

Dominance hierarchy as integral to reproductive suppression; an adaptation consequent to the evolution of the male

A theory that the function of dominance hierarchy is the ranking by 'mate value' enabling individuals correspondingly to differentially (physiologically) (self-) suppress reproduction; and that this is a key manifestation of testing males in the service of filtering (eliminating deleterious and retaining enhancing) genetic material from the reproductive group -- this being the process that is either the reason for which the male mating type evolved or its major consequence and reason why separate mating types were maintained.

By Steve Moxon (*Correspondence address: stevemoxon3@talktalk.net.)
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Abstract

Dominance hierarchy (DH) is often thought to result from competition for resources and to function to bias access to or control over them, thereby reducing fitness lowering mutually unproductive contest. I theorize that albeit in some species resources may be allocated according to rank, this is merely a by-product of DH, not its root or function.

A more empirical and consistent conceptualisation of dominance -- which reveals DH to be fundamentally same-sex -- indicates DH instead to be a means of allocating mating access. Same-sex individuals ranked by 'mate value' enables not just corresponding opposite sex mate choice but, more fundamentally, physiological reproductive self-suppression of each individual to some corresponding degree. This varies along a continuum from in some species (most 'co-operative breeders') a 100% reproductive skew with total suppression of all individuals bar the sole breeder, to in most others a gradient down the length of the DH.

DH thereby makes wider sense as a major part of the process of testing males so as to 'filter' genetic material of the reproductive group to eliminate/ retain what is deleterious/ enhancing; this being the process that is either the reason for which the male mating type evolved, or its major consequence and reason why separate

mating types were maintained.

That DH and differential physiological reproductive suppression are integral is illustrated by looking at the extreme end of the continuum in 'co-operative breeder' species to see how the two phenomena vary with the permutations of elements of their various social organisation.

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Introduction

There would appear to have been a potential major fitness problem across the animal phylogeny that as a result of (and in the process of producing) male reproductive skew, male intra-sexual competition for mating access inevitably tends to include a large element that is mutually unproductive. Some form of social organisation to restrain what otherwise would be a free-for-all could rectify this, and dominance hierarchy (henceforth DH) fulfils this.

Male reproductive skew stems from the fact that whereas the female is necessarily the limiting factor in reproduction and females do not markedly vary in the number of offspring they produce, the male is potentially a prodigious reproducer. Consequently, males fiercely compete intra-sexually, usually in marked contrast to females. This is to try to take advantage of the potential heavy male reproductive skew on the one hand, and on the other to avoid the reproductive oblivion that displacement by such successful males would entail.

Males potentially could act directly to obstruct other males from getting the chance to mate, displace males who were in a position to mate, and intimidate other males from behaving towards them in like manner. Inevitably many males who were smaller, weaker, less driven, etc; would be eliminated from the competition through injury or death, or would have given up because of the risk of this; or simply could not muscle

in on the mating game. However, many males higher in fitness would be closely matched. Even for the strongest males, there would be a distraction if not a more serious hindrance from the business of mating. In defeating other males, even the highest status males would risk serious injury and even death from adversaries who may have little to lose. As well as these risks, a large element of such conflict would be at best unproductive -- a mutual waste of effort by all parties.

It is this restriction to an explanation in terms of competition over sexual access, instead of applying to any and every resource over which there may be competition, that distinguishes the position here from the consensus but ill-considered account of why DH would be adaptive. (As to why the consensus explanation taking in resources generally is false, I will return at the end of this exposition when I play devil's advocate to my own hypothesis. As to the nature of dominance and DH, I will outline after this introduction.)

The behavior of most males within a DH in ceding much, and in some cases all, reproductive opportunity to a minority, is not in some way altruistic. A skewed outcome of some kind of advantage to a minority does not mean that the majority necessarily has incurred a cost, even in the absence of any relatedness to provide inclusive fitness. Possession of any rank in a DH confers an overall benefit to its holder. The alternative to DH of 'scramble' competition to mating access likely would result in injury or even death for many lowly males, so at worst a lowly rank offers a refuge. Then there is the more pedestrian (non-injurious, non-fatal) mutually unproductive contest that DH precludes. For the least fit, the toll this takes alone may be highly significant. Lowly rank may enable an individual to bide his time until he is better equipped to ascend the ranks. Any position is a platform offering the potential to climb the hierarchy, and males are so highly motivated to compete with other males because of the potential for enormous reproductive pay-off, that they are prepared to take very long-shot bids to gain high rank. In humans, for example, this can easily take over a man's life, becoming something of an end-in-itself, even if this turns out to be fruitless to the point of being the route to reproductive oblivion. That only a minority of men ever succeed in such bids is factored in to the 'cost-benefit analysis', as it were, of the evolved behavior. To the individual male, it is worth the risk of being amongst the, say, nine out of ten who fail, for the chance of being the one in ten who succeeds. From both positive and negative considerations -- from both hopeful and defensive perspectives -- there is always a strategic advantage to membership of a DH.

As there is no need to invoke any model of altruism, there is therefore no need to look to a 'group selection' model -- not that 'altruism' cannot be explained in terms of 'enlightened' self-interest; but actually in any case this would not be a problem given the collapse of the debate about 'group selection' with contemporary multi-level selection theory that accommodates both the gene-centred and level of selection or 'vehicle' approach (as Dawkins distinguished). The consensus now is that in general 'group selection' will occur as long as the selection pressure at the higher 'group' level exceeds that at the lower level of the individual organism, even if the selection pressure is in respect of benefits that are realised only in the long-term, which clearly would be the case here. This is 'lineage selection',¹ which works not through selection of the trait with long-term advantage over the trait with short-term advantage, but indirectly by selection of what serves to reduce the latter's occurrence. 'Lineage selection' is how the 'policing' of DH evolved⁶, which is to say how to an extent DH evolved, as I'll now briefly explain.

Notwithstanding that there is a strategic value to membership of a DH even for low

ranking males, there is inevitably a problem in that tactically a low ranking male has an interest in opportunistically trying to subvert the DH. If a male's ranking entitles him to little if any mating opportunity, then he is likely to consider clandestine attempts to mate. With most agonistic behavior obviated by the social organisation of the DH, a

low ranking male might hope to avoid the serious punishment he would have expected if the context of all attempts to mate was a free-for-all. So a DH entails a potential tactical 'free rider' problem, which needs to be policed. A universal mechanism is required that triggers punishment for transgressors: either agonistic responses to check or correct, or exclusion from the social group.

This is where the social psychology of 'cheater detection' mechanisms comes in. Recent separate experimental work by Linda Mealey² and Denise Dellarosa Cummins³ has demonstrated that such mechanisms are employed in humans specifically against lower status individuals,⁴ being disengaged -- reversed, indeed -- in relation to the behavior of those of higher status. The extent of 'violation detection' varies according to the status of both the individual observed and the observer. Low status individuals will always be subject to 'cheater detection', and profoundly so by others of higher status. This would seem to be a mechanism that has evolved specifically to police the male DH, given that status differentials are not evident amongst women unless they are given male sex-typical status tags.⁵ It is also known that not only do people tend to withdraw attention from low status individuals, but that we have a neurochemical reward/ punishment mechanism to reflect rewarding or punishing others according to their status. So it is that if you deal harshly with others perceived to be of lower status, then your stress indicators and stress hormones fall and 'reward' hormones flow in their place. If, on the other hand, you attempt to retaliate against a person perceived to be of higher status, then stress levels actually rise. The same mechanism is evident in various primate species, which is what we would expect for a 'policing' mechanism for a social structure as phylogenetically ancient as DH.

The picture I've drawn thus far of DH is a too simple picture, however, in failing to consider that male reproductive skew is *the result of* DH; DH apparently being a product of the process behind why sex and the male evolved. As I outline below, it is becoming clear through a synthesis of theory that the male mating type evolved to act as a 'genetic filter' for the whole lineage: to both 'filter' out deleterious genetic material from the lineage and complementarily to retain genetic material that is beneficial. It is in the service of this key function of the male that DH would seem to be a behavioral adaptation, giving DH a more fundamental origin than has been supposed. The genetic quality of individual males is revealed through forcing mutual competition, and this is the basis of mechanisms to then skew reproductive outcome in proportion to rank achieved in the DH, thereby eliminating/ incorporating genetic material from/ in the lineage. It appears, therefore, that the solution to the theoretical problem of mutually counter-productive male intra-sexual competition would have been *already extant*, having itself arisen as an adaptation in the wake of the innovation of sex and the male mating type to help to produce the reproductive skew, a consequence of which DH should ameliorate. The upshot is that DH appears to be less a solution to a problem as I initially framed it, than the mechanism that mediates male reproductive skew.

I should deal here with possible objections to the notion of 'acting for the whole lineage'; this again raising the old spectre of 'group selection' or even of the perennial journalistic faux pas 'for the good of the species'. I mentioned above that contemporary understanding is in terms of multi-level and 'lineage' selection -- that is,

that selection acts across both level and timescale. But it also acts within the confines of a finite local reproductive group, which means inevitably some degree of inclusive fitness also needs to be taken into account. What this all adds up to is that the perspective needed is one that is simultaneously 'gene-eyed' and of the whole local reproductive group -- population genetics. The imperative in biology is gene replication: the maximising of it; and the context of this necessarily is not a theoretical infinitely large gene pool but a real one, that is usually of no great size and with the complex interaction within it over time that precludes usefulness in taking any snapshot view. That DH facilitates reproductive skew in the service of maximising gene replication within the reproductive group, means that the mechanism of DH is not just the process of rank ordering: associated with -- intrinsic to -- it must be the subsequent skewing of reproduction in relation to rank.

The core proposition of the hypothesis that I outline below is that differential reproductive suppression and dominance hierarchy are integral to each other, constituting a unified system whereby the one with the other would make much more sense; and it is a complementary argument as to how DH arose -- as a consequence of the emergence of the male mating type -- apparently before it was co-opted for the purpose of differential reproductive suppression. I include this complementary, subsidiary argument (towards the end of the exposition) because of the light it sheds, notwithstanding that the core proposition does not depend on it.

Before I develop the argument I first have to tackle the concepts of dominance and DH to get a firm handle on just what they are.

Dominance is often misconceived because of the way in which data is collected

The concept of dominance and DH originated with Thorleif Schjelderup-Ebbe, who discovered and studied the 'pecking order' of chickens in the early part of last century.⁷ As Omark⁸ found in his review of the literature, functionality of DH is almost always implied in any definition. According to Omark:

"A dominance relationship can be defined as existing if an attack by one individual is followed by flight or submission by the other individual However, assuming this functional relationship between dominance relations and prior access to some environmental feature, like a mate, is not the same as demonstrating that this assumption is valid. Dominance relations may have other functions; so the assumption must be tested and other factors explored."

Fitness maximisation is usually explicitly included in the definition; notably in that by E.O. Wilson:⁹ "the assertion of one member of a group over another in acquiring access to a piece of food, a mate, a place to display, a sleeping site or any other requisite that adds to the genetic fitness of the dominant individual." Omark discusses the pros and cons of a definition including fitness, but given the ubiquity of DH and that it requires certain specific cognitive attributes of all participating individuals and even in very lowly species, that appear to have evolved for the purpose; then DH would be an adaptation -- albeit that the DH that arises from dominance interactions is epiphenomenal in that it is created without any supra-individual level of organisation beyond dyadic interaction of participants with the minimal necessary neural equipment. (I will expand on this shortly.)

How dominance/ DH is conceived is bound up with the problem that as with any phenomenon under investigation it is necessarily the case that until it is more fully understood we are stuck with a merely provisional definition of what the phenomenon actually is. This is informed by the practical difficulties of how data is collected, sometimes to the extent that the 'operational' definition of the phenomenon in effect becomes the definition of the phenomenon itself.

The central problem with the concept of dominance is that it is a relationship, and the data is necessarily relative. Much confusion has ensued from the conceptual error of treating dominance as if a combination of attributes that help an animal to achieve dominance was itself dominance; and even that dominance is a personality trait. Having said that, it is not unreasonable to posit an inherited degree of predilection to dominance in the form of a basal testosterone level; but given male intra-sexual contest occurring from infancy onwards (from the age of 18 months in humans) then it is difficult to distinguish between dominance as a personality variable and a model where dominance and basal testosterone level are reciprocal.¹⁰ The relativity has made it hard to get a handle on the process behind dominance in the brains of the parties to the relationship. The 'working definition' of dominance at its narrowest is simply the victory of an individual in a single contest, irrespective of what the contest is about, either directly or indirectly. Less narrowly conceived, dominance is a more general relationship of an individual to others, which is gauged by looking at a series of encounters between the individual and a number of others across different scenarios. With sufficient observation it is possible at least in theory to find the individual's rank in the DH.

However, given that researchers do not know quite what they are looking at, then there is the likelihood that an observed interaction is one where dominance is only one factor, and not even the major factor; or where dominance is not in play at all. So when we try to assess an individual's rank it may well be that data is confounded and we get only a poor approximation. On the narrower definition, where we are looking at a single encounter, or at many individuals but only re instances of just one type of encounter; then it may be that the data we get is entirely spurious. This would mean that in studying any (supposed) DH, the placement of constituent individuals, or the degree of linearity, may alter markedly according to what type of interaction is being assessed. There is now research demonstrating this very problem.¹¹ This is just what we would expect if dominance concerns only one subset of what has been taken to be a wide range of types of encounters appropriate to study; as we have (I argue) with dominance being concerned only with sex, and with other matters such as resource allocation consequently being at most indirectly connected.

An encounter is often taken to be one of dominance simply because of an apparent victory, without checking for signalled submission/ dominance, or (if this was an initial encounter) even if any sort of contest took place. Notwithstanding that submission/ dominance signals are observed, it does not necessarily mean that the interaction was one of dominance, because we know that such signalling has been co-opted for other social behavior, such as courtship. Much of what is taken to be signalled submission/ dominance is not so. Simply avoiding conflict is taken as evidence of submission: an animal may be said to have run away, when actually it simply declined to initiate engagement.

The problem is that we can't filter out spurious instances, because all instances, spurious or otherwise, are dominance interactions according to the operational definition. Dominance is defined circularly. This leads to the tendency to broaden the conception of dominance rather than to narrow it down so as to usefully give

clues re a theory of mechanism and function that can lead to testable predictions.

Where dominance is assumed but is not applicable: it's not inter-sexual

Absurdities ensue, such as the notion that the human mother-infant relationship is one of dominance -- that it is not qualitatively different to peer-to-peer dominance -- with the mother invariably dominant. This comes unstuck as soon as you consider that in most mother-infant encounters the infant 'calls the shots', as it were. The infant demands to be fed and 'wins'. The mother usually if not always responds by preparing food or by yielding up her breasts to allow the infant to suckle milk. There is no mutual signalling of dominance/ submission, but this is thought not to be necessary for dominance to be inferred. By the operational definition you would conclude that the infant is dominant to the mother. Yet the mother-infant relationship is clearly an affiliative one, where neither party is competing with the other for the purpose of attaining rank in a DH. The bond is so strong that it would be superfluous to have any mechanism to compel the mother to provide resources; and competition over sex between a mother and her daughter cannot be at issue as the daughter is not sexually mature. When human offspring do reach sexual maturity they disperse from the family, and have by then long been part of a peer group of which the mother is not a part. Furthermore, daughters usually disperse from the natal group altogether.

There is a more common instance of an assumed dominance interaction that is less obviously false but on examination indeed proves to be so: that between the sexes. It is instructive to focus on this generic supposed interaction because the absence of it is consonant with the model here of dominance being concerned with reproduction and the necessary sex segregation of DH. So it provides a fault line between the consensus model and the one proposed here. If DH concerns the spectrum of resources, then it might be expected that the sexes would cross-compete; but if, as I contend, DH concerns sex -- ranking for the purpose of intra-sexual differential fertility suppression -- then the sexes would have every reason for same-sex competition but no reason to cross-compete.¹² Indeed, for a number of obvious reasons, it would be counter-productive. So we have here a prediction -- a mutually exclusive prediction, indeed -- of the model, that DH is a same-sex phenomenon; that there is one DH for males and an entirely separate one for females.

There has been much study of what is assumed to be dominance between the sexes where males 'give up' food to females. This is a type of encounter between the sexes where researchers have consistently made a firm conclusion that dominance is at issue. It is routinely asserted that one sex (in the great majority of species the male, but in several species the female) is always dominant to the other. That is, all individuals of one sex supposedly are dominant to all individuals of the other. A moment's reflection on why it would be that dominance in whichever direction is 100% immediately shows a flaw in this notion. A total one-way asymmetry in dominance between two very large normal variant sub-groups of an animal species that must to some extent overlap in relevant criteria (such as body size between males and females) implies that some factor other than dominance has become salient; indeed that dominance is likely irrelevant to the interaction.

Researchers reveal in their contradictory statements that they are confused about what is going on. It is said that, for example, chimpanzees have separate male and female DHs, but also that young males first dominate females in a series of

encounters and only then join the male DH at its foot and seek to climb it. The ring-tailed lemur is also said to have separate male and female DH, but that the females are dominant to the males. What we are being told here about both chimpanzees and ring-tailed lemurs is a contradiction. Either the DHs are separate and males and females do not have cross-sex dominance interactions, or the DH is as one and there is inter-sexual dominance.

The most interesting cases are those species, like the ring-tailed lemur, where 'female dominance' is supposed. In these cases, this is despite the fact that there is sexual dimorphism in size in favor of the male, making the interpretation of dominance still more unlikely. For the very reason that it is supposedly 'female dominant', the gray mouse lemur recently has been closely researched (by Ute Radespiel¹³). Only a single interaction in an entire study was judged an exception to what Radespiel termed 'female dominance'. 'Female dominance' supposedly was the case 99.9% of the time. Radespiel also notes that only in a small number of instances did both animals show any aggressive behavior. In other words, the males were very rarely aggressive to the females, even when the opportunity was there to reciprocate aggression from females.

The factor independent of DH which had become salient in Radespiel's study is plain to see. She explains that because it is so hard to keep a group together in the close confines of captivity, then: 'group formation took place on the first day of oestrus of one of the females'. By this, as she states, she means that this was the first time that the sexes met; beforehand animals had been kept in same-sex twosomes. The study is deeply flawed at the outset because it was conducted at the precise point when relations between the sexes were at their most atypical and intense, being sexual.

'Continuous spatial proximity between the sexes so far has not been observed in the field', Radespiel admits. So the very nature of inter-sexual interactions observed in the study may be a wholly artificial scenario. This possibility fits with the data from the study that most conflict occurred not as usually expected between the sexes in connection with food, when a proximal reason for conflict might be salient; but simply 'in the spatial context'. Spatial context conflict exceeded the combined conflict from all the other scenarios, and the definition of agonistic conflict had to be defined down to include simple approach/ avoidance, let alone chasing/fleeing (which can be observed between the sexes in young children, where we know there is self-segregated separation of DH according to sex). Radespiel claims only that 'dominance relationships can *potentially* (my italics) develop in the field'. She elaborates: 'In contrast to the captive situation, however, the submissive partner can more easily prevent an escalation of conflicts by fleeing and avoiding the dominant partner'. Equally you could interpret -- or, rather, you could *better* interpret -- that any kind of encounter is simply avoided, and a question of dominance or submission simply does not arise.

The ring-tailed lemur is a classic case of a species where there are inter-sexual encounters during feeding. The species is very well documented in this respect. There is even a David Attenborough BBCTV wildlife documentary¹⁴ investigating the species re this topic. When a male is feeding near to females, a female might come and take food from out of his hands. Far from an agonistic encounter, the female hardly so much as snatches the food, whilst the male not only does not resist but remains quite placid and unresisting. It is not even a case of giving the food upon request, because there is no active yielding. The encounter is simply a non-interaction. The film confirmed the entirely separate DHs of the males and females, showing fighting amongst the females both within the troupe for rank and between

troupe for territory, with the males taking no part whatsoever in this. Males are seldom anywhere near the females, often not even within the same territory. Attenborough pointedly stated: "the males do not fight except over females". They never fight *with* females is the crucial point.

There has been a lot of discussion about 'female dominance' that is apparent only in the context of feeding, being actually male deference in female 'feeding priority'. This was the conclusion by Kappeler¹⁵ re cross-sex aggression in lemur species generally. White¹⁶ concluded that male ring-tailed lemurs defer to females because they thereby become preferred mates. Pochron and Wright¹⁷ summarized their work on a species of lemur known as the Milne-Edwards' Sifaka, that: 'despite behavioral similarities between intra- and inter-sexual aggression, dominance within sexes differs fundamentally from dominance between sexes'. Their insight was that the probability of winning an intra-sexual dominance contest was for mammals generally higher with age, so if the nature and function of cross-sex aggression was similar, then outcomes should show the same relation to age. For sifakas, victories indeed do increase according to age in male-male encounters, but there is no relationship whatsoever in the case of cross-sex interactions. 'This supports the hypothesis that intra- and inter-sexual aggression play markedly different roles in lemur society.'

There is some ducking of the issue here. If dominance in the intra- and inter-sexual scenarios apparently 'differs fundamentally' and it plays 'markedly different roles', then there must be a question as to whether there is indeed dominance interaction in both contexts; of whether in fact they have anything sufficiently in common to be regarded as in any way similar phenomena. The picture is interestingly complicated in the

Mongoose lemur, where there are high levels of female-on-male aggression (but little male-on-female) apparently related less to feeding priority than to mate monopolisation by females.¹⁸ This is a fascinating evolutionary basis for the 'mate-guarding' behavior that is thought to explain the now overwhelming research evidence of a preponderance of domestic violence in the female-to-male direction in humans.¹⁹ John Archer²⁰ has proposed that a view of 'mate guarding' as male behavior is far too restricted and that there is a distinct female variety of the phenomenon. There is scope for much of what usually little inter-sexual aggression there is in any species to be explained not by dominance but by 'mate-guarding'.

The conclusion that male 'yielding' of food to females is not dominance but a non-interactive operation of female 'feeding priority' resonates much further afield. Many large mammals and birds show far more than a mere avoidance of conflict over food, in a marked divergence of the sexes between either the types of foods they eat or the modes of foraging for it, or even changed morphology (physical aspects). Some bird species have different types of beaks according to sex, so that the sexes have no option but to forage in different ways or for different foods. The most well-known case of this in behavioral form is that of the giraffe, where the males put out their long necks vertically to forage only in the high branches, whereas females (whose necks are just as long) take leaves at heights no more than they can reach by putting out their necks horizontally. The standard explanation for such sexual dimorphism is sexual selection -- female choice of male-male competition -- but natural selection of behavior to obviate resource competition is now also thought to be important, albeit that it is as yet little studied. This is known as the resource partitioning hypothesis of sexual dimorphism.²¹

That the potential problem of the sexes of the same species usually seeking the

same foods in the same local environment has in many cases resulted in a specific evolutionary adaptation, usually to change behavior, utilising and underlining the separation of male and female; is another ramification of the female being the limiting factor in reproduction.

There are clear reasons why the sexes have evolved not to engage in terms of dominance

There are strong selection pressures against cross-sex dominance interaction, if indeed cross-sex dominance interaction could in any way make any sense. As the limiting factor in reproduction, for a female it would be worse than pointless to risk injury through agonistic behavior towards males if there was any risk of retaliation in kind. It is not just that males are usually physically superior (the much fiercer intra-sexual combat of males usually ensures a pronounced sexual dimorphism in body size and strength, albeit not a non-overlapping one) but that the relative weakness of females has implications for susceptibility to injury. As the sex which has to appeal to females so as to be selected, for males not only would agonistic behavior towards females likely be directly counter-productive, but would risk retribution from other males who would seize the opportunity to curry favor with females and to display their fitness. Any marginal benefit of an immediate reward such as food would be nowhere near worth the risk, and even the profound benefit of (forced) sex is likely to be more than offset by the consequences. This drives male deference to females, which is an entirely different phenomenon to submission, being either a simple non-engagement in recognition of the other's interests (being bound up with a male's own), or the signalling of an instrumental yielding. The contrast between intra-sexual dominance-submission and *inter*-sexual male-to-female deference was common parlance in human society until recently, and it has been shown in analysis of human behavior.²²

The remaining possibility to explain inter-sexual behavior that may look like dominance is what clumsily might be called behavioral 'leakage' from intra-sexual behavior. It may be that individuals of the opposite sex encountering each other outside of a mating scenario are confused -- many species may not be able to sex each other -- and behavioral routines normally employed *intra*-sexually are evoked. Initially there could be rank registering/ checking as default behavior, as if all encounters are provisionally assumed to be same-sex. Even if the interaction that follows is simply non-engagement, the nature of this may be different according to sex if you consider that how individuals decline to engage others of the same sex may differ markedly for males and females. For a male, non-engagement is necessarily through mutual signalling re dominance-submission, because given that males have a mutual relative rank in a pronounced DH, then if rank is in doubt a contest will result. Males do not just ignore each other. If one animal simply withdraws, then the other is likely to assume that this is to avoid a test of dominance in which the withdrawer would likely prove sub-dominant, so he will try to press the apparent advantage and test for a submissive response to establish his dominance. For males, simple non-engagement therefore brings about the opposite of what you might expect: it ups the ante. The costs of not exhibiting submission are in the normal circumstances -- of intra-sexual potentially agonistic competition -- likely to be significant and in some circumstances could even be fatal.

Of course, in interacting with females, in my model there is no male-male DH rank at stake, so to avoid the possibility of an inappropriate dominance contest and aggressive behavior, the evolutionary process presumably will have selected either uncoupling of male intra-sexual behavior at this point, or alternatively a mechanism to engage such behavior only if there is positive identification of a male individual. The latter would be the most reliable, and indeed this would seem to be the solution that has evolved. Certainly this is evident in mammals. If you 'knock out' the gene in male mice that is necessary for detecting male scent, then the male mice behave as if all others encountered are females, and instead of trying to repel males they may try to mate with them.²³ So there is a default mechanism that all conspecifics are treated as female and therefore not engaged with in terms of dominance, unless there is evidence to the contrary.

For a female, non-engagement in an inter-sexual encounter would not need to come with such default baggage, because unlike for males there is no significant cost attached to dominant style behavior in any normal circumstance, given that female-female competition is nothing like as agonistic as the male-male variety, and there must have evolved strong damage-limiting de-escalation devices because of the selection pressure attending being the sex which is the limiting factor in reproduction. Aggression within limits is likely to bring positive results for a female if it is interpreted by males as a demand for preferential treatment, with a possible pay-off for the male in mating terms. The worst outcome for the female may well be merely the neutral one of being ignored.

It can be envisaged that sex differential cost considerations mean that if the sexes do at times engage outside of a mating context, rather than simply ignoring each other, males may act apparently submissively and females may act apparently dominantly. To call this a dominance interaction though, clearly would be to misunderstand the nature of the interaction.

To re-focus on the wider point: if the sexes indeed do not engage with each other in terms of dominance, then this provides subsidiary support to the hypothesis I set out here; being a 'prediction' that mutually excludes that of the consensus model.

Dominance hierarchy is a real phenomenon, and one tied to reproductive suppression

The nature of dominance is one thing, but the nature of DH is another. It needs to be established that DH is a real phenomenon and not an artefact of observation, and that it is a phenomenon that is actively constructed through mechanisms present in the individuals who make up the DH, and that therefore it is not merely an incidental epiphenomenon. It must also be established that rank correlates with reproductive success. Then we can begin to look for a link with differential reproductive suppression.

Dominance hierarchy is the social organisation of males (primarily, but it may also be of females; and in species where there is no male sociality, exclusively female) in the wild in species as far back down the animal phylogeny as the pre-insect phyla of molluscs and crustacea. Crayfish in particular and also shrimps have been well studied to confirm that in the wild males form DHs. What is more, the rank they achieve is the basis of mate choice by females.²⁴ A DH necessarily entails as the

minimum neural requirement of participating individuals the ability of each to store data on the outcomes of past encounters with a range of individuals to be carried forward re future contests. This is mediated by the neurochemical octopamine.²⁵ The registering of wins and/or losses ('winner'/'loser' effects)²⁶ enables an individual to cumulatively arrive at his own relative dominance; and the same process common to all participating individuals is the minimum requirement to produce a DH: either a clear ordinal series or less clear cut (varying in the degree of linearity) according to the use of either what are called 'winner' or 'loser' effects or of both. Computer modelling²⁷ confirms these minimum requirements and also shows that nothing beyond the behavior of the individual participants is required -- there is no supra-individual level of organisation per se -- so in this sense DH is a self-organizing system, as computer modeller Charlotte Hemelrijk claims. Indeed, we could call DH an epiphenomenon of the social psychology of individuals; individuals who need have no conception of the DH other than their own dyadic interaction when dominance becomes salient. Selection actually does in effect act on this epiphenomenon: operating intrademically on the whole reproductive group via the dominance hierarchy that results from individual action.

In a sense then it would not be incorrect to refer to the evolution of DH per se, but strictly we shouldn't refer to the evolution of what is an epiphenomenon, notwithstanding that it is anything but merely incidental to what 'concretely' has evolved. A parallel here would be consciousness, which is likewise at least in some respects a non-incidental epiphenomenon of brain process integration, and without thinking we happily refer to the evolution of consciousness. In any case, being convenient shorthand for what otherwise would have to be a clumsy long-winded expression, I will use the shorthand of referring to the evolution of DH throughout this exposition.

The effect of DH indisputably is to reduce agonistic behavior through ritualisation and staged escalation of what few encounters are required to establish the DH. A further refinement would be to get round the necessity of having to go through every permutation of pairing combatants. This is just what is achieved in species higher up the animal phylogeny through the evolution -- apparently for this very purpose -- of the cognitive ability of 'transitive reasoning',²⁸ where males are able to 'fill in the gaps' and thereby more easily arrive at a sense of their own rank within the local population as a whole by merely sampling the range of adversaries within the reproductive group.

The neural/ hormonal mechanism(s) of self-assessment of rank is not understood: we know it is complex. The basics in insects and a theoretical model that works in simulation have been discovered, as I have just outlined; but further up the phylogeny it would be expected that there is more complexity, making detection let alone understanding of the system more difficult. Several hormones are involved, notably testosterone, cortisol and serotonin. Each hormonal component is difficult to tease out given various feedback processes with more/less sensitised or blocked receptors, of which there may be more than one type. There may be (certainly in the case of cortisol) different mechanisms for short- as opposed to long-term elicitation and secretion, which have very different impact. The problem of unravelling what is going on with several interacting hormones is compounded by the dynamic nature of DH. A DH may be in its formation stage or be in some sort of flux, or some members may be falling or rising in rank. In some species DH can be more or less permanently unstable whereas in others it tends to be mostly stable.

In humans, the 'winner'/'loser' 'competition memory' necessary for the establishment

of a DH appears to be reflected in fluctuations in testosterone levels.²⁹ When men compete, their testosterone levels increase before the competition proper begins, and this is in response not to the task per se but to how they rate the chances of their opponent winning. Then after the competition, winning males have heightened levels of testosterone and losers have lower levels. This disparity in levels continues afterwards. This is not found in females, whose testosterone levels indeed do rise before a contest, and markedly so, but only in relation to how difficult they perceive the task; not according to how difficult they regard their opponent. Afterwards the levels of the female winners and losers do not significantly differ. There are other hormones involved in the 'competition memory' mechanism in men. It is known that before contests the cortisol levels in men differ according to their status or relevant skill: markedly higher resting levels of cortisol are the result of the persistent losing of contests experienced by lower status males. This also is not found in women. From what we know of human sex difference in terms of which sex competes for -- and is chosen sexually according to -- status, this is just what we would expect.

It is clear that in the hormonal mediation of competition in men, there is a contribution to the machinery of establishing and maintaining status hierarchies. Just how testosterone, cortisol, and serotonin interact in men is as yet a confusing picture. Serotonin is known through most of the animal phylogeny to be concerned with a more permanent registering by an individual of his/her relative rank. What is not in doubt is that there is something going on in men that has no counterpart in women.

That DH rank correlates very strongly with reproductive success is overwhelmingly evidenced,³⁰ though there is also research that shows little if any correlation in some species. This can be explained by the crude methods often used; not least the proxy measure of relative number of matings, which necessarily will not take into account clandestine extra-pair mating between dominant males and female partners of lower ranked males, and any ability of high ranking males to monopolise mating at especially fertile phases of the female cycle.³¹ It is only very recently that genetic techniques have become available whereby precise parent-offspring relationship can be ascertained, but although evidence of the correlation between rank and reproductive success is in the course of being progressively revealed, reviews³² have shown the correlation to be very strong. It would be still stronger if to fully assess reproductive outcome there was taken into account not just the number of offspring but also their quality. High ranking males will tend to mate with females of a correspondingly high 'mate value', so will produce offspring that are far fitter than average that will themselves stand a very good chance of being future high rankers.

The degree of relatedness to mates is another major factor. In-breeding is avoided for obvious reasons, so producing offspring will be far more restricted in species where social groups contain a substantial proportion of close relatives, yet low rankers may resort to in-breeding as their only option, thus producing very low quality offspring. Any model necessarily is complicated by kinship. The simple condition that all individuals within the reproductive group are unrelated rarely pertains: there will always be a degree of kinship within any social group, and in some species -- the 'co-operative breeders' which I discuss below -- this kinship may be its major feature. This introduces the very important factor of inclusive fitness, and this will strongly drive adaptation. When it comes to 'co-operative breeder' species, being cognisant of the factors that determine the breeding system is essential to make sense of relative reproductive success. A further complication is that indeed DH rank often will not fully correlate with reproductive outcome even taking into account all of the above factors, because although female mate choice is primarily according to male DH rank, in

many species it also includes a subsidiary element of reliability: the perceived propensity of a male to help in the care of offspring.

There is, then, little difficulty in establishing that DH -- or what produces it -- is an adaptation, and that this adaptation essentially concerns reproduction in that DH rank correlates with reproductive success. The question now is *how* DH rank correlates with reproductive success? There is no direct causal link without an additional mechanism. Is it simply that the principal female mate choice criterion is male rank? A co-evolution of male effort to gain status with corresponding female mate choice might be thought to suffice to skew reproductive outcome so as to maximise (within usual constraints) gene replication in the reproductive group. But this is far from an inexpensive or simple mechanism, and ubiquitous though this has become, it is not the most direct way of achieving reproductive skew. A much more direct way would be to couple DH rank with the level of fertility in the same individual, so that the ability and/or propensity to mate is correspondingly calibrated. Female mate choice would be an additional mechanism. Just as being behaviorally constrained by rank makes strategic sense for all individuals, regardless of how low a rank is achieved; so too there is strategic advantage to (self-)suppressing fertility. Indeed, if ranking is for the very purpose of differential allocation of reproduction, then the two go hand-in-hand in any case. The way that DH is policed with respect to attempts at tactical subversion manifests mainly as preventing males from mating.

We know for a fact that physiological reproductive suppression exists across the range of the animal kingdom; notably in the extreme and therefore obvious cases of 'co-operative breeder' species. However, there has been no discussion as to whether it always coincides with the presence of a DH, nor as to whether reproductive suppression is integral to DH. If such a coupled mechanism exists, we don't know what degree of coupling to expect; just that there would be to some degree the *differential* reproductive enhancement/ suppression of individuals according to rank, with the alpha allotted a full or possibly even enhanced reproductive role and lower ranks relatively progressively more suppressed. Conceivably this could be either through control by the alpha (or by a coalition of high rankers) of other individuals -- a 'dominant control' model -- or by individuals inhibiting their own mating effort and/or fertility autonomously -- a 'self-restraint' model. These alternative models thus labelled have been used in the context of the special case of 'co-operative breeder' species. In many of these species, there is the simplest form of reproductive suppression whereby all individuals are suppressed bar a single breeder of one or both sexes. So there is a 100% maximum reproductive skew. The 'dominant control' model might seem to make intuitive sense in this scenario, but it looks less apposite if such systems simply represent the extreme of what is a continuum where the usual case is a reproductive suppression *gradient*, whereby a single individual at the apex of a DH somehow would have to be able to calibrate the reproductive state of others to varying degrees. The 'self-restraint' model would not be through *cognitive* 'self-restraint', of course, given the lack of neural complexity of the lower animals that utilize DH. Albeit that selection operating on simple decision rules can often lead to sophisticated context dependent behavior, a simple autonomous neuro-hormonal mechanism within each individual is all that is required, directly impacting on an individual's own reproductive physiology, and possibly also working indirectly through behavior -- sex drive and wider behavioral propensity to seek sexual partners.

The theoretical dichotomy between 'dominant control' and 'self-restraint' is rather a chimera in that DH cum reproductive enhancement/ suppression is in the interests of all individuals within the reproductive group, so to place on any individual the locus of control or restraint is a misnomer. At root there is neither control nor restraint per se; no polarisation between two contrasting types of mechanism. A range of mechanism

is likely to be apparent, reflecting both general level of evolutionary development and adaptation through specific ecology; but I suggest that a trend in the whole phylogeny towards an autonomous automatic mechanism would be expected given that this is most parsimonious. It may be that mechanism evolved from interactive agonism, which then became pheromonal signalling by the alpha (or by the alpha and fellow high rankers), before the mechanism was then rationalized to one that no longer required signalling and was instead self-sufficient. The more gradation -- the closer the correspondence between DH rank and level of reproductive suppression/enhancement -- the greater would be the efficiency of the mechanism. However, as to what degree there would be a correspondence between rank and fertility suppression/enhancement would be subject to practical problems and cost considerations of the mechanism against the diminishing returns of progressively finer tuning, and the extent to which factors other than DH rank contribute to determining reproductive success (notably male signalling of reliability to offset to an extent lack of high status).

Just such a gradient of reproductive suppression corresponding to DH rank has been found to occur in bee, wasp and ant species, amongst females -- these being peculiarly all-female societies, with the males excluded from the colony and surviving as free-living individuals whereas the females have a highly unusual ultra inter-relatedness producing extreme 'co-operative breeding' systems (further discussed below) whereby there is a sole female breeder but with others waiting in the wings to take over. So although it appears that reproductively it is 'winner-takes-all', rank amongst the females determines the *degree* of suppression of ovarian activity compared to the full functioning of the sole breeder. The level of fertility of each individual in the DH is signalled chemically (pheromonally) from the external body surface or cuticle in the form of methyl branched alkanes and alkenes referred to as cuticular hydrocarbons (CHCs), of which the topmost ranked individual and egg layer has more and of a wider range. The amount and range of CHCs decrease as the DH descends from alpha down to delta or epsilon. Below this, other individuals are unranked and sterile and have no CHC signature. This has been extensively researched by Thibaud Monnin,³³ who confirms that 'recently, studies have also shown that insects can detect and discriminate between slightly different CHCs.' Monnin explains thus:

'The CHC profile does not simply indicate whether or not an individual reproduces; it advertises its level of reproductive activity. Indeed, CHCs vary gradually from the profile of a sterile individual to that of a partially fertile individual, and up to the profile of a fully fertile individual. When a sterile individual becomes fertile, its CHCs change accordingly; and, conversely, when a fertile individual becomes sterile its CHCs change in the opposite direction. However, the correlation between fertility and CHCs is not always perfect, because they do not vary at the same rate. This does not mean that the correlation is weak, or that CHCs are not an honest reflection of fertility.'

This works (as Monnin concludes) as 'honest signalling' -- that is, it is accurate because it would be against the interests of all concerned for it to be otherwise and instead for cheating to occur. The system on the face of it might seem to be one of 'dominant control' but equally can be interpreted as one of self-calibration of fertility on the 'self-restraint' model, given that individuals are merely responding to information about the fertility of others. The 'honest signalling' here is *not* owing to the very close inter-relatedness (see below) of the individuals within the reproductive group in these species and the consequent inclusive fitness considerations as may be supposed. The extraordinarily close inter-relatedness is the basis of the extreme skew in reproductive suppression, *not* the fact of differential reproductive suppression itself. There would be differential reproductive suppression even in the complete

absence of any inclusive fitness considerations. Given the gene-eyed view of the maximising of gene replication within any reproductive group in which the level of fertility is linked to fitness, then a mechanism whereby an individual calibrates his (or her) own fertility according to dominance rank could evolve in any reproductive group of any species, even if there is low or no inter-relatedness.

The tight linkage between DH and reproductive suppression is illustrated by the fact that whereas, for example, queenless ants establish a DH agonistically and then signal their dominance and consequent reproductive state 'honestly' by pheromones; honey bee workers do not contest physically at all, but contest instead by using pheromones mimicking those produced by queens that suppress ovarian function.³⁴ This results in the losers of contests being directly rendered -- or rendering themselves -- sterile: the two-stage process of establishing rank and reproductive suppression are here as one. Apart from beautifully showing that ranking and reproductive suppression are part-and-parcel of the DH mechanism, this is also interesting with respect to the suggested overall evolutionary path towards an internal mechanism. Here agonistic behavior, which is proxy for 'mate value', has been completely replaced by another proxy for 'mate value' which combines with signalling inclusive of the reproductive suppression process. Given that all is 'honest signalling' then there is no reason why in turn signalling cannot be completely replaced by an internalised signal, as it were -- a hormone rather than a pheromone -- whereby the process becomes entirely autonomous. All that is needed is for each individual to register its own rank and to differentially reproductively suppress itself accordingly. It is immaterial whether this is mediated by a signal from another individual or a signal generated internally. The difference is merely one of sophistication -- or, rather, simplification.

That DH and reproductive suppression are connected is revealed by other lines of evidence. The mediation of this connection by key neurochemicals has been demonstrated. Juvenile Hormone integrates dominance position with reproductive status in primitively social wasps and bumble bees,³⁵ and higher up the phylogeny serotonin provides a direct relationship between dominance and reproductive *enhancement* by the stimulating of release of luteinizing hormone-releasing hormone (LHRH).³⁶ This is interesting in that it shows that high ranking individuals may have not merely a non-suppressed but a boosted potential to reproduce. So conversely, sub-dominance by this mechanism will by hormonal cascade result in low levels of luteinizing hormone, which studies have shown is key to physiological reproductive suppression (see below). Serotonin we know is the chemical that mediates DH rank, even in animals more lowly than insects, such as crayfish; and it is perfectly antagonistic to octopamine, which as well as being behind experience-dependent plasticity of aggression -- 'competition memory', if you will -- also triggers the production of Juvenile Hormone in insects.

Primitive species aside, cortisol is or has been generally thought to be the key to a mechanism of reproductive suppression, and it is beyond doubt that sustained elevated levels of cortisol have this effect,³⁷ and in all higher animals, including humans. Sustained elevated levels of cortisol are characteristic of lower status males. Cortisol is the hormone behind the body's longer-term stress response -- as opposed to the 'fight-or-flight' response mediated by adrenaline (epinephrine) -- which keeps the body at a more sustained readiness for action by gearing up to produce glucose from otherwise inaccessible stores of fat. Cortisol secretion in the short-term is superseded by a positive feedback control system for long-term production, and it is this that is responsible for the elevated resting levels of cortisol in

lower status men. This accounts for the sex difference in cortisol responses to psychological stress.³⁸ Compared to women, men react with higher levels, and these levels are maintained for much longer before falling back. Such is the preparedness of men that their levels rise merely in anticipation of the psychological stress situation without actually having to perform the task. The sex difference re cortisol has led to the suggestion that the stress response evolved in each sex for different reasons, and there is research that now supports this.³⁹ It may be that the somatic stress response evolved into a reproductive suppression device first in males and then latterly and only partially in females.

This physiology is common to higher animals certainly as far back down the phylogenetic tree as fish.⁴⁰ In cichlids, once a hierarchy is established, the cortisol levels of the more dominant fish drops precipitously (despite their repeatedly chasing away males and attempts to attract females), whereas the non-dominant males' cortisol rose to very high levels and stayed there for the rest of the study. Dr. Sabrina Burmeister⁴¹ has studied the gene mechanisms of this and she confirms that: 'The basic mechanisms that control reproduction in fish and in humans are the same and may be in all vertebrates'. However, this would seem to be a rash conclusion. Just because the fluctuation of cortisol levels appears to be in higher animals similar to what it is in fish, does not mean that a more elaborate mechanism has not superseded a simple stress based physiological suppression of reproduction, even if indeed the system in cichlids is as simple as it appears. It may well be that with the evolution of social systems, heightened stress levels do not so simply coincide with low rank, so it would become necessary to have a mechanism of physiological reproductive suppression that was not based on cortisol; just as the mechanism that had been employed in insects was open to being superseded in the wake of the evolution of a physiology of stress utilising cortisol. Even so, a mechanism utilising cortisol is a usual working assumption, so I will look in more detail at this and at what the objections themselves reveal. Before this, however, I want to look briefly at the curious impact of sustained elevated cortisol levels in humans and what this reveals.

The epidemiology of the stress dimension of reproductive suppression

Sustained elevated cortisol in humans as well as directly causing lowered fertility (as would be the case in any animal) leads to 'insulin resistance' and then to the 'metabolic syndrome'⁴² which entails the range of serious disease to various organ systems in middle-age -- not to mention middle-aged spread -- that men are all too familiar with, and largely accounts for the substantial lower life expectancy of men compared to women. (Across the developed world the sex difference ranges from five to fifteen years.) The deleterious effects on health seem to be down to a chain of unintended consequence, as it were; but the impact on fertility being more direct (that is, other than the impact that poor health has on fertility indirectly) has more the appearance of being by evolved 'design'.

Though we cannot say that there is a causal connection other than as an 'unintended by-product', as it were; the cortisol that is associated with fertility suppression has an impact in humans that can be seen indirectly across the general population by epidemiological studies of general ill health. The 'Whitehall' study⁴³ of 18,000 men in the Civil Service that Sir Michael Marmot began in 1967, by the late 1970s revealed that men in the lowest employment grades were much more likely to die prematurely

than men in the higher grades. An even bigger and longer follow-up study, 'Whitehall II',⁴⁴ was then started in 1985 to find out what underlies this 'social gradient' (as it was dubbed) in death and disease, and to include women. A striking 'social gradient' of

a constellation of ill health that Marmot terms the 'status syndrome', he concluded must be related to the extent of an imbalance between the control that men felt over what they did in the job, what demands were stacked upon them, and what rewards accrued. But in not considering how the men first got into and then failed to escape these lowly jobs, Marmot appears to have mistaken the signature for the cause. Is it not something inherent not so much in the job that causes ill health but in the individual who holds it -- that is, his relative dominance, as arrived at through the course of his earlier life? The job would be merely symptomatic, as it were.

The big surprise for the researchers was that the 'social gradient' only applied to men. For women, 'social gradient' related not to their grade at work but to their situation at home. The 'social gradient' at work was a male phenomenon. It is not that no 'gradient' was found for women, but only a shallow one. On the face of it, this looks simply that the same mechanism applies to women as to men except that it is just much less pronounced, but there is more to it than this.

The model I have outlined entails a separation of DH: male and female DH is entirely separate. We also know that the criteria for mate choice is radically different according to sex, with only men competing for status. So regarding an hierarchical work environment where status is key, then we would expect a relationship between health and rank only to apply to men and not to women at all, except that the criteria for female ranking in their own DH may be correlated weakly with job status in some way through their male partners, given that female attractiveness assort with male status.

Where women fit in has been looked at by Amanda Sacker⁴⁵ et al:

"In women, social class based on individual employment relations and conditions showed only a weak gradient. Large differences in risk of mortality in women were found, however, when social position was measured according to the general social advantage in the household. ...The Office for National Statistics' new measure of socioeconomic position is useful for assessing health inequality in men, but in women a more important predictor of mortality is inequality in general social advantage of the household."

In reply to editorial comments about their paper, the authors spell out further:

"There is something about either the material or the cultural advantage or disadvantage of household circumstances that affects women's health more strongly than their own occupation. Also implicit is the assumption that there is a stronger correlation between the male (than the female) partner's occupationally defined social class and the general social and material advantage and lifestyle of the household. Given this hypothesis about the source of health inequalities in women, and the existence of an independent measure of household advantage, to rely on the husband's occupational class as a proxy for household advantage would not have been appropriate."

Previously, the best fit that could be obtained for women was by placing them according to the husbands' occupation,⁴⁶ but endorsing Sacker et al, Marmot⁴⁷ writes: "A measure that reflects general social standing best predicts the social

gradient in women". What is going on here is in accord with known sex differences⁴⁸ and consistent with a complete separation of male and female DH.

Questioning stress mediated reproductive suppression

Notwithstanding that sustained elevated cortisol levels certainly cause reproductive suppression in higher animals, to assert that it is stress that is central to mediation of an evolved reproductive suppression mechanism common to all higher animals, is really just informed speculation. There is little direct research on this question, and of research into a specific mechanism there is little to show that cortisol is pivotal (whereas there are studies showing the centrality of luteinizing hormone.⁴⁹) Nevertheless there is a consensus that for species where there is a clear dominance system, then the disproportionate stress experienced by sub-dominants is key; but the consensus has broken down regarding the special case of vertebrate 'co-operative breeder' species in the wake of a research programme by Scott Creel et al. As one of his team, Jennifer Sands, remarks⁵⁰: 'The fact that elevated glucocorticoids (cortisol, corticosterone) levels can compromise reproduction does not mean that this is the normal mechanism by which social subordinates are reproductively suppressed'. Quite so. Sands is referring to research into vertebrate 'co-operative breeders' such as wild dogs showing that cortisol levels are higher not in (what have been supposed to be) dominants as expected, but in (what have been supposed to be) subordinates. The conclusion is that in some species stress may be a cost of dominance that subordination avoids, and that therefore stress cannot mediate reproductive suppression at least in some species; but this would seem to be a claim too far for several reasons, quite apart from whether or not the dominants/sub-dominants were in fact so (whether there was in fact DH in the species studied).

The crucial difference between dominants and subordinates is not levels of circulating cortisol but sensitivity of receptors to cortisol, which is greatly reduced in dominants. Consequently cortisol levels may be similar or actually comparatively raised in dominants, even though the impact of stress is felt most by the sub-dominants.⁵¹ What is more, it is known that dominants have a more pronounced short-term cortisol profile than do sub-dominants; this being adaptive for dominants in that they are readied to quickly aggress if it is necessary. This elevated cortisol level, which can last for hours, is likely to be confused with basal levels. Creel et al are aware of these complications and have tried to take them into account, but it would be expected that with more complex social systems, the corresponding complexity of neuro-hormonal mechanism will tend to mask the role of any particular component. Albeit that cortisol seems to be key, certainly it is not the whole picture.⁵²

It remains the case (as Creel points out) that subordinates and not dominants are the more stressed in all species so far studied bar some (but not all) vertebrate 'co-operative breeders'; so stress still appears to be key as is usually supposed. The issue then is how to explain the exceptions rather than to challenge the rule. Even without the points I've just made above, this would seem not to be difficult. For a start, we know that insect 'co-operative breeders' have very short dominance hierarchies consisting of just a few of the individuals within the reproductive group, and that some other species such as crayfish have been found to have an elite of 'super-dominants' where contest is much more intense. At the apex of the crayfish male DH there is a contest for 'super-dominance', whereby there is a DH within a DH

with the top five ranks of a 'super-dominant' and four subordinates fighting it out.⁵³ Under the circumstances of either a short DH or 'super dominance', high ranking individuals will be more stressed than the majority of same-sex individuals because they are either not ranked at all or ranked in a more low key DH beneath the 'super dominants'.

'Co-operative breeders' are distinguished by the very high inter-relatedness of individuals in colonies. This makes possible in these species a total reproductive skew so that only the alpha female/ male ever mate. The extraordinarily high 'inclusive fitness' not only explains the alloparental care that is a principal feature of 'co-operative breeder' colonies, but also the very much reduced competitive behavior; which in turn accounts for the low cortisol levels in most individuals: the seeming anomaly in dominants having high cortisol compared to sub-dominants. More profoundly, it is highly questionable that non-breeding animals are sub-dominant at all. If social organisation is not a peer group of unrelated individuals but a family, then it might be expected that as in human families the parents sustain stress in heading the family, whereas offspring are relatively stress free. So it may be that here DH either is not an appropriate characterisation or a too simplified view of what is going on, and that if there is any reproductive suppression it is (as Creel suggests) of a different nature to that achieved through DH. (I will discuss this forthwith.) It is known that in many or most species of 'co-operative breeder' there is no physiological reproductive suppression, so on my model this would fit with there being no DH in man or most 'co-operative breeder' species.

A major confusion is that it is often assumed by researchers that physiological reproductive suppression is by the 'dominant control' model, and that this is by pheromones, whether or not research has shown for the species under study that this is the case. (Either a pheromone has been shown to be in operation, or it is assumed that there is such a mechanism though as yet undiscovered.) The assumption is that physiological reproductive suppression is *caused* by pheromones from a dominant animal, rather than that the pheromone acts merely as an 'honest signal' to inform the sub-dominant animal of its sub-dominance in order that it can suppress its own fertility. The problem then arises that in the absence of any discovered pheromonal basis of reproductive suppression, when nevertheless infertility is apparent, it may just be inferred that if the suppression continues when the dominant individual is not present, that instead of physiological reproductive suppression by 'dominant control' there must be an in-breeding avoidance mechanism.⁵⁴ Yet if, as I suggest is the norm, there is instead physiological reproductive suppression by an internal hormonal mechanism as the result of low rank in a DH; then similar observations may be made. Reproductive suppression would also continue in the absence of a dominant individual, mimicking an in-breeding avoidance mechanism.

It would appear that this is what is sometimes being correctly identified as not in-breeding avoidance but a general suppression of fertility -- that is, in respect of all opposite sex individuals, both related and unrelated -- attributed to 'self-restraint', but with the inference that this is somehow cognitive and behavioral rather than physiological and automatic. This has led to theories of 'decision-making' culminating in a 'commitment model of self-inhibition'⁵⁵ which is a game theoretic 'social contract' between the (supposed) 'sub-dominants' choosing either to commit to complete self-inhibition of reproduction or to do so partially, in exchange for a concession from the (supposed) 'dominant' not to impose other costs of sub-dominance, and involving assessing compliance and the possibility of 'cheating' within bounds. Inherent in this model is a misunderstanding of the nature and function of dominance: that

dominance and reproduction are unrelated.

The model also begs the question of specific mechanism, and its applicability to lower animals. Most tellingly it would appear to be a decidedly unparsimonious alternative to understanding 'co-operative breeding' systems instead of regarding them much more as all-of-a-piece with the systems utilised by the great bulk of species. A 'commitment' model would necessitate non-breeders or relatively suppressed breeders monitoring the situation to check if things have changed such that it would be more appropriate to commence breeding or to increase it. For those individuals 'allowed' to breed to a limited extent, there would be checking that indeed they were breeding only up to the allowed ceiling. It is not so much the feasibility of this that would be problematic as the costs involved; which would suggest an autonomous and automatic mechanism as being superior.

It would be instructive to look at some examples of species where reproductive suppression has been found. The most studied in this respect are the 'co-operative breeding' species where the usually 'winner takes all' reproduction is reproductive suppression at its clearest. The variety of arrangements in these species in which it manifests both clouds the issue and provides a series of in effect controlled experiments of how dominance and physiological reproductive suppression relate to each other in an ecological setting, and could prove a good if rough preliminary test of the hypothesis. Though the reproductive suppression is at the extreme of the continuum, these exceptions in this respect may turn out to be less exceptional than somehow illuminating a wider rule.

Unusual social systems help to reveal common reproductive suppression mechanism

The most well-known higher animal 'co-operative breeding' species is the wolf. It is clear that contrary to the usual view that wolf groups have an alpha male and alpha female, in fact dominance plays no role. The most telling research questioning the concept of dominance re a 'co-operative breeding' species is that by L David Mech.⁵⁶ His long-term studies of wolves in the wild are the most comprehensive and most up-close in the literature. Mech habituated animals to the presence of himself and his team from 1986 to 1998, and concluded as several other researchers had noted in the 1940s and 1970s, that the wolf pack is in fact a family. Almost all recent research on wolves has been of captive packs made up of adult animals from various sources, but Mech found that in the wild: '... young members constitute a temporary portion of most packs, and the only long-term members are the breeding pair ... unless a maturing pack member inherits a position that allows it to breed with a step-parent in its own pack, sooner or later it will disperse and attempt to breed elsewhere ... Because most wolves disperse before two years of age, and almost all before three years of age, there would be no source of sexual competition within most packs'. The notion of an alpha male and female here is, in Mech's own words, 'particularly misleading', given that 'dominance contests with other wolves are rare, if they exist at all'. Certainly there are no agonistic encounters.

Mech recorded what were apparently active and passive submission postures and gestures, but noted that: 'submission itself may be as important as dominance in terms of promoting friendly relations or reducing social distance'. He found 'active submission and food-begging indistinguishable', and indeed that it also acted as 'a

food-gathering motivator'; that all individuals tried to retain any food they possessed irrespective of which other wolf challenged it, the supposed 'alpha' included -- all wolves freely so challenging any other wolf. This would be unheard of in a DH. After large prey kills: 'pack members of all ranks (ages) gather around a carcass and feed simultaneously, with no rank privilege apparent'. Indeed, young pups are fed preferentially by both their parents and older siblings.

Dominance/ submission behavior in the wolf apparently has been reduced to signalling to aid affiliative and division-of-labour behavior. It would appear that not the behavior itself but the attendant signals have been co-opted for a purpose other than dominance/submission (just as dominance/submission behavior has been co-opted in many species for the purposes of signalling in sexual scenarios; and, conversely, just as in some species pseudo-copulatory behavior is employed to signal dominance/ submission). It is not that wolves don't retain a dominance/submission behavioral repertoire, because interestingly wolves *do* have the facility to form a DH in the artificial circumstance of captivity when several unrelated sexually mature individuals of one sex are forced to live together. In the natural state, however, an affiliative family social organisation with dispersal upon sexual maturity is evidently more appropriate and precludes or obviates the need for DH.

That there is no competition over reproduction in wild wolf packs means that there would be no purpose served by a DH, and consequently there is not differential stress that adversely affects non-breeders. This would explain in this species the seemingly anomalous findings about cortisol that Creel highlights. We also know (as Creel points out) that there is no physiological suppression of reproduction. It is not needed given that all animals other than the breeding pair are not sexually mature. Again this fits with there not being a DH, according to my model.

As with the wolf, the naked mole-rat⁵⁷ is a 'co-operative breeder' with sole breeding pair reproduction in a family group, but there is a crucial difference in that animals do not disperse but remain within the natal group upon attaining sexual maturity, and research shows that there is no in-breeding avoidance mechanism. (An in-breeding avoidance mechanism is common in 'co-operative breeders', achieved not through kin recognition per se but by a simple proxy mechanism of the shared smell that animals living in a close colony gain. This is not reproductive suppression, of course: it is a simple uncoupling of sex re a category only of opposite sex individuals -- those with whom the colony smell is shared). So there would be nothing to stop intra-sexual competition over sex. Consequently, the naked mole-rat *does* have recourse to DH and there *is* physiological reproductive suppression in both sexes.

So what happens when only one sex disperses? This is the case for the meerkat,⁵⁸ and also for the dwarf mongoose.⁵⁹ Meerkat males must disperse to become a sole breeder in a colony, and they stay within their natal colony to bide their time until they become fully mature, in the meantime possibly breeding with extra-colony females. We know that the males are not physiologically reproductively suppressed, and this would fit with them not requiring a DH. The females remain in the natal group -- and indeed, no female can join another group -- so there must be female intra-sexual competition, and we know that they *are* subject to physiological reproductive suppression. Presumably they do have to form a DH. A long-term detailed study by Cambridge University researchers, as very well documented in the 2005 BBC TV series, Meerkat Manor, would appear to confirm this. Admittedly, there are complications to this analysis in that reproductive suppression in female subordinates appears to be induced less by physiological means than it is behaviorally; and it is not clear that there is no in-breeding avoidance mechanism.

The complication of only partial dispersal is evident in the Damaraland mole-rat,⁶⁰ and it is sex differential: twice as many males disperse as do females. That this limited dispersal is not sufficient to preclude competition for breeding in males is shown by the presence of (what is suspected to be) male-only in-breeding avoidance. The combination for females of low dispersal and absence of in-breeding avoidance means that intra-sexual competition is a problem, and so it is that for females (but not males) there is physiological reproductive suppression. This would imply on my model that females (but not males) have a DH, though given the sort of misinterpretation seen in study of the wolf, there is insufficient detail in the published research to be clear if this is so. To cloud the picture further, there is an element of caste⁶¹ (a proportion of individuals become 'infrequent workers': they do not engage with the colony either as alloparental carers or in any way reproductively, and instead disperse). This echoes the evolutionary pattern in social insect 'co-operative breeders', which according to species may utilise either DH or caste to bring about reproductive suppression; the means of reproductive suppression via caste being distinguished by it being *irreversible* and from the outset of an individual's life, as opposed to the situation where individuals are totipotent and a DH is required as a prelude to any differential reproductive suppression. It is known that there is an evolutionary relationship between these two systems because they are modulated by the same hormonal system. Clearly, caste would obviate the need for DH in other than the reproductive caste itself.

In several species of 'co-operative breeder' there are further factors at play making interpretation difficult. For example, in pine voles and several other species, there is no oestrus until it is induced by the presence of an unfamiliar male. In general, it can never be certain that in studying species in the wild that all of the multiple factors at play in a particular breeding system have been identified. Nevertheless, albeit that research methodology and preconceptions have confused the issue of the presence or absence of DH in some cases, the data on species of 'co-operative breeder' appears to be consistent (at least not to be inconsistent) with the hypothesis that where there is potential conflict over reproduction in either sex, and where there are no other means to preclude it; then both a DH and physiological reproductive suppression are apparent in individuals of that sex. The aforementioned problem of inferring in-breeding avoidance when instead there may be the physiological suppression mechanism I propose, together with the confusion between family structure (where there is dispersal upon sexual maturity and therefore no sexual competition) and DH, means that interpretations of reproductive behavior systems in the discussion sections of these studies are liable to be confused or false.

There are invertebrate as well as vertebrate 'co-operative breeders'. So, for example, the queenless ant⁶² (above mentioned and already in part discussed) lives as a family with a sole breeder and, like the meerkat and mongoose, the males disperse whereas the females remain in the natal colony. The males play no part in the social organisation at all; it's an entirely female one. The only option for a queenless ant female to reproduce is to get to be the 'gamergate', as the sole breeder is known, which is the passport to mating with one of the free-living males from outside of the colony. So there has to be a female DH, but there is a special complication: queenless ant females are ultra co-operative because of the unusual reproduction method they employ (along with most ants, bees and wasps) of haplodiploidy, whereby females have closer relation to their sisters than to their own offspring (sharing not 50% but 75% of their genes). The colony is not only a collection of sisters and daughters, but also 'supersisters'; everyone is closely related to the 'gamergate'.

These inclusive fitness considerations make for not just stability but also unusual co-operation. It is in the general interest that no new 'gamergate' usurps the present one, because this would mean subsequent offspring being from a different male, which would be much less related to the body of workers than those currently being produced. This is why the 'gamergate' remains in place until either she dies or she becomes senescent and her rate of reproduction substantially falls. A would-be usurper in any other context is immobilized by workers, and results in the would-be usurper losing her rank and being unable to take part in any future contest. The upshot is that notwithstanding that all members of the colony are fertile, the DH is very short: just a handful of individuals out of the whole colony that have the size/strength to potentially accede to the sole breeder position. The great bulk of the colony is made up of workers with no status. The DH, alpha through delta or epsilon, is the result of contest to determine relative strength. It is not instrumental competition over food or any resource, but purely to determine rank. Once the alpha is established, then agonistic encounter ceases to be a feature and instead pheromonal communication takes over. The alpha has a distinct pheromonal signal that marks it out to other high rankers, and the alpha controls any attempt at usurpation by chemically marking the offender so that workers can identify it as requiring immobilization. Each of the handful of individual high rankers has a different pheromonal signal according to rank, and, therefore, fertility. There is no internal hormonal reproductive suppression through DH, but instead a mechanism that achieves the same thing by a DH facilitated chemical signalling to animals that police the DH externally (they are not in the DH themselves) because they have a direct interest in the current breeder continuing in that role. They act behaviorally to indirectly suppress reproduction in any individual other than the breeder. This might be envisaged as a precursor to a fully internalised mechanism along the lines of what I propose.

That the DH applies only to a handful of individuals is a notable feature of this social organisation. If this were also a facet of some mammalian 'co-operative breeders' then that would be another reason why cortisol levels would be higher in high rankers. If most individuals were not ranked at all, then they would not suffer the stress of being sub-dominant, whereas the stress of competition would be experienced by all of the few ranked individuals. Alternatively, perhaps there may be a DH on top of a DH: the 'super dominance' as seen in male crayfish? Research into short DHs in 'co-operative breeders' has shown that the length of these short DHs can be predicted by the degree of relatedness of colony members and the size of the colony.⁶³ It would be expected, therefore, that in species other than 'co-operative breeders', where individuals are not very closely related, that the DH would extend to include most or even all members of the reproductive group. Without very close relatedness, a 'winner takes all' reproductive system whereby there is a sole breeder would not be adaptive, and instead a graded reproductive suppression tied to rank indeed would be. It would be expected that such a graded reproductive suppression mechanism has evolved, as in my model.

The female-only social structure (a female but not a male DH) widespread in insects would seem to be a complication to my thesis that DH is required primarily as a male adaptation. Female-only social structures in such evolutionarily ancient species might suggest that DH more than just being co-opted for the female had evolved originally not as an adaptation for the male but instead for the female. However, haplodiploidy reproduction whereby society is all-female is a special case, and the prevalent view is that haplodiploidy is an evolutionary sideline that evolved from normal sexual reproduction, and is prevented from being evolved in mammals and probably in all vertebrates.⁶⁴ (Haplodiploidy -- and the related parahaplodiploidy -- is a powerful instance

of an arrangement that enhances the role of the male as genetic 'filter' for the whole lineage, as I discuss below.) DH that was an adaptation for the male can be co-opted for the female. In any case, as I have already pointed out, there are indeed phylogenetically more ancient species that have DH, and I explain below that DH would appear to have evolved quite primordially in the wake of the evolution of sex and the male. (Even if this was a precursor social system, it would be another helpful complication in providing an already extant mechanism ripe for exploitation by species where males became members of the social organisation; this being highly adaptive for the male especially, for reasons I have outlined. My thesis would be helped in that it reduces the selection pressure needed to evolve the neural apparatus necessary for more extensive DH and the refinement of individual recognition.) Where female DH does occur, often rank is determined mostly by the mother's rank: female rank is largely heritable. This makes sense when you consider that female 'mate value' is simply degree of fertility, and contest would serve little purpose. Yes, of course, attributes that contribute to male rank are heritable, but not as simply so; and in any case, the main value of DH is to sort out and amplify what differences there are between males for the purpose of eliminating/ retaining genetic material on the male (not the female) side of the lineage.

The research on different 'co-operative breeding' species shows that it is not a social organisation of family that precludes or obviates the need for DH, but the opportunity to reproduce outside of it. There is no point in having a DH to apportion differential fertility when fertility is not going to be a factor until individuals have escaped into another setting. It is by contrast important to have a DH when the family setting will remain the only milieu in which any individual can hope to secure reproductive opportunity. This contrast is consistent with my hypothesis regarding the function of DH, as is the interesting finding that this same contrast is evident within a species: the wolf normally in neither sex forms a DH, but will readily do so when artificial conditions force competition for reproductive opportunity that in the natural state is absent. There is even a case of a 'co-operative breeder' where familial organisation and DH occur entirely separately and simultaneously *within the same social group*: the alpine marmot. This species forms extended family groups but due to territory take-overs these groups usually contain unrelated individuals. The adults of both sexes attack only unrelated same-sex individuals, which unlike the individuals belonging to the extended family group were reproductively suppressed. In this way parallel social systems emerge whereby the individuals of one system are physiologically reproductively suppressed whereas individuals of the other system are not; notwithstanding that all individuals from both systems co-reside. Tellingly, this species was singled out by Creel as being unusual in 'co-operative breeders' in showing relatively elevated cortisol in sub-dominants. In a study by Hacklander et al ⁶⁵ the identification of sub-dominants, as opposed to extended family members, is accurate, and so they were able to tease out the parallel systems. That the possibility of the same kind of parallel social system occurring in other species does rather make interpretation of data from other species still more complex, and would further help to explain why a generic link between DH and physiological reproductive suppression has not been spotted. Another kind of parallel social system suggests itself and may be an additional confound to study: the possible existence of parallel DH/reproductive suppression and an in-breeding avoidance mechanism. Could a 'co-operative breeder' species have an in-breeding avoidance mechanism through colony smell for all natal same-sex individuals, and additionally and separately re non-natal group members, a DH and associated reproductive suppression?

Perhaps the most instructive 'co-operative breeder' species for my argument is the queenless ant, in that it reveals with some clarity DH formation as clearly separate from and a direct prelude to reproductive suppression. This is the very two-stage

linked mechanism that I propose, albeit very different in detail; separate but the one following the other. 'Co-operative breeders' are interesting in that they are collectively the extreme case of a 100% reproductive skew instead of a gradient of reproductive suppression: usually only one individual of a sex reproduces, and where there is reproductive suppression, all other individuals are completely suppressed. However, in some species there is more than one individual of a sex that simultaneously breed, and this may be despite the fact that one individual is the alpha, and other breeder(s) the beta, or the beta and the gamma. Here we have a simple case of a gradient of reproductive suppression so that there is some correspondence between rank and physiological fertility other than simply the all-or-none situation of the sole breeder and the colony of alloparental helpers. Consequently there is a grey area between species that are 'co-operative breeders' and species that are the more usual 'social but unrelated', as it were, where there is a gradient of physiological reproductive suppression. This indicates that reproductive suppression systems belong on a continuum with a degree of shared mechanism.

Albeit that (some) 'co-operative breeders' may in some details have a different mechanism, I contend that there is no fundamental difference as Creel would seem to suggest. 'Co-operative breeder' species are currently considered as a group to be a special case in having a set of mechanisms that mark them out as a distinct subgroup of animal phylogeny; whereas it would seem that they belong within an overarching parsimonious explanation of reproductive suppression.

How the evolution of sex and the male sheds light on the function of dominance hierarchy

I now want to turn to the subsidiary argument that sets the scene as to why at root DH evolved, and for the purpose of differential reproductive suppression. This concerns the role of DH in the function of the male mating type. The standard explanation of sex, that compared to asexual reproduction it increases genetic variation and consequently adaptability, on the face of it would seem to be very broadly right once there is taken into account the complexities in natural populations of finite size, spatial structure, and genetic drift; and that sex appears to be favored in some but not all conditions.⁶⁶ Furthermore, selection is multi-level, with what is of long-term advantage winning over what would seem to be greater short-term advantage by 'lineage selection'.⁶⁷ However, the broad explanation of increasing genetic variation and consequent adaptability is the *outcome* of lineages having recourse to sexual reproduction, rather than the explanation of why it is that a lineage should have recourse to it. The standard explanation masks the precise problems that sex solves, not least why there is the need for differentiated male and female mating types.

Sex solves two problems. The first and most crucial is the problem that besets any system of iterated replication: a steady build-up of replication errors. These would accumulate in a (asexual) lineage leading eventually to the progressively poorer functioning (if not their death) of all individuals in the lineage and the lineage's extinction. This is not so much of a problem in species with a relatively simple genome where reproduction is fairly cost free. We see this in the fact that many simpler species are obligate asexual reproducers. Here, whole lineages can simply die out leaving the fitter ones extant. Moving up the phylogeny, for species with a more complex genome, reproduction is costly and at a low rate, and losing a lineage

may mean the extinction of the species in a whole locale or habitat, and possibly the loss of the species itself: extinction. So it is that there are species that introduce periodic sexual reproduction after several generations of asexual reproduction. With further evolved genomic complexity there emerges obligate sexually reproducing species: asexual reproduction has been completely jettisoned.

However, lineage extinction is not avoided simply by recombination -- recombination alone being mistakenly regarded as the contribution of sex. Recombination, we now know, is present in mitosis as well as in meiosis, so that in diploid asexual populations deleterious genetic material is unmasked through recombination reducing complementation of alleles. Recombination also leads to the evolution of self-promoting genetic material and hence to intra-genomic conflict. It would seem that loss of complementation and the unmasking of recessive deleterious (especially self-promoting) genes is what sex -- that is, meiosis -- came into being initially as the mechanism to counter.⁶⁸ This might be called the short-term problem that sex solved. As Archetti points out:

"sexual reproduction is necessary only for the *spread* of the recombinogenic element to other individuals in the population, it is not necessary for its *origin*: what is required for its origin is only diploidy and the existence of the DNA repair machinery."

The more comprehensive recombination that meiosis produces mixes up replication errors, repeatedly diluting them amongst the mass of genetic material rendering them less synergetic (supposedly), and thereby slowing down the impact of the relentless build-up in the lineage of replication errors, but at the expense of tending actually to maximise their retention. Inasmuch as some instances of recombination will produce individuals who through their deleterious genetic make-up will be consigned to reproductive oblivion, then deleterious material will be lost from the lineage; *but* the overall genetic load in the lineage will tend to remain high -- higher than it would be in the absence of iterated recombination -- consequently depressing the fitness of the lineage overall. It is not unlikely that there would still come a point when the lineage would be destroyed. This problem is compounded by the coincidence, found in computer modelling,⁶⁹ that a system with built-in robustness to disruption (such as the genome necessarily has against both replication errors and the shuffling of genetic material in sexual recombination), engenders increased interactivity of components. In the jargon, 'negative epistasis' is increased. This will work antagonistically to sexual recombination in tending to nullify the effect of recombination to render deleterious material less synergetic. Deleterious material becomes *more* synergetic. In the end, then (modelling confirms), dilution doesn't work. Instead, what is required is the very opposite: the concentration of deleterious material so as to polarise adverse impact on a minority of individuals in the lineage to the extent that they fail to reproduce and take with them the unwanted genetic material upon their death.

This perhaps counter-intuitive insight is behind recent thinking about in-breeding.⁷⁰ Researchers had been puzzled that it was hard to find evidence of any negative impact of in-breeding. It was realised that in-breeding actually provides a benefit in increasing homozygosity, whereby harmful recessive genes are much more likely to be unmasked and thereby removed -- or 'purged', as is the refreshingly non-technical term for this. A problem would arise if some of those individuals 'purged' were female, because the female is the 'limiting factor' in reproduction. This gives a selective advantage to any system where 'purging' is not conducted on the female side of the lineage. The obvious solution, given that a recombination process is an iterated partitioning into two halves of a lineage, is to bring together deleterious

material to be quarantined as much as possible in the male half of the lineage, from where it can be discarded through the reproductive oblivion of a minority or even a majority of individuals without having any overall impact on the reproductive potential of the lineage. Indeed, the impact on the reproductive potential of the lineage would be progressively positive the more that males are lost from the base of the male dominance hierarchy upwards, because the more that male reproduction is confined to high 'mate value' individuals, the better is the quality of offspring, without compromising on their number.

This would appear to be why sex evolved to be not between identical hermaphrodites (obligately out-breeding), but between the two separate mating types of male and female. Sexual reproduction is thus not simply meiosis; and what distinguishes it beyond mere meiosis is the role of the male, as pointed out in a ground-breaking paper by Wirt Atmar,⁷¹ who argued that none of the various theories of why sex evolved explained why *the sexes* evolved. Atmar's argument pertains to the function of the male as it came to be; not to why disassortative mating types initially emerged. Just as with meiosis, initial origin is a different phenomena from that which is thought then to have extended and maintained it. Models show that anisogamy can emerge from initially undifferentiated adult individuals because there are different advantages for having small than for having large gametes.⁷² The smaller gametes produce more mutations per generation, thereby providing the foundation of anisogamy and sexual dimorphism in the function of the male as I outline below.

Atmar's explanation (as he originally outlined it) to be more precise is *part* of why sex and the male evolved. The process serves not only to highlight and eliminate deleterious genetic material, but complementarily it serves also to highlight and *retain* genetic material that by mutation and/or recombination *enhances* the genome. (Indeed, Atmar considers this a secondary function of sex and the male in a private e-mail correspondence loop to which I have been part.) And here the synergy found in computer modelling of systems robust to disruption works not antagonistically but itself synergetically with the thoroughgoing recombination in sex.

This is the second problem that sex solves: of how to better optimize to the changing environment and to out-compete rival lineages in the 'reverse entropy' of evolutionary advancement. The two problems that sex solves are of course essentially one in that the reduction of deleterious genetic material is a mirror image of increasing enhancing genetic material; and it can be seen why in crude terms it is said that sex is explained by increasing genetic variation. And there is a third related take on this: the 'red queen' notion of changing environment requiring the genome to keep pace. All three related categories of theories of the origin, or rather maintenance, of sex boil down to the genome being out of kilter with the environment in which the individuals for which it codes have to survive and reproduce; whether it is the genome that changes (though replication error or recombination) or the changes are in the environment itself.

The very important selective advantage of a process that capitalises on mutational and recombinational change is the basis of a theory or theories that had been ascendant that sex evolved so as to win an 'arms race' with parasites. Parasitisation was put forward as the likeliest candidate to explain the evolution of sex because this was an evolutionary 'arms race' that was thought to provide on its own sufficient selection pressure to account for the adaptation. It was the ultimate 'red queen' hypothesis. But if you combine the rather specific problem of how to out-compete parasites with the other selection pressure to optimise in the context of a changing environment, and place together with the still more important need to eliminate

deleterious genetic material; then there is in total more than ample selection pressure to account for the maintenance through evolution of sex and of the male. Theory had been too myopic. A divisiveness in search of mutually exclusive prediction is necessarily how scientific enquiry proceeds, but now it is apparent that all of the various theories that had been put forward to account for the evolution of sex are complementary; being subsumable under this overarching understanding.⁷³ Furthermore, there is apparent interplay between sex and genetic architecture such that sex and recombination have affected their own evolution.⁷⁴

The male acts as a 'filter'; metaphorically speaking, as a sieve with a mesh of an appropriate size to catch and so retain genetic material for the furtherance of evolutionary development, as well as to allow to fall through and so reject newly acquired and recurring defects.

The male fulfils his role in several ways. First (or should that be last?) there is more rapid and overwhelmingly greater overall gamete formation in the male than in the female. This produces many times as much replication error and mutation than in the female (from double to 100 times, depending on the species; about six times in humans). Many of these male gametes will be unviable from the outset and are thus eliminated from the lineage. Those male gametes that survive spermatogenesis and development in readiness for ejaculation, upon being part of the semen introduced into the vagina then have to find their way up the vagina, through the cervix and up the uterus and thence to the female gamete. This curious long journey of sperm through the extremely hostile environment of the female genital tract now makes sense. A vanishingly small fraction only of the tens or hundreds of millions of sperm ever get near the ovum. The most efficient will get to the ovum first but often even then not one will fertilise the female egg. On some occasions just one will manage to do so. The sperm will have been severely tested for their metabolic vigour and against other performance criteria. The sperm themselves require the basic genetic material of life for their own propulsion, to find their way to the ovum, and to penetrate and fertilize it; so those with any defects in the more essential parts of the genome don't make the journey. Of those that are in contention, there is selection according to degree of viability -- less in the sense of unviability as in any enhanced viability that the process of spermatogenesis may have revealed. So it is that there are 'positive' as well as the 'negative' aspects to what the process of sex and the male 'filter' performs at this stage. The problem is that most of the genome will not have been tested: the male in the adult stage is required for this.

Of the zygotes that successful sperm produce, half will make male individuals, and these themselves have the function also to act as a 'filter'. First, males are vehicles to expose defect (or enhancement) by being more genetically heterogeneous than are females. Much key genetic material (and key variant genetic material) other than the basic material that has already been tested in the male gamete ahead of formation of the zygote, is contained within the sex chromosomes; and whereas females are XX, males are XY. This un.masks recessive genes in the male that are hidden in the female. For the genes on the autosomes, however, this is not the case; even though most are not dichotomously dominant or recessive as is supposed, but somewhere in between, so that they will express to some degree whenever there is heterozygosity. This will result in the creation of some further reproductively compromised or unviable males (and conversely, some reproductively enhanced and 'super viable' males); but given that the heterozygosity of the autosomes will be to the same degree in females as in males, then, sex chromosomes aside, there will be as many potentially reproductively compromised females as males, which is fitness reducing in that it comes up against the problem of the female being the 'limiting

factor' in reproduction. This is where DH would appear to be adaptive.

To differentially expose this material in males necessitates the behavioral adaptation of male intra-sexual competition. If male adults are tested under conditions of metabolic stress, just as were sperm; then genetically defective (and enhanced) individuals can be identified. Behavioral adaptations of male intra-sexual competition can be not just in the mating process but in anticipation of this throughout the life cycle. Most primitively, male intra-sexual competition is confined just to the courtship antecedent to mating, as in the bee (albeit that this is a case of an adult which is not a zygote -- the male bee is haploid, and as such is homologous with sperm).⁷⁵ Bee courtship consists simply of the queen leading her suitors on a chase, with her criteria for mating simply to yield to the male who first catches her. In almost all other species, the adults are true fused gametes (zygotes) but the same testing under metabolic stress is evident.

Such crude testing of males in the mating process has broadened through evolutionary time to encompass behavior much wider than the mating process proper. Social organisation of males has become a precursor to mating in sorting males by degree of viability, in both the 'positive' and 'negative' senses. Most obviously this manifests as DH (and/or territoriality: DH and territoriality being very closely related). Here again, competition at root involves metabolic stress. The less viable males usually are not seriously unviable, but they are marked out. Of course, simply marking out is only half the process: there must be a subsequent mechanism that results in corresponding differential reproductive outcome. Indeed, this should be considered as part-and-parcel of the DH mechanism. DH can serve to exaggerate differences between males that may be nearly negligible in absolute fitness terms: it has been conjectured⁷⁶ that a DH will emerge even if individual participants have no differences in pre-existing attributes that may predispose to (or hinder) gaining dominance. That DH often appears to stretch out differences both negative and positive to highlight what may from usual perspectives seem small and insignificant, is to the good because the finer are the distinctions then the greater is the proportion of deleterious material that can be eliminated from the lineage if DH is used as the basis of reproductive enhancement/ suppression. This serves to maximise the overall gene replication of the reproductive group. That is, there is maximisation of replication of genetic material/ combination that is enhancing, and corresponding minimisation of replication of deleterious genetic material/ combination through 'purging'.

The evolution of differentiated mating type, with the relative disposability of the male, set in motion the progressive polarisation of the sexes whereby the major investment in offspring was made by the female rather than by the male. This is reflected in gamete production: males can make billions of tiny spermatozoa for every large egg made by a female, and from even before fertilisation the rest of the development and early life of offspring takes place within or very close without the female's body, as gestation gives way to the female providing nutrition from her own body for a considerable length of time even after the offspring is born. The law of comparative advantage has driven the sexes apart so that for females there is concentration of effort on post-fertilization, rendering mating irrelevant for most of their reproductively active lives; whereas for males usually most or almost all effort is concentrated pre-fertilization. The consequence is an enormous potential reproductive skew within the male mating type, and by contrast little skew amongst females. This further drives male intra-sexual competition introducing the problem of the element of mutually unproductive conflict which is where I came in. DH becomes adaptive in respect of what it has itself produced: it is a self-reinforcing system of social organisation.

Dominance hierarchy is explained in terms of the evolution of the architecture of gene replication itself, as well as in terms of maximising gene replication of the reproductive group.

A prediction of the subsidiary hypothesis re the evolution of the male mating type is that in all species the combined impact of natural and sexual selection will be significantly greater on the male half of the lineage than on the female half. It is becoming clear that this would appear to be true even in seeming anomalous cases, notably some birds species, where there is an apparent 'sex reversal' in males assuming the role of parents, and females being more intra-sexually competitive and displaying to the opposite sex. The reason for this supposed 'sex reversal' is the very high attrition of eggs in some ground-laying birds adapted to hostile environments. With the female gamete being individually far less valuable than is usual in biology, the female has to produce many more and of a greater variety to ensure a handful of offspring. This obliges males to take on the parental role, and to do this solo. Males are selected not just for vigour but also for their willingness and ability to solo parent. This is a great extension of sexual selection, and the reason it has been achieved in birds is that it is facilitated by the sex chromosome system of birds, that is not the usual XX/XY system but a non-homologous ZZ/ZW system, where the male rather than the female is homozygous. It is this sex chromosome homozygosity that allows males to better hold on to -- not to lose -- genetic material that predisposes to co-evolved sexually selected attributes.⁷⁷ This is just as well, because in the ZZ/ZW system males do not have the sex chromosome heterozygosity that better exposes genetic material to selection as in the XX/XY system. Overall, it appears that males in these unusual species are as in other species more strongly subject to selection than are females, and the male as ever continues to function as the 'filter' for the lineage as a whole.

The understanding of sex I have outlined here is interestingly consonant with the recent findings about mitochondria.⁷⁸ Mitochondria are the organelles within cell cytoplasm that provide the most vital function for all animal life of respiration, and unlike all other organelles they are controlled in part by DNA contained within the organelle itself, as well as by DNA in the cell nucleus. In the rare species that are isogamous, mitochondria from both parents are present in the zygote and this results in conflict between them until at some point in embryological development all of the organelles from one parent have been eliminated from all of the cells, leaving those of the other victorious. This has been precluded in almost all species by virtue of the fact that they are *anisogamous*: by ensuring that the mitochondria of only one parent get into the zygote. And it is always the case that the parent who bequeaths all (or almost all) the mitochondria is the female. Mitochondria are always passed down the female half of the lineage.

It seems that mitochondria are partitioned away from the 'filtration' system of the male side of the lineage. Is this because they are such elemental constituents of the organism that it is either too risky and/or pointless to subject their genetic coding to likely alteration and subsequent culling through the male 'filtration' system, and that instead they are passed from generation to generation intact? It appears that mitochondrial DNA experiences lots of change even without sexual recombination, because it mutates at 20 times the rate of nuclear DNA. In the absence of sexually mediated nuclear DNA repair mechanisms, mitochondrial DNA consists of multiple copies, so that even if there is repeated damage to a section of DNA and each subsequent replacement, there is usually yet another in reserve. This is an expensive but more foolproof insurance policy than that which nuclear DNA has through sex.

But it is not that mitochondria do not undergo selection. On the contrary, they undergo very heavy selection. Unlike the attributes of males (as adult or as sperm), the selection here of a female attribute occurs hidden away *within* the individual, in the embryonic stage of development. A fertilised egg has about 100,000 mitochondria, and these apportion between dividing cells so that soon there are only about 200 per cell left. All those mitochondria that function relatively poorly are effectively discarded through apoptosis (programmed cell death). Only if the remaining mitochondria are of high quality is there a live birth. This weeding out stage is the lesser one, however: most mitochondria are discarded in the female adult's oocytes as these develop.

Out of the millions of oocytes in the embryo, only up to 200 are ever ovulated during a woman's lifetime. It is thought that there is a particular problem stemming from the dual control of mitochondria by DNA in the mitochondria themselves and in the cell nucleus, and that there is a problem in getting these to neatly dovetail for optimal functioning. The oocytes are the testing ground for achieving this close match. This would explain the need for a single genetic set of mitochondria: if the set in the oocyte have developed the necessary close match with relevant nuclear DNA, then the last thing needed is an injection of a whole new set of mitochondria from the male gamete. Presumably, this model also implies that there is gene imprinting of the relevant nuclear DNA, so that only the relevant genes from the female parent are activated.

This solution of the problem of replication error accumulation in mitochondria has been put forward as the origin of sex, but whether or not there is any truth in this, certainly it points up how inordinately expensive a mechanism this extreme redundancy would be to eliminate accumulation of replication error in a whole complex genome. This 'quarantining' in the female is complementary to the male 'filtration' system, and provides 'circumstantial evidence', as it were, for the function of the male.

No resource (unless you so consider sex) could have eclipsed sex to explain DH evolution

Finally, I will play devil's advocate in returning to the consensus model of DH as a means of reducing mutually unproductive conflict over resources, to see if, after all, this may be likely to be at the root of why dominance and DH evolved; putting to one side for now that DH would seem to have arisen as a consequence of the evolution of the male mating type. For the sake of argument I will treat sex not as if it were a goal (the proximate goal for the ultimate imperative of reproduction) but as if it were a resource like any other, so as to compare it with (other) resources to see if there is anything other than sex that is likely to be so intensely fought over that a system to differentially apportion it could be a serious candidate for the reason why DH evolved.

What is distinct about sex is not only that males are very strongly and perpetually driven to have sex, but that it is invariably scarce. Sex is scarce in all circumstances. It is not just the small number (if any) of mating opportunities that is the problem, but also the highly variable quality of sexual partners. Available sexual partners are scarce, period; but they also become progressively scarcer the higher their quality. These dimensions of scarcity always pertain, and when environmental conditions

change so that (other) resources also become scarce, then the stakes re sex become yet higher still. Additional constraints serve to skew reproduction further, with only the very fittest individuals likely to have any chance of breeding successfully. Indeed, the possibility suggests itself that the proposed self-calibration of fertility is differentially contingent on environmental conditions, so that reproduction is more strongly skewed when conditions are adverse. This may explain the precipitous population collapse in mammal species known as 'plague mode', but this is an under-studied and contentious topic that I do not wish to explore here.

The only obvious possible rival resource to sex as being such a bone of contention that it might have driven the evolution of dominance, is food; but food differs from sex in both the motivation to secure it and its scarcity. Unlike sex, generally for most species food is not in constant short supply, it is spread liberally throughout the environment, and controlling access to it would be difficult if not impossible. In marked contrast to sex, food suffers from very rapid diminishing returns. Males have almost unlimited energy when it comes to sex with different partners, but no amount or variety of food stops animals from being very quickly satiated. So it seems that sex, in the degree of both desire for it and its restricted availability, is unique.

More fundamentally, the contrast in scarcity between sex and (other) resources is rooted in the imperative of maximisation (of gene replication) that is peculiar to sex. There is no corresponding maximisation imperative to the consumption of food, which is geared to the body's homeostasis, and is therefore self-limiting. Sex for males effectively has no upper limit, with even the physiological capacity being considerably elastic according to the extent of variety in available sexual partners (though albeit that semen is produced continuously, satiation with sex may set in, with the body perhaps requiring some rest so as to replenish stores of semen).

The impact of the unique scarcity of sex is itself unique: it directly limits gene survival and reproduction. With sex, if a male is lucky to be in a near winner-takes-all situation then he can bring about large genetic multiplication by fathering a good proportion of the offspring of the entire reproductive group. At the other end of the scale, the intense competition between males prevents many males from mating at all. By contrast, with respect to food, with less fierce competition a 'scramble' element creeps in: a male animal can much more easily grab some food on the sly than he can surreptitiously usurp another animal's mating opportunity. Yes, there might well be times of extreme environmental stress as regards food supplies, and such a time might well be a survival critical moment; but genetic annihilation through lack of access to sex is nearly always the bigger problem. There is no corresponding genetic proliferation through access to food as that afforded by access to sex.

This strongly suggests that no mere resource is likely to be the basis of the evolution of DH. It does not mean that differentially acquiring food and other resources does not become tied up with DH. High rankers often have privileged control over resources. But it's an extension, if you will, of the function of DH, not its root. That this mere extension could have usurped the original function seems unlikely when, quite apart from the perennial salience of the selection pressures that brought DH into being, you consider that the way that social life of higher animals has evolved around DH further entrenches the centrality of sex. With greater co-operation, male policing or 'cheater detection' that was introduced to tackle the tactical 'free rider' problem becomes more efficient. Together with other mechanisms such as sperm competition and preferential access for dominants to female in estrus, this makes it still harder for an animal to subvert the DH to attain sex by 'scramble', thus making it even more imperative for any and every individual to be a member of the DH as a co-

operative venture re sex. Not only in comparison can an individual more easily avoid the indirect control over food by the DH and so obtain food by 'scramble', but the need to resort to such a tactic is lessened due to competition over food diminishing as sharing emerges evolutionarily as instrumental to social bonding.⁷⁹ It would seem that as evolution progresses up the phylogenetic ladder, selection pressures would serve not to undermine but to further reinforce dominance as an instrument of sex rather than for it to be co-opted in the service of other ends. It would be expected that DH would not be co-opted to serve another imperative.

There is evident a cultural problem in finding the correct perspective in this discussion given that misinterpretation re sex/ resources is all too common in biology, and mostly this is just misplaced emphasis; highly effective in clouding the issue it is nevertheless. It is often assumed in behavioral/ ecological study that competition over resources is primary, even when what is being studied is competition to reproduce. Take a 1995 study⁸⁰ on reproductive suppression in badgers. The authors mention that 'females competed for breeding status, but that there was little competition among females thereafter', yet concluded that 'reproductive suppression appears to be a response to female/female competition for resources, rather than a need for co-operative care of the young'. They were focused on aspects of the ecology, to choose between alternatives of what the degree and/or skew of reproduction was contingent upon. But individuals do not compete over food in order to decide who reproduces. Instead, it is decided which individual(s) is to reproduce and she/ they then is/ are given or allowed access to the wherewithal in terms of food to do this successfully. Likewise, generally in 'co-operative breeders', the background to competition to reproduce and consequent reproductive suppression is the need for alloparental care; but it is not competition over alloparental care that produces reproductive suppression. Instead, the females compete for the privilege of being the breeder, and when that is decided then all other individuals act as helpers. So the reproductive suppression is essentially a result of competition to reproduce, and any ecological consideration is merely the background to this. Yet the authors confirm that they don't see it his way:

'Only females in relatively good condition bred successfully following a very dry summer, when food availability was low. However, when food availability was high, following a wet summer, females were in better condition on average and breeding success appeared to be related to social status. We suggest that this reflected a difference in the structure of competition between the two years.'

Yet the 'structure of competition', as they put it, is always the same process and for the same goal of reproduction, with only contingency that may change. This mistaking what is merely contingent for what is mainly at issue, is quite usual, and is not an insignificant part of why thinking about sex/ resources with respect to dominance and DH is so muddled.

Re-drawing the false picture of dominance

Underlying why, regarding dominance and dominance hierarchy, the wood is not seen for the trees; what decisively biases in favor of the false consensus model of dominance is the unusual contemporary cultural setting of discussion. This is the consensus within the intelligentsia that in coming to terms with the failure of the political prescription of what can perhaps best be described as neo-(pseudo-) Marxism to galvanize ordinary people, requires the invention of unlikely insidious inter-personal 'power' relations. Most notably is that supposed between men and

women, especially in the context of the family (which has come to be viewed as the root locus of the 'power' manifested in 'capitalism'). This has led to misidentifying the major social sub-group of disadvantage; viz, women generically. It's the view within all facets of the establishment that has taken hold without ever understanding, defining or even describing what this might be -- let alone how it could square with evolutionary theory -- not least through its congruence with the social psychology of 'policing' the male hierarchy, which is *the* most deep-seated prejudice. Anthropomorphized on to the animal kingdom more generally, the notions about dominance and DH that this fostered became the lens through which human social behavior has been re-examined. The bogus insight of a profound 'power' asymmetry between the sexes has far-reaching ramifications in falsely framing enquiry into social matters generally.

Dominance and DH have been poorly understood, and in general little attempt has been made to study in humans what we know is social psychology common to higher animals generally -- and pretty well the entire animal kingdom. By a truly un-blinkered examination of DH we can start to perform the invaluable service of rectifying the wider misunderstanding of social structure that is behind this impasse. With the consequent genuine furtherance of social justice, instead of actually promoting social *injustice*, the benign political ramifications of a proper understanding of dominance cannot be overstated.

Notes / References

(I've restricted references to those supporting a point that is or may not be obvious or is contentious, or is though likely familiar, particularly important. Rather than as is customary to exhaustively reference every point no matter how subsidiary and/ or minor, this has the advantage of drawing attention to key, non-obvious or contentious aspects that otherwise would be lost in a forest of distracting superscript. Re the social/ reproductive systems of individual animal species, I have tended to include only one or possibly two examples of papers, given that several similar papers dealing with closely related research are readily searched for and available on-line.)

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term provided lineages that give rise to cheats at a low frequency are more successful over the long term than are lineages that give rise to cheats at a high frequency." (p241).

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