sex (with the male an appreciating asset and the female a depreciating one), in itself provides a basis for pair-bonding in the female interest.

In the male solving the female's problems of both unwanted engagement by lower mate-value males and her quickly falling fertility, the trade-off he succeeds in making against his own relative lack of mate-value results in the female not assortatively mating according to a full corresponding opposite-sex mate-value – that is, in terms purely of 'good genes'. Instead, the female has made a compromise to accept a male with a mate-value made up of 'good genes' plus the ability to provide a mate-guarding service plus durability as a pair-bond partner. To have sex with males possessing a mate-value truly corresponding to that of her own – that is, purely in terms of male 'good genes' to correspond to fertility – the female would need to eschew her pair-bond partner to seek extra-pair sex. And this is not difficult given the actual nature of the male pair-bond partner's mate-guarding – to not include keeping at bay males of higher mate-value than his own. Female physiology drives women to seek extra-pair sex at the very point in their cycle when sex is most likely to lead to pregnancy [eg Gangestad & Thornhill 2007]. The female has the pair-bond partner's genetic complement to fall back on if the tactic of extra-pair sex does not bear fruit.

If the pair-bond indeed is an adaptation functioning to achieve at least one successive conception with the same male, then the pair-bond would have to be of a certain (minimum) duration to encompass the several stages from the commencement of courtship to the second birth. The length of these stages can be assessed (in populations as near as possible to the ancestral), added together; and the total compared to Fisher's conclusion of the pair-bond lasting four-years on average. Fisher's estimate would appear to require an adjustment, however, in that there is no account taken of the period of courtship before marriage; and therefore this duration should be added. Unfortunately, quantifying cross-culturally is extremely difficult given the enormous variation, both individually and according to society, and often wildly contrasting measures by different researchers studying the same population, as with China [Zang 2004]. There seems to be little if any reliable and comparable data. All that can be said is that the average length of contemporary courtship is years rather than months: two years or more in the USA [Whyte 1990]. Another problem is that pair-bonding cannot be taken to be from the very beginning of courtship, given that it would require some elapse of time to form; but there seems to be no data on this, despite courtship having been broken down into twelve stages [Morris 1972]. It would appear that the time taken from first meeting to the establishment of a pair-bond is completely elastic. Taking all into account, in augmenting Fisher's average pair-bond length, an appropriately cautious stretching would be to five or six years from four.

To compare with this, data is needed on the sequence of courtship, sex, conception, gestation, birth, lactation and resumed cycling and sex, ending with a second conception; this in populations living in conditions as near as possible to those that pertained ancestrally. The major contributor here is the duration of lactation: the age of weaning. This is too variable for a cross-cultural average to be meaningful, but at two-and-a-half years it is surprisingly long, with the natural duration before 'self-weaning' being still longer at three to four years [Dettwyler 1995]. The significant duration for the present calculation is that portion of the lactation period before cycling is resumed, which depends on the frequency of suckling – short bouts of frequent suckling trigger a complete suppression of reproduction [Konnon & Worthman 1980]. This is assured in 'hunter-gatherer' societies because the mother has the child with her all of the time, enabling the child to suckle at will. However, as the child gets older and less dependent, then feeding frequency presumably declines, thus triggering renewed cycling and the mother becomes fertile again.

To avoid these indeterminacies regarding lactation (and to reduce the number of other stages to take into account between the first and subsequent birth, which have their own uncertainties); instead, use can be made of the data on the actual inter-birth intervals of extant hunter-gatherer societies. There are reports for several of these: all being three to four years [Kaplan et al 2000]. [This reveals that lactation must be shorter and less reproductively-suppressive than might be expected.] From this data, to arrive at the overall length of time between the start of pair-bonding and the second birth, there would need to be added the nine-month duration of gestation, the 'fecundability' period – the time taken for regular sex to lead to conception; and any elapse of time between the beginning of courtship and the commencement of penile-vaginal sex. 'Fecundability' is, in modern societies at least, four to six months on average [Hutchins 2011]; so I will factor into the calculation five months in respect of this. As for courtship, based on evidence from extant hunter-gatherer societies, a reconstruction of ancestral marriage practice shows unregulated courtship rather than arranged marriage to be ancestral [Walker et al 2011]; and without the various factors contributing to protracted courtship in agricultural and 'developed' societies, ancestrally courtship presumably would be very much shorter; months rather than years. There is no readily accessible data, however, save for a mention that for the Hadza courtship is 'brief' [Marlow 2004]. In the absence of data it can only be assumed that the Hadza are representative. 'Brief' suggests just a few months, and a guesstimate of four months would seem reasonable. Also difficult to assess is the point during courtship when penile-vaginal sex commences and the 'fecundability' period thereby begins to apply, creating an overlap, which needs to be taken into account; but inasmuch as marriage does not coincide with the onset of fertility, in at least some hunter-gatherer societies any sex before marriage is proscribed and absent; eg the Hamza [Unrau 1971]. Consequently, it is reasonable not to factor this into the calculation (that is, for it to be ascribed a value of zero).

Even simplifying through using the inter-birth interval leaves major uncertainties, then, in the durations of other stages that have to be taken into account; but to add them up is to arrive at a very rough but not entirely uninformative overall duration with which to compare the augmented measure of pair-bond length based on Fisher's findings. The total based on the above conservative guesstimates is four-and-a-half to five-and-a-half years, which is close to corresponding to the five to six years for the pair-bond that is Fisher's four-years together with the omitted courtship period. Using less conservative guesstimates that go beyond averages to be in line with better guaranteeing that most or the great majority of couples reproduce twice, would increase the calculated 'first sex to second conception' duration to equal or surpass the pair-bond duration based on Fisher's findings. In this regard, most notably the 'fecundability' period required to ensure not merely half but 90% of couples conceive, would double to ten months the five months factored into the calculation. This alone would bring the estimated ancestral 'first sex to second conception' duration to match the Fisher-based findings.

So the data regarding the duration of pair-bonding and a quantitative estimate based on a rationale as to its basis are not in discord. They are together consistent with ensuring the conception of a second child with the same father, and therefore not inconsistent with a female fertility model of pair-bonding. [If female fertility indeed is the adaptive explanation, it would not be expected that the evolutionary process would still further extend the duration of pair-bonding to ensure three or more offspring by the same male. The very many competing selection pressures would entail diminishing returns for any specific adaptation within the context of the suite of all others. In any case, other forms of affiliation can 'piggy-back' pair-bonding, in effect extending it by augmentation or replacement.] The length of the pair-bond thus both assessed and estimated is about the same as, or rather longer than what would be required to ensure male provisioning during lactation (which is Fisher's own explanation of her findings) [Fisher 1989]; but (to reiterate) provisioning has been excluded from being a candidate in its being antecedent to the evolution of pair-bonding.

The understanding of male mate-guarding turned on its head so that in humans what had been taken to be proprietorial control by the male instead is *by the female*, is evident in the literature. That there is mate-guarding by women as well as by men and that they are very different in nature has been recognised [Archer et al 2001, and personal communication 2005]. There is female mate-guarding in other primate species in the form of high-level unilateral aggression; eg the mongoose lemur [Anzenberger 1993]. That the human female rather than the male is the 'controlling' partner is the case in 90% of couples [Coleman & Straus 1986], and even in terms of what are perceived to be male sex-typical forms of 'control', women at least match men [Graham-Kevan & Archer 2009] — so if there were also factored in any distinctively female forms of 'control', then presumably women would be revealed as the more 'controlling' partners. Other research reveals that men are obliged simply to give in and agree in the face of women taking overall charge of the relationship in a 'domineering' manner [Vogel & Murphy 2007].

The need for 'control' within the pair-bond self-evidently can precipitate as intimate-partner violence, and with 'control' being overwhelmingly by the woman, then it would be expected correspondingly that intimate-partner violence is predominantly female-perpetrated. This indeed is what is revealed by several converging lines of evidence and a sum total of evidence [Moxon 2011]. Physical violence is women's preferred mode of aggression in domestic situations (in complete contrast to men, who back away from engaging in physical aggression in any situation where a female would be the target) [Cross, Tee & Campbell 2011]. This explains why, despite huge sex-differentials in both upper-body strength (conferring far greater hitting power to men) and body-frame weakness (rendering a profound susceptibility to injury to women), there is almost no sex-differential in intimate-partner injury rates – slightly higher for women [Archer 2000, Mirrlees-Black et al 1998,] or a difference that is not significant [Capaldi & Owen 2001], or nil [George 2003]. Yet *even if rates of male and female perpetration of intimate-partner violence were similar,* the sex-differential in injury rates would be expected to be double an order-of-magnitude (x20); that is, 95% of injuries would be sustained by females [Dixon 2012]. This indirectly reveals a very large preponderance of female perpetration of intimate-partner violence. Furthermore, at levels of violence where serious injury occurs, victims are much more likely to be male [Felson & Cares 2005]. The data for intimate-partner violence is well understood to suffer from a highly sex-differential reporting bias, with men compared to women having less willingness to report to police by a factor of ten [Stets & Straus 1990], because women but not men self-perceive victimhood. Consequently, couching surveys in terms of crime or personal safety evokes a victim response in women but the very opposite in men; but even after removing such demand characteristics men still under-report compared to women [Archer 1999]. Given the proportion of male victims of intimate-partner violence as formally recorded by police is consistently 40% [eg Thompson 2010], then if the very large sex-differential in the propensity to report were factored into the crime data, there would be shown an overwhelming preponderance of male victims of intimate-partner violence.

The greater importance of the pair-bond to women compared to men is belatedly showing up in research, that in being of indirect measures of the emotional investment in pair-bonding detect implicit genuine attitudes. The results may appear counter-intuitive, but this is because of the popular context of *direct* measures of *explicit* attitudes, which in failing to exclude (and instead creating) demand characteristics are worthless. Simple surveys of attitudes to marriage inevitably strongly evoke perennial prejudices couched in contemporary political fashion. Also uninformative are divorce statistics regarding the sex of the initiator, because formal separation proceedings are likely the response to de facto separation initiated by the other partner, or to the other partner's indifferent inertia – and to very strong financial and child-custody incentives. The key new research on *indirect* measures is by Dunbar and associates: in analysing patterns of mobile phone use, it was found that not only do women invest far more heavily than men in a pair-bond, but also persist with it as their principal focus fully twice as long as do men – fifteen years as opposed to seven [Palchykov et al 2012]. Another window is provided by a major cross-cultural study in which wives were shown to be more worried about their spouse's infidelity than were husbands [Shattuck et al 2012], notwithstanding the clear major male concern of cuckoldry – the importation of a genetic complement from outside the pair-bond – which is an objective male fear without a parallel for women. The authors ascribe their results to a greater likelihood of male extra-pair sex, but questions as to the reality of a sex difference in propensity to obtain extra-pair sex aside – and note that the male can seek excessively and not obtain; whereas the female can obtain very easily with little if any seeking required – the profound sex differences in the evocation of jealousy surely would be expected to be evident here; *males* rather than females being sensitive specifically to sexual rather than emotional betrayal [eg Sagarin et al 2012]. With females having less fear of the very sort of infidelity in which males usually indulge, then Shattuck et al's findings would seem to be rooted in men's lack of concern for the integrity of the pair-bond. The research by Sagarin et al is the culmination of an extensive literature on sex-differential aspects of jealousy, which has been in part a debate as to whether there is indeed a real sex difference rather than some artefact of study. Their meta-analytic review of both real-life studies and hypothetical scenarios confirms a real sex difference. Not that this was ever in doubt with one of the most common conversational staples being of the woman 'standing by her man' despite his infidelities whilst the man may well desert at the first sign of the female partner's infidelity.

This 'deal-breaker' nature for the male of female extra-pair sex is easily explained. Notwithstanding the lack of male investment in offspring, the female partner's extra-pair sex completely negates the male's investment of sexual effort over time in this one particular pair-bond. Instead, the male could have been in a different pair-bond, with a faithful partner, and/or simply mated promiscuously (which for men ancestrally would be highly reproductively profitable). To not quit the pair-bond upon discovery of infidelity would be to compound this opportunity cost by a likely further loss of the same kind, as the female may well then enter a long period of non-fertile gestating and lactating another male's offspring before resuming cycling. Furthermore, it is not just that the male cuts his losses and avoids further opportunity costs; but he is likely to gain an opportunity windfall, as it were, in acquiring a *more fertile* new pair-bond partner. With the typical male mate-value trajectory being upwards in line with rising status with age (as his 'good genes' over time manifest more in status), then in a new bout of assortative mating the male may well be able to find a replacement partner of a correspondingly higher mate-value – higher fertility – than was the former partner even at the beginning of that pair-bond; let alone at the time of the dissolution of the pair-bond, by which time the former partner's mate-value would have declined in proportion to the pair-bond's duration. So it is that the discovery of a partner's extra-pair sex is a clear 'deal-breaker' for the man, though not for the woman because of what she would lose in dissolving the partnership. By contrast with the male ex-partner, the new pair-bond partner the female ex-partner likely would acquire would be of a lower mate-value than her previous partner, given that she had acquired her former partner when younger and nearer the peak of her fertility. The consequence would be a significantly lower fitness for all of her subsequent offspring. The upshot is that whereas the male readily quits a pair-bond on discovery of his partner's infidelity, the female is likely to attempt to keep the pair-bond intact, even with repeat infidelity by her partner.

Pair-bonding as male mate-guarding to thwart lower mate-value males would complement concealed ovulation/oestrus, in that this can serve the very same function, rather than that usually assumed either of ensuring male investment or counteracting infanticide by males. [For a full review of the competing hypotheses re concealed ovulation/oestrus, see Thornhill & Gangestad 2008.] Neither of these putative explanations would seem to apply in the human case, given the absence of any evidence of male-perpetrated infanticide of offspring of a still-lactating female to force a resumption of cycling (presumably because no such phenomenon exists), and with the advent of male provisioning being in the wake of the evolution of the pair-bond rather than the basis of it. It may be that pair-bonding and concealed ovulation/oestrus evolved in tandem. In rendering males unable to detect the short monthly window of fertility when it is potentially fruitful to gain social and sexual access to the female, lower mate-value males would have to expend effort continually; and this time, effort and risk – for what anyway for such males is a very long-shot bid to obtain sex – would be problematic if not prohibitive. That for humans this may well be the function is indicated by what seems to be the obverse of keeping at bay lower mate-value males, in the body of research revealing that human ovulation/oestrus actually is not entirely hidden but subtly evident [eg Tarin & Gomez-Piquer 2002]. With the female being most receptive to extra-pair sex with high mate-value males at the most fertile point in the menstrual cycle [eg Gangestad & Thornhill 2007], then if ovulation/oestrus were to be detectable only by preferred males – perhaps through the female being proceptive and allowing a male she favours to get particularly close – then the mechanism can be discriminating in both discouraging low mate-value males and encouraging high mate-value males.

There would seem to be an instructive long evolutionary history to these adaptations in homologous behaviours in the orangutan. This is the sole ape species other than the human to display concealed ovulation/oestrus, and it also has a form of (proto-)pair-bonding. Not only do orangutans have sexually exclusive consortships that can be of comparatively long length (up to seven months) [Utami et al 2002], but the same individuals pair up between child-rearing, and adolescents establish long-term affiliations prior to future consortships [Grehan 2006]. These similarities might be thought merely homoplasious were it not for the new finding that the orangutan is the extant higher primate species closest to the extinct common ancestor of all apes, owing to its having evolved very slowly (in comparison to all other ape species) since that split [Locke et al 2011], and therefore this species is highly indicative of human ancestry. Specifically regarding mating systems, that of the human is now shown likely to have evolved not from a chimpanzee-like ancestor but from one much more like the gorilla or orangutan [Nakahashi & Horiuchi 2012, Geary & Bailey 2011]. [The gorilla is polygynous, the orangutan short-term polygynous.] This is in accord with a substantially greater overall behavioural and morphological similarity, revealing that humans are evolutionarily closer to the orangutan than to the chimpanzee/ bonobo [Grehan & Schwartz 2009]; albeit that this contradicts what had been taken to be irrefutable molecular evidence, and controversy has ensued; but generally, constructing phylogenies based solely on genetics (and sampling very small fractions only of coding regions of the genome) entails assumptions and methodologies now criticised [eg Carvalho & Craig 2011]. There is also recent further important evidence against human-chimpanzee genetic closeness in the almost complete non-similarity of the human and chimpanzee Y-chromosome [Hughes et al 2010]. Even so, it is not necessary to accept greater human-orangutan than human-chimpanzee genetic proximity in order to to accept human-orangutan homology of mating systems. The balance of evidence is that concealed ovulation/oestrus and pair-bonding in orangutans and humans are likely homologous rather than homoplasious.

The problem both mechanisms would appear to address for female orangutans is that of ‘forced’ copulation by ‘unflanged’ (low status) males [Knott et al 2010]. These rarely result in conception, but this would appear to be because of these very counter-measures. When most fertile, females can form a consortship or ingratiate themselves with ‘flanged’ (high status) males, whose ferocity to other males deters low mate-value males from approaching attendant females; the effort in any case being rendered much less worthwhile by concealed ovulation/oestrus. The above-mentioned usual hypotheses re concealed ovulation/oestrus are even less potentially applicable to the orangutan than to the human; there being no investment at all by orangutan males in their offspring, and an extremely long – seven-year – inter-birth interval, which is several years longer than the three-year lactation period, rendering infanticide ineffective to bring the female back into sexual receptivity (thus explaining why infanticide has never been observed in the wild) [Beaudrot, Kahlenberg & Marshall 2009]. It would seem, then, that concealed ovulation/oestrus and pair-bonding may well be related mechanisms that evolved far back in the phylogeny – to the beginning of the ape radiation, if not beforehand – to deal with the problem for females of social and sexual attention from lower mate-value males.

This review reveals that a major correction would seem to be required to the understanding of the nature of mate-guarding and the human pair-bond. That hitherto what (at least in retrospect) is an obvious different understanding of male mate-guarding has not been appreciated, suggests compromise by political considerations completely out of place in science. The all-pervasive ‘politically-correct’ totalitarian mindset in its extreme-feminist core insists on an ideological model of ‘patriarchal’ [*sic*] ‘power’ to the exclusion of a scientific understanding from the underlying biology. This prevents any coherent analysis of social structure and dynamics; especially in respect of how the sexes inter-relate, as in mate-guarding and pair-bonding. Indeed, it leads to accepting complete falsehoods. It is ironic that this has eclipsed the key role of female choice, which determines both the pair-bonded and extra-pair sex partners of the female. Female choice is revealed to be central in recent modelling of the evolution of pair-bonding [Gavrilets 2012]. The model’s assumptions are the same as the findings or assumptions in this review: female choice, female fidelity but with extra-pair sex, male heterogeneity, assortative mating, and a key male contribution. Though in the model’s case this is provisioning, the model should work just as well if the element of male contribution instead was mate-guarding (in terms of preventing access to the female by lower mate-value males).

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