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DOMINANCE HIERARCHY IS MALE-SPECIFIC:

IT IS NOT BI-(INTER-)SEXUAL OR FEMALE.

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ABSTRACT

Dominance hierarchy (DH) is never bi-(inter-)sexual. Rare ostensible female dominance (over males) is not even amenable to modelling, and actually is male non-engagement in dominance terms (deference, not submission). Any female hierarchy is not DH, as it is not contest-based, but from either mutually signalled differential fecundity or maternal rank inheritance. Otherwise, apparent female hierarchy is either non-dominance-based first-among-equals -- winner-takes-all -- sociality of a female sole reproducer, or a loose artefact of ad hoc resource competition. DH entails neuro-hormonally processing winner/loser effects, for which there is evidence only in males, and requires the Y chromosome's SRY gene. Male-specificity is anticipated from the male root function of genetic filtration / mutational cleansing, necessitating male ranking in terms of genomic integrity.

Keywords: dominance hierarchy, male-specific, contest-based, male deference, winner effect

DOMINANCE HIERARCHY IS MISCONCEIVED THROUGH ITS WORKING DEFINITION

A full century on (1922-2022) from the inception of the concept of dominance hierarchy (DH), remarkably it is still beset with serious misconceptions, none of which even were broached when marking the centenary in the special themed issue on DH of *Philosophical Transactions of the Royal Society* (compiled and edited by Strauss, Curley, Shizuka & Hobson, 2022).

Generally understood as a significantly stable, linear and transitive rank ordering of the (same-sex, usually male) individuals of a group, created by a partial permutation of mutual contests, DH has the putative function of differentially allocating resources generically (and, in a rationalised and ritualised way, to reduce agonistic interaction). This longstanding operational (working) definition of DH is undermined empirically when attempts are made to determine a DH within any group of conspecific individuals. This suggests the nature of DH as usually assumed is merely a derived or subsidiary function hiding a narrower, core one; and/or unrelated phenomena are being included within an umbrella too loosely labelled DH. Funkhouser et al. (2018) complain that “dominance ranks depend on the behavioral context, and many studies have derived different rank orders for the same group across different measured behaviors (Norscia & Palagi, 2015; Vervaecke, De Vries & Van Elsacker, 2000; Bayly, Evans & Taylor, 2006; Paoli, Palagi & Tarli, 2006)”. *Context-dependent* hierarchy is a well-recognised phenomenon and thus termed (e.g Nagy et al., 2013; Hewitt, Macdonald & Dugdale, 2009). Finding similarly that DH is “situation- or resource-specific”, Lanctot & Best (2000) point out that “… dominance measurements that were conducted in similar environmental contexts, regardless of the response variable recorded, ranked animals similarly”. The problem, then, is not modes of measurement, but of the unacknowledged differences in what is being measured, with competition scenarios mistakenly regarded as being generic.

This pervading issue with DH has so long been recognised that there is a now thirty-year-old review of pertinent studies by Fedigan (1992), who neatly summed up the problem of taking as generic observation of conflict over a particular type of resource (the most obvious one, of food):

> *In fact, it has been found that food tests do not generalize to other conflict situations in any consistent way. Not only does the test-situation only exist in the artificial laboratory-test*

> *setting, it has been found that priority to food does not necessarily correlate with priority to other incentives, and that dominance determined through dyadic tests does not generalize to dominance relationships for the same individuals within the group as a whole. … Rather than peeling away the layers of the behavioral onion, to arrive at the core of an underlying 'real' dominance rank or dominance relationship, it can be argued that the experimenter has in fact created the dominance relationship.*

DH IS ABOUT REPRODUCTION, NOT RESOURCES, SO IT CANNOT BE BI-(INTER-)SEXUAL

Taking all observations of competitive (or seemingly competitive) behaviour as ubiquitously pertaining to the formation or maintenance of DH is likely to encompass far more than the phenomenon at issue. It's a superficial, top-down view, when examination bottom-up from biology is required to ensure a clear, deeper understanding; if not, indeed, to uncover the actual function that otherwise may have been largely or wholly hidden. Given that reproduction is central to biology, its differential allocation a priori is the chief candidate for the function of DH, rather than reproduction somehow being considered just one type of resource in a range of them, with all being allocated differentially by DH. Reproduction is, after all, the supreme goal, not a resource. Resources are means to ends, and all ultimately are instrumental to reproduction. This basis of DH was put forward by the present author in 2009 as a formal hypothesis, including that differential reproductive self-suppression mechanism appears to be integral to DH, which last, if accurate, would strongly support the core hypothesis. [Note the present updated review of DH is to better specify its nature (as male-only), not to revisit integral reproductive self-suppression (which would be for another paper).]

The function of DH pertaining to reproduction rather than resources entails DH being same-sex, given this is necessarily the nature of competition over reproduction, with individuals attempting to better assert or display their mate value relative exclusively to same-sex others, so as to be preferentially chosen as a sexual partner by those of the opposite sex deemed to possess sufficient mate value. Given that the female is the limiting factor in reproduction, it would be expected that competition over reproduction would be very different according to sex. Unsurprisingly, to cite the title of a 2015(a) review by the present author, *competitiveness is profoundly sex-differential, consistent with being biologically based and within-, not between-sex*. No sense can be made of inter-sexual competition, including that which supposedly is indirect. If a strategy employed by one sex interferes with that of the other (sexual conflict), this always resolves to *intra*-sexual competition. [This is revealed in considering even an extreme form in male-perpetrated infanticide (to render the female sexually receptive); among lions, for example. The mother as well as the male achieve fitness gains in terms of offspring quality (essential given an extremely high offspring mortality rate; more important than number) relative to same-sex rivals.] The reality of DH as being same-sex (and usually if not overwhelmingly specifically male) is attested by this being so well and long recognised as hardly to require comment or even acknowledgement, so although it is explicitly stated in the literature, such is uncommon.

That DH is a same-sex phenomenon is confirmed by the discovery of a mechanism whereby sexual behaviour is default, to be overridden, in males, by behaviour relating to DH only if encountered other individuals are not of the same sex. The research of Stowers et al. (2002), echoed by Leypold et al. (2002) and Kimchi, Xu & Dulac (2007), shows that in a mammal model there is a profound (so almost certainly evolutionarily highly conserved) neural algorithm whereby sexing precedes any consideration of how to engage an encountered conspecific other. In male individuals there is then applied a decision rule whereby if the other individual is female, courtship behaviour is employed. Should the other individual instead be male, engagement is in DH (dominance-submission) terms. This root decision-making architecture precludes any possibility of bi-(inter-)sexual DH. Elaborating the mechanism of this mating/aggression switch, very recently there has been the outlining of what would appear to be both its basis neurally (Yamaguchi et al., 2020) and in terms of the pertinent hormonal receptors (Olivier & Olivier, 2022).

By this analysis, DH can be properly understood as a ramification of sex and the sexes, stemming from what has been dubbed the *genetic filter* (Atmar, 1991) or *mutational cleanser* (West-Eberhard, 2005) root function of the male, in turn from the function of sex and the sexes to maintain genomic integrity (Moxon, 2019, after Gorelick & Heng, 2011). [Sex and the sexes do not function to create variation as assumed. That notion arose from a vast over-estimation of the variation produced by sexual reproduction, in a false analysis of meiosis by Weismann back in 1891 (Gorelick & Heng, 2011; Gorelick & Villablanca, 2018). An historical mistake has been missed and forgotten, not least through its seeming utility in providing a major source of variation to drive evolution, thereby underpinning the theory. Entrenchment ensued with the great volume of research on the major question as to what can be the utility of sex given its twofold extra cost in comparison to the asexual mode. The paradigm persists despite (the above authors review) overwhelming evidence from many disciplines and fields that it is asexual reproduction that creates the greater variation.]

This male core function entails male same-sex assortment according to relative absence of deleterious genetic material (rather than relative presence of *good genes*, which is the obverse, lesser consideration; a corollary and less accurate criterion -- a proxy), to allocate differential sexual access and facilitate corresponding female mate choice. Male same-sex DH is necessary to facilitate this.

Note that with its concerning reproduction and not resources, DH is not only same-sex but likely also male-specific, in that males compete primarily for reproduction, whereas females compete primarily for resources. See Benenson & Abadzi (2020), specifically in regard to the human case. Williamson et al. (2018) point out that in contrast to females:

> *"males typically compete first for mates and only compete for resources insomuch as they provide further access to mates. Recent work in house mice suggests that this pattern exists in mice as well, with females not engaging in any more agonistic behaviors when given the opportunity to compete for males (Weidt et al., 2018) (p122-123). Females have distinct evolutionary mechanisms from those of males that drive intra-female conflict, as they compete primarily for resources to increase chances of survival for themselves and their offspring, where males compete primarily for mates (Stockley & Bro-Jørgensen, 2011)" (p332-333).*

MALE HIERARCHY: THE NEED TO CONTEST, NOT TO REDUCE IT

It becomes apparent that in an important sense a superficial view of DH is so badly mistaken as to be an inversion of a proper understanding of the phenomenon, in that rather than it being damped down, conflict instead needs actually to be generated in order that relative mate value -- male relative mate value, that is -- can be tested and a rank order established in these terms. This is evident in a profound sex dichotomy in stress response, as reviewed in 2015(b) by the present author: *Stress mechanism is sex-specific: female amelioration or escape* *from stress to avoid compromising reproduction contrasts with male utilisation or in effect manufacture of stress to fulfil male genetic filter function*. Once established, a hierarchy itself further drives conflict between individuals of near-adjacent ranking, and does not reduce conflict between individuals ranked far apart. The latter have little or no reason to engage in contest, given the chances of a rank reversal are so very low. The disparities underpinning the rank differential would be so apparent that thus cementing them in DH ranking hardly would be a requirement to preclude the low-ranked individual from mounting a challenge. This is not so in the case of more nearly adjacent rankings, however; the very opposite occurs. Here it is the rank ordering itself that might prompt renewed contest, with a rank being such a reliable overall summation of an individual’s strengths. It is by virtue of the closeness in ranking that a lower ranked individual might well consider challenging another individual of higher albeit not too dissimilar rank, to try to switch their respective rank order, given the potential gain outweighs any costs of losing, making it worth the risk. Note, given transitivity, that this one contest may do for the other potential contests in a permutation of those dyads within the compass of the rank differential between the two individuals. By contrast with the significant potential gain, there would be no direct cost of losing in terms of ranking, albeit its subordinate aspect is underlined in a loser effect (see below), corresponding to the winner effect (again, see below) that would be yet another pay-off if the contest were successful.

A usual assumption, then, that DH functions to ameliorate agonistic interaction, does not make sense, so appears to be false. With DH in place, however, it is then available for co-option secondarily to differentially allocate resources of whatever type. As resources can be instrumental to reproduction, this would have utility in reproductive terms as a derived, subsidiary function, and here there would be a service of rendering unnecessary any fighting that otherwise may occur. However, resource categories differ in how relevant they may be to reproduction, so it would be anticipated that there may be contest entirely outside of DH, and/or the strength or reliability of any employment of DH might vary correspondingly. Thereby are accounted the problems in determining any consistent rank order and linearity outlined herein at the outset: of their varying according to context.

FEMALE HIERARCHY IS NOT CONTEST-BASED

Given that the *genetic filter* function is purely male -- in effect quarantined on the male side of the lineage away from the female (necessarily so, owing to the female being the limiting factor in reproduction, through gestation, lactation, etc; making it important to avoid any further hindrance) -- then there is no basis here for female same-sex DH. Neither would it have any basis in corresponding competition over female mate value, as this is by the narrower criteria of fecundity, which is not indicated by fighting ability or any general measure of quality. Instead, a combination of signs of developmental stability encapsulated in bodily symmetry and of physiological fertility in youthfulness (what in human terms we would call *beauty*) would sufficiently indicate fecundity; with this being immediately all too apparent in physical appearance. Any facet of fecundity that is not visible could be mutually signalled. No behavioural, attitudinal or ability testing is required. Consequently, there would be no utility in a contest-based female hierarchy in respect of reproduction.

Neither regarding resource allocation: with the female necessarily having evolved to be risk-averse, thereby to avoid any compromise of fecundity, females hardly would be adapted to engage in agonistic contest if its purpose is merely its own subsequent reduction. Not only may injury risk not be sufficiently reduced with ritualisation of combat, but initially determining relative rank would entail a higher level of agonism necessary to reveal salient individual differences in fighting ability, requiring a great deal of physiological effort, not unlikely to significantly threaten fecundity. Even if there were a benefit to the female of ameliorating agonistic contest, the determination of rank itself would risk driving an escalation of agonistic interaction to a level well above that from which the female subsequently would be spared by the adaptation.

The only contest-based agonism for which it would be worth females taking the risk of significant injury is the winner-takes-all scenario of determining sole breeder status. But rather than a hierarchy, this would be a sociality of what could be dubbed *first-among-equals* (winner-takes-all): one apex individual with everyone else equally non-eminent also-rans. A DH would be an alpha plus a beta, a gamma, and a delta, etc. -- a multi-ranked order. Albeit a DH may not be perfectly linear, in featuring shared ranks, especially further down the hierarchy (it may vary in steepness along an egalitarian-despotic dimension), this is entirely different to no hierarchy at all and a single apex individual, which indicates a very different mode of formation. Either way, then, in the female case, proper agonistic contest and DH seem not to go together. Any apparent female DH is likely to be either contest-less hierarchy or ad hoc low-level competition.

A contest-less ordering of reproductive privilege in terms of relative fecundity, inasmuch as it isn't self-evident, could be achieved simply through mutual signalling. Alternatively, it could be the outcome of ad hoc competition over resources, where females avoid the risk of compromising their fecundity by contesting other than agonistically, or with no more than mild agonism. Yet this would provide no utility in outcomes of contests being registered in a way that impacts on future encounters. No value would be conferred by DH to females, unlike for males. Theoretically, there appears to be no conceivable utility to females of the contest-based determination of consistent hierarchy that would be adaptive for males.

Just such a sex dichotomy in reality for humans is recognised by Benenson & Abadzi (2020) in the title of their paper, *Contest versus scramble competition: sex differences in the quest for status*. Zilkha et al. (2023) outline something similar: they find in mice "sex-specific behavioral strategies to establish a stable hierarchy … wild females are characterized by more pro-social behavioral traits, whereas wild males seem to be characterized by agonistic behaviors, social abstinence, and hiding (p9) …. the social organization formed in male mice is mostly dependent on their degree of aggression. In contrast, social organization formed in female mice seems to depend more on social factors such as familiarity and physiological factors" (p10). "Specifically, males engaged in significantly more agonistic and less pro-social behaviors compared with females, in both lab and wild mice …" (p2). Zilkha et al. point out (citing multiple studies re each species) that their findings are widely applicable: "Similarly, extensive sex differences in the dynamics and behavioral strategies undertaken to form hierarchies were also found in other mammalian species, including hyenas, foxes, rhesus monkeys, baboons, and even humans" (p10). Stockley & Bro-Jørgensen (2011) concur with Zilkha et al. that females employ far less aggression and instead use alliances competitively. And in a major set of studies of hierarchy in mice, Williamson et al. (2018) find that "females indeed exhibited significantly less aggression than males, as is demonstrated by their scores on the various measures examined". Even more profoundly, in a social insect species (in this case a paper wasp), Brown (2019) finds no aggression at all in the replacing of the dominant individual by a successor.

THE SOLE REPRODUCING FEMALE DECIDED BY FERTILITY SIGNALLING

Social insects are the great bulk of species featuring ostensible female DH. In most cases there is a sole breeder (a queen), in an afore-mentioned first-among-equals (winner-takes-all) sociality (a pre-eminent individual with all others un-ranked also-rans, not an alpha + beta + gamma + delta, etc., as in DH). There also may be a deputy: a potential replacement queen. That in some species there appear to be a handful of apex individuals in a seeming short hierarchy, is likely an over-interpretation of a queen plus a deputy and one or two others who fell not far short of them in fecundity. Communication of social information is via a set of complex organic chemicals on the outer surface – cuticle -- consequently known collectively as cuticular hydrocarbons (CHCs). These very recently have been shown in several species to encode fecundity indicators, that in their mutual comparison between individuals decides who becomes the sole breeder, without any agonistic contest. “There were no dominance hierarchies”, conclude Abril & Gomez (2020), instead “intrinsic physiological differences among queens”. *Cuticular hydrocarbons correlate with fertility, not dominance* is the title of Izzo, Wells, Huang & Tibbetts’ (2010) paper on a wasp species. Leonhardt et al. (2016) outline that “In communal or facultative eusocial species where several females compete for reproductive dominance, the relationship between CHC profile and ovarian activity informs both competitors and potential helpers about the reproductive potential of each female and can be used to establish dominance and induce helping behavior.” In confirmation, Honorio, Châline & Chameron (2019) find there are “pre-existing differences in putative fertility signals”, and that “idiosyncratic differences in a putative fertility signal (and therefore presumably in ovarian activity) between workers in the queen's presence reliably predict the outcome of reproductive conflict after queen loss”. Yagound et al. (2014) elaborate: “status discrimination abilities were in fact sufficient for the establishment and stabilization of linear hierarchies. The observed level of accuracy allowed fine-scale discrimination of all top rankers' hierarchical status. ... Low-ranking workers did not exhibit such fine-scale status discrimination. We moreover showed that a putative signal of fertility, 13-methylpentacosane, precisely labelled the workers' position in the hierarchy”. Building on this, Yagound et al. (2015) state: “Furthermore, this compound might play a key role in the establishment of the reproductive hierarchy, since workers with low fertility at the onset of hierarchy formation already have relatively high amounts … individuals with experimentally increased amounts of 13-MeC25 triggered less agonistic interactions from top rankers, in accord with them ‘advertising’ higher status”.

More revealing still, *cuticular hydrocarbon profiles differ between ant body parts*, to cite the title of a 2021 paper by Sprenger, Gerbes, Sahm & Menzel, building on the discovery of location-specific cuticular hydrocarbon signals in a social insect by Wang, Goodger, Woodrow & Elgar in 2016. This would appear to account for the various forms of particular physical interactions between individuals that have been assumed to be agonistic contest but, without imputing function, more objectively are rubbing or grasping manoeuvres involving different, specific body parts. For a listing and description of these, see Monnin & Peeters (1999). Albeit their classification is specifically in respect of an ant species and its relatives, similar pertains across social insects. The key body parts involved are the antennae and the mandibles, both sets of which are known to feature sensory organs (sensillae) to detect CHCs (e.g Ozaki & Wada-Katsumata, 2010), and mandibular glands themselves produce oderants (Ferguson, 2021), as do antennae – hence antennal so-called duelling or boxing.

Sasaki et al. (2016) find in an ant species that the great bulk (86%) of interaction features antennal duelling, with most of the rest (10%) involving the mandibles. Honorio, Châline & Chameron (2019) describe what is usually denoted biting as being “when the individual uses its mandibles to grip a part of another individual’s body. In most instances, biting was prolonged … with no apparent damage or cuts, and we consider this behaviour ritualized biting”. This is, as the authors thus label, a grip rather than a bite, and with no more obvious ostensible agonistic behaviour in social insect repertoire, it is a more than merely plausible hypothesis that social insect ostensible agonistic interaction in general actually is to facilitate the tactile contact required to accurately detect honest fecundity signals.

THE SOLE REPRODUCING FEMALE DECIDED BY MERE CONVENTION

A class of modes of determining the female sole (or parallel multiple) breeder(s) is dubbed *convention*-based dominance, as termed and neatly summarised by Tibbetts, Pardo-Sanchez & Weise (2022), (though again, note, the absence of either hierarchy or contest means it is misleading and unwarranted to employ *dominance* terminology):

> *In societies with convention-based dominance, individuals have unique attributes that single them out as the next dominant, (e.g., age, tenure in a group, or maternal rank) without reflecting intrinsic characteristics that allow individuals to win contests (Lewis, 2008; Horrocks & Hunte, 1983). For example, some social insects determine dominance based on the seniority convention. The oldest worker is the most dominant and will take over if the queen disappears (Strassmann & Meyer, 1983; Taylor et al., 2020). Nepotistic hierarchies are common dominance conventions where dominance rank is inherited from the mother. Juveniles acquire status immediately below their mother, with younger offspring outranking older siblings (Holekamp & Smale, 1991). … Although nepotistic hierarchies are considered convention-based, rank inheritance depends on support from mother, kin and coalition members to ensure offspring acquire the appropriate rank (Strauss & Holekamp, 2019; Chapais, 1992).*

Tellingly, while inheritance of rank by females from their mothers is known for many species, there is no corresponding case of inheritance of rank by males from their fathers (Mattison et al., 2019). Inheritance from the mother, like succession by age, occurs only for females, not for males, in line with neither inheritance nor age concerning contest, hierarchy or dominance.

Convention appears to apply in particular when individuals are closely related, and, therefore, there are inclusive fitness considerations. A coalition of close relatives is familial sociality, and the pre-eminent female of a family hardly could be considered to be at the apex of a DH. Familial relations are in terms of age-based seniority and the simple scramble of sibling rivalry, not dominance, for which there is no use, as reproduction (sexual access) is not at issue, with mating being extra-familial, as it has to be to avoid in-breeding depression. Even a derivative DH function of ameliorating aggression is not needed, as close relatedness (consanguinity) would preclude fierce rivalry, and when, in some species, it is necessary to cull weak offspring, amelioration of ferocity would be the very antithesis of what is required.

A famous case of falsely imputing female DH when sociality instead is familial is that of the wolf. L David Mech, the pre-eminent authority on the animal, had previously described the wolf in DH terms, but completely revised his position upon discovering all groups in the wild are established by mating and having offspring, so that rather than an alpha female (and male) the supposed top-ranked individual should be designated *breeder* or *mother/father* (Mech, 1999). Long before, Mech (1970) had realised that what had been taken to be submission actually is simply a food-begging gesture or a food-gathering motivator by offspring to the parents (who monopolise food in order to allocate it, making sure younger offspring get their share). Agonistic behaviour is more or less confined to driving offspring away from the group upon their reaching maturity. Instead of a DH there is simply seniority (age-based ranking). Issue is taken with Mech's position by Cafazzo, Lazzaroni & Marshall-Pescini (2016), who claim there is DH, yet agree there is age-based determination, which being convention-, not contest-based hierarchy, is a hallmark of familial sociality, not DH. In any case, Cafazzo et al.'s work is in respect of captive wolves, and it's the contrast with wild populations that is Mech's point. It is well recognised that in general across fauna, the close confines of captivity engenders repeat conflict that would not occur in the wild, to the point that natural sociality can break down, with some individuals becoming withdrawn through the experience of multiple negative encounters. There is no reason to assume this is sub-dominance in a DH if the species does not display it outside of captivity. In the wild, Mech's conclusions appear likely to apply across the Canidae family of species, with even domestic dogs (dogs long bred in captivity) also being known to have an age-based tolerant hierarchy when feral (Bonanni, 2017). As already mentioned, some social insect species also have age-based female hierarchy (e.g., Bridge & Field, 2007).

The meerkat is another case in point: the sole-reproducer female is determined by seniority, primarily, and secondarily, weight (Thavarajah, Fenkes & Clutton-Brock, 2014), without contest. It would seem in effect that differential weight given optimum reproductive age and experience is a ready-reckoned proxy for fecundity, settling the matter as to which individual is to take the reproductive crown without need of agonistic interaction. Weight would be an excellent indicator of overall condition and stored reserves available to be utilised in feeding and protecting offspring. Meerkat communities consist of the single breeding female and her mate, with everyone else non-breeding alloparents, most if not all individuals (of both sexes) being the pair's offspring. This is essentially familial sociality. [Note the males don't form a DH, as they have been well tested (after dispersal from the natal group upon reaching sexual maturity), in having to survive and thrive either individually or among fellow male rovers to the point of out-competing other males in achieving sufficient weight to show a pre-eminent genetic fitness (genomic integrity), thereby to join a group as the sole male reproducer.]

DH IN ITS MOST NOTABLE COMPONENT, *THE WINNER-LOSER EFFECT*, IS MALE-SPECIFIC

Finding "a sex-specific mechanism underlying social hierarchies in mice", Van den Berg, Lamballais & Kushner (2015) conclude that this is "whereby males are strongly influenced by prior experience, whereas females are reliant upon intrinsic attributes". By prior experience the authors mean previous contest, of course. Furthermore, the male-only facility to make use of these they find arises from the Y chromosome's SRY gene, so the mechanism cannot be female, as anyway is clear from its being known to be mediated by testosterone. This facility is known as *the winner effect*, when a prior win provides a physiological (and, in higher animals, a psychological) boost to future winning, and/or *the loser effect* when a prior loss provides a physiological (and, in higher animals, a psychological) brake, predisposing to future losing. By contrast, for females there are no such shifts, and instead each encounter entails mutual assessment anew, irrespective of past dealings. Without carrying over of an impact from one encounter to another, there is no basis for ranking in females. Hierarchy may be aparent and it may be fairly linear, but it would be simply an artefact of differences between individuals according to basic criteria that are so obvious as not to require the sort of testing to uncover underlying difference in which males engage.

Winner-loser effects are shown to produce a DH in modelling using cyber interactants in a computer simulation known as *DomWorld*. With no predication other than the ability of interactants individually to process *winner-loser effects*, then (as long as there is no constraint on the option to escape) the result is a self-organising hierarchy of similar linearity to DH in reality (Van Haeringen & Hemelrijk, 2022). As *winner-loser effects* are also the basis of hawk-dove game theory, unsurprisingly, similar results are obtained in thus modelling DH (Huang & Wu, 2022).

In real living interactants, a *winner effect* has to be “evolutionarily wired” (Morgulev & Avugos, 2020), with specific neuro-hormonal circuitry required to process it (Robertson, 2012), now more fully outlined (Choi et al., 2023), necessitating a genetic basis, of which there are clear indications (e.g Franz et al., 2015), and which van den Berg’s team confirm. That the mechanism is implicit and not through rational acting is shown in human males by Kubitz, Page & Wan (2023). It cannot be cognitively sophisticated, because *the winner effect* has been found in invertebrate as well as vertebrate species (Hashikawa, Hashikawa, Lischinsky & Lin, 2018). It’s long been well-documented across fauna (e.g Fuxjager, Oyegbile, & Marler, 2011; Mesterton-Gibbons, 1999). All of these findings are exclusively in respect of males, and in human males a number of studies find a *winner effect* across a range of contexts, from sports to board games and elections, as summarised by Gorelik (2023), revealing it to be ubiquitous in male-male competitive scenarios.

The contrasting *absence* of a female *winner effect* is newly evidenced in mammals. Dai et al. (2022) point out that “… while in male mice repeated attacks lead to an increase in aggression (*winner effect*) and preference to the winning-associated context, such behavioral changes are not observed in female mice (Aubry et al., 2022; Hashikawa et al., 2018)”. So profoundly lacking is a *winner effect* in females that Hashikawa et al. posit it is through attack failing to provide reward to females. There has accumulated a sufficient body of research into this phenomenon in humans to conduct a meta-analysis. Over the past 35 years, research into the impact of competition outcome on testosterone concentrations in humans reveals an effect only in men and not in women (Geniole, Bird, Ruddick & Carré, 2017; Geniole & Carré, 2019).

This extends to *loser* as well as *winner effects*, albeit there is a study where although there was no female *winner effect* instead a female *loser effect* was found (Casto et al., 2020), but finding even a *loser effect* in women makes this an outlier among studies. Not even a female *loser effect* is found by Abad-Tortosa et al. (2019), whereas it is well evidenced by numerous studies in men, complementing *the winner effect*. Page & Coates (2017) (and Gauriot & Page, 2019) looked at both *winner and loser effects* in tennis players of both sexes and found “these effects did not exist among women, a finding consistent with the hypothesis that androgens mediate winner and loser effects”. Cohen-Zada, Krumer & Shtudiner (2017) found likewise with judo. The same sex dichotomy pertains in considering prestige dominance (Cheng, Kornienko & Granger, 2018). That there is both a *winner* and a *loser effect* specifically in male mammals is shown by Chase, Bartolomeo & Dugatkin (1994). The few rodent studies there have been show no female *loser effect* (Hashikawa, Hashikawa, Lischinsky & Lin, 2018).

Authors increasingly are denoting *the winner/loser effect* as *momentum*. That for humans this is psychological (rather than merely physiological) is outlined by Clark & Nilssen (2021), citing in particular Iso-Ahola & Dotson (2014), who conclude “the influence of psychological momentum seems to be greater for male than female performers”.

Even considering not testosterone but instead what is normally considered the female sex hormone, estradiol, Scaia et al. (2018) find that whereas in males there are higher circulating levels of estradiol after winning, there is no such change in females. So, with estradiol too there is no basis of a *winner effect* in women; again, only in men. Likewise in considering not testosterone on its own but in conjunction with cortisol – the dual hormone hypothesis (Knight, Sarkar, Prasad & Mehta, 2020). A meta-analysis of studies investigating this by Dekkers et al. (2019) is supportive in the case of men but not women (for whom there is an almost negligible correlation in the data). Knight et al concur that there is “stronger support for the dual-hormone hypothesis in males than females”. The only support for a female *winner effect* here is in terms of an exception proving the rule: in the case of the “special population” of the minuscule proportion of the female population who compete at Olympic level (Casto, Hamilton & Edwards, 2009), which would be explained by a necessarily highly unusual extent of masculinisation of such women (hyperandrogenism), possibly mild congenital adrenal hyperplasia (CAH), producing profoundly aberrational hormonal profiles.

Strikingly, then, there is no evidence of a female *winner effect* – little if any for a *loser effect* either: any form of momentum – despite the enormous ideological motivation for it to be demonstrated. Certainly, there is a dearth of published studies, and this is likely through null findings failing to interest journals (as is generally the case, and specifically in respect of this topic, given the ideological implications). Countless investigations will have gone unpublished, and countless potential investigations will not have commenced given researchers’ anticipation of null findings. If a female *winner effect* indeed were there for the finding, this would be prominent in the published literature starting many years ago. Albeit impossible to prove a negative, it is possible now at least provisionally to conclude that there is no *winner effect* in the female; that is, *the winner effect* is male-specific; likewise, regarding even a *loser effect*.

The profundity of the sex dichotomy in respect of *the winner/loser effect* is revealed by Gorelik (2022) in pointing out that “it is not winning per se that precedes a testosterone boost; rather, showcasing dominance over potential reproductive rivals seems to be the main cause”, and that “… research on the effect of winning on men’s sexual interest suggests that testosterone may likewise be upregulating men’s sex drive in anticipation of greater reproductive opportunities (Gorelik & Bjorklund, 2015; Markey & Markey, 2011; Markey & Markey, 2010)”. What is known about *winner/loser effects* further reveals that not resources but reproduction is what is at issue with DH.

OSTENSIBLE *FEMALE DOMINANCE* IS INHERENTLY IMPLAUSIBLE

A useful test of DH as being not bi-(inter-)sexual, but instead same-sex (indeed, male-specific), and requiring contest -- and to be a hierarchy, not simply first-among-equals (winner-takes-all) sociality -- is to examine the ultimate manifestation of the still standard view of DH in the unusual putative phenomenon of *female dominance*. This is where, in a few species, females supposedly are dominant to males either wholly (all females dominant to all males) or partially (a minority of females dominant to a minority of males). If even the proverbial exception to prove the rule is absent here, then the rule would be strong indeed. Should the new understanding of DH herein be accurate, then imputation of *female dominance* would be the clearest inappropriate application of the standard view.

That the notion of *female dominance* (over males) not only is a priori theoretically misguided in terms of an understanding of sex and the sexes but makes no logical sense, is clear from the corollary that in the usual case (in the vast majority of species: all those not supposedly female dominant), there would be correspondingly *male dominance* (that is, over females). Even assuming there could be such a thing as bi-(inter-)sexual DH, there would not be 100% dominance in one direction, given that in most species there is a degree of overlap across the sexes in measures of key factors (e.g. size, weight, and associated strength) that in males greatly contribute to gaining dominance. If dominance were inter-sexual it would be anticipated that in all species, other than the most extremely sexually dimorphic, a small proportion of males (the most sub-dominant) would be sub-dominant not just to most males but also to a minority of females. A coterie of females would be sufficiently large, heavy and (especially if unusually masculinised) strong to outdo a minority of males in these male very terms, thereby to be dominant over them. That across species this is very much not the case, and certainly not generically, demonstrates that a relationship other than dominance pertains between the sexes. If *male dominance* does not exist, then neither can *female dominance*.

To try to account for rare *female dominance*, Lewis (2020) puts forward a wider conceptualisation, of "female power", in terms of "leverage", in particular through a male-biased sex ratio. Lewis is quite vague, though intimates this power involves sexual favours, yet this is implausible. The female already has leverage in being the limiting factor in reproduction through being the gestating and lactating sex. Inclusive fitness considerations of local reproductive output require evolved mutualism (accounted for by any of several empirically equivalent theoretical outlines – without entailing group selection) to drive male protection of and/or giving precedence to the female. This could be a facility that is initiated or upped according to fecundity. Its absence would be to the detriment of local reproduction generally, thereby negatively impacting individuals within the local group generically, either indirectly and/or directly.

OSTENSIBLE *FEMALE DOMINANCE* ACTUALLY IS MALE DEFERENCE

The most well-known species said to sport *female dominance* is the spotted hyena, yet according to McCormick et al. (2022) "without any observed provocation" males "submit" to females, begging the question of why males would signal subdominance in the absence of signalled dominance. It would seem the male is simply deferring to the female, as males would be expected to do. It's possible males employ a sub-dominance signal to acknowledge registering a female's presence and will not compete with her for food or other resources, in a co-option for want of a more specific signal to indicate non-engagement in dominance terms. McCormick et al. state their study was to try to decide between "intrinsic attributes" (aggression) and social support for the basis of male-female interaction, and “were unable to assess the leverage hypothesis”. In any case, hyena females do not contest for rank and instead acquire it by convention, in this case by inheritance from the mother (e.g Engh, Esch, Smale & Holekamp, 2000), so if there is hierarchy it is not DH, and hence there could not be a dominance-submission interaction even in principle.

A male act of deference is explicit non-engagement. It is nothing to do with female leverage. Not initiation of courtship or signalling of male mate value, if anything it is a signal of non-courtship; a retiring gesture indicating insufficient own mate value to warrant initiating courtship. Male deference is fairly obviously evolved male consideration for or protectiveness towards the female. That male deference has been assumed to be sub-dominance (submission) is likely through there being little or no difference in the form of the behaviour from that observed between males where the function indeed is sub-dominance. A staple of the evolutionary process is that forms, whether morphological structures or genetically based behaviours, are forever being co-opted for different function; exaptation, to use the term devised by Gould & Vrba. Selection forces can work only on what is already present, utilising different aspects or combinations, possibly aided by a new or hitherto non-utilised mutation. All evolution is co-option (or exaptation) of some kind. McLennan (2008) sums this up as “… traits that had evolved under one set of conditions were co-opted to serve a different function under a second set of conditions. … Behavior, like morphology, has both structure (what it looks like) and function (what it does). Julian Huxley, a founding father of ethology, had the fundamental insight that behavioral displays often evolve in one context, then change function later in evolution”. What is here seemingly male sub-dominance is a co-option of the same or similar form to become functionally a quite different signal more appropriate for the context: to reassure the female that the male is not going to behave agonistically or in some other obstructive or deleterious manner towards her.

Most *female dominant* species are lemurs (that for brevity are here considered together, though papers cited may be in respect of one particular species). Depending on the species, they display a range of putative *female dominance*, from complete to merely partial. Yet the behaviour is anything but that of dominance-submission. Males are very rarely aggressive toward females, even if provoked, according to Radespiel & Zimmerman (2001), who also find that the males simply avoid females, so that invariably the female prevails (in 99.9% of all encounters). Film of lemurs in TV documentaries (e.g BBC *Wildlife on One*, 2002) show males placid and non-resisting when females simply take food out of their hands, in what is no sort of agonistic or any kind of interaction, with neither active yielding nor request. “Dominance within sexes differs from that between sexes”, Pochron et al. (2003) argue in respect of a sexually monomorphic (same-sized) lemur species, where “If females win a disproportionate number of interactions, it is likely that males allow this to happen”; this being in feeding contexts, where “males may trade off the immediate caloric reward available to winners for increased reproductive success” [p182]. If inter-sexual outcomes were in terms of dominance, size would be a major factor in who wins contests, but maturity, not size, is determinant (Voyt, Sandel, Ortiz & Lewis, 2019).

It has long been concluded that the phenomenon indeed is simply male deference, through female feeding priority (e.g Kappeler, 1993), or more widely “cost asymmetry” (Dunham, 2008), or both feeding priority and “reproductive strategy” (White et al., 2007). White et al. found that the top-ranked male deferred the most: the inverse of what would be expected if the sexes were in a dominance relationship. The conclusion of male deference is reaffirmed in the conclusions of the most recent studies/reviews, by Grebe, Sheikh & Drea (2022), and also by Kappeler, Fichtel & Radespiel (2022), who state that there is “spontaneous male submission in the absence of female aggression and linked to female sexual maturation”. In other words, specifically to fertile females, males are deferent; that is, they signal non-engagement in dominance terms. Males hardly could be submissive (sub-dominant) anyway, given the apparent absence of a male DH: Bauer (2004) describes the male interactions as “unstable over time due to male migration and extreme male-male competition during the brief mating season (Budnitz and Dainis, 1975; Taylor, 1986; Sauther, 1992; Sauther and Sussman, 1993; Pereira, 1993; Gould, 1994; 1997”. Males are not sufficiently together to establish male DH as claimed. Neither would the female hierarchy appear to be a DH: Bauer finds that establishment is according to age and weight, adding that it is also according to aggressiveness, but it needs to be considered if any agonism is the exercise of rank already established through age and weight criteria, in which case ranking would not be established by contest, and there would be no female DH.

White et al. argue that females have evolved to be more masculinised in order to better compete intra-sexually for unusually restricted food availability, given the high energetic demands of lemur species (though both this restriction and the demands are disputed in the literature). On this view, female-female competition gives rise to *female dominance* as a by-product. However, that the phenomenon here indeed is the male yielding rather than the female actively prevailing, is shown by the hormonal profiles of male lemurs: “unusually high estrogen concentrations year-round potentially facilitating male deference via male-initiated affiliation” (Grebe, Sheikh & Drea, 2022). Male estradiol levels are described as not significantly lower than those in females, which is highly unusual, indeed likely unique to some lemur species.

Verreaux’s sifaka, actually another species of lemur, is supposedly completely *female dominant*, but this is contradicted in reports of its behaviour. Lewis, Bueno & Di Fiore (2022) point out that “While 96% of the acts of submission were directed from males toward females, females only won a third of their conflicts with males. … evoking submission does not translate into winning a resource. Indeed, intersexual power is dynamic, contextual, and dependent on the individuals in the dyad”. Voyt, Sandel, Ortiz & Lewis (2019) write:

> *Power relationships between mature females and males were unambiguously female biased. Female reproductive maturity, and not body mass, predicted intersexual conflict outcomes. Once reproductively mature, females almost never lost to males, except when females had not yet had an infant survive past weaning. Our results are thus consistent with the hypothesis that female leverage characterizes social structures of adult Verreaux’s sifaka more than female dominance.*

Again, a result of 100% unidirectionality is also consistent with a phenomenon other than dominance-submission being at play (as explained above). Lewis (2019) reveals the supposed subordination signals given out by males are other than they seem: “… males respond to aggression by females with ‘chatter’ indicating ‘subordination’, but the pattern of ‘chatter’ is quite different to that amongst females”. If male supposed submission signals are very different from any signals females use to each other, then the basis of submission signalling cannot pertain to any form of inter-sexual hierarchy, DH or otherwise. In any case, there first has to be established if either sex actually has a DH, and also if males and females have sufficient social proximity for there to be a putative inter-sexual DH. With males in this species dispersing upon sexual maturity to join other males as a floating group, then the sexes are too separated to be able to form a putative inter-sexual hierarchy in any case. Again, no sense can be made here of a notion of female dominance.

FEMALE DOMINANCE CANNOT EVEN BE MODELLED

Modelling that purports to show primate *female dominance* (Hemelrijk, Wantia & Isler, 2008) actually is a failure, being circular and anyway based in assumptions so implausible as to have nil ecological validity (that is, no application to the real world). Reviewing work using the *DomWorld* simulation of interacting cyber agents, Bryson, Ando & Lehmann (2012) conclude: "Contrary to Hemelrijk et al. (2008), *DomWorld* could never account for complete *female dominance*, unless the starting condition had the females already in a dominant position" [p19]. The strange inbuilt assumptions of the model (perhaps the least of which is that the level or intensity of aggression is set only slightly higher for males than for females) lead to the highly implausible outcome that "the female would have a one-in-three chance of defeating an agent very much her superior. This high number of 'improbable' outcomes is what creates the dynamicism of the ranking system in *DomWorld*" [p19]. Furthermore, *DomWorld* actually produces nothing more than "a perfectly random dominance hierarchy ... The apparent rise in *female dominance* is only a trend towards complete randomness" [p19]. Bryson, Ando & Lehmann further outline in detail other key problems with the *DomWorld* simulation that together irretrievably undermine any claim for its reflecting a basis in reality for *female dominance* ever to emerge. They explain why the model produces more *female dominance* as the proportion of males increases:

> *Adding males to the system increases the rate at which random order is achieved because males have a higher StepDom [the level or intensity of aggression set for a cyber agent in DomWorld] than females and thus the average amount of 'violence' per interaction increases with the proportion of males. Since the experimental run times are truncated at an arbitrary but fixed period of time before the ordering of agents is perfectly random, the rate of change determines the proportion of dominant females. [p19]*

With no attempt to address, reply to or acknowledge Bryson et al.'s outline of *DomWorld*'s fatal flaws by those continuing to use it as the basis of research, a recent flurry of papers employing it make no useful contribution to the literature on supposed *female dominance*, serving only to perpetuate the notion despite its being shown to be chimeric. Even if were accepted the falsehoods that there can be a bi-(inter-)sexual DH and that the sexes essentially are interchangeable with only small differences between them, there is nonetheless no feasible model that produces *female dominance*; only one employing outlandish assumptions designed to generate that outcome, if not embodying key facets of the outcome within the model itself.

CONCLUSION

Recent research provides further evidence to bolster the analysis of the phenomenon of DH as being invariably intra-sexual (never inter-sexual – not either rare female dominance or presumed usual male dominance), and, further, that DH is male-specific. That is, DH proper – a hierarchy that is formed through contest, not first-among-equals (winner-takes-all) sociality, and that is linear and transitive – is male-only, with any female hierarchy, when not more apparent than real, a quite different phenomenon: merely signalled relative fecundity, or by maternal inheritance (or some other convention), or ad hoc resource competition. This is in keeping with the function of DH to allocate reproduction rather than resources, in the service of the male *genetic filter* function, leaving the hitherto assumed function of DH to reduce agonistic interaction pertaining not to male actual DH but to female sociality, that anyway is other than DH.

This analysis hardly is of mere theoretical interest, as it relates directly to profound new understanding of sex and the basis of the dichotomy of the sexes, without which sense cannot be made of sociality and behaviour (human or animal). Current hegemonic extreme ideological notions have led to nonsense notions about human social behaviour, that will come to be seen as outlandish historical mistake. Meantime, scientific investigation and its dissemination may not survive growing totalitarian censure preventing informed debate.

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AUTHOR PROFILE

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

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