

Sperm and Post-Copulatory Competition for Females' Reproductive Tracts among Male Insects and Vertebrates

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Abstract-The paper presented and discussed the general evolutionary understandings of post-copulatory competition issues that are found among males when they are competing who is going to be the first, as well as the last, to having intimate contact with females. In particular, the whole discussion of this article focuses on the presence, or not, of male sperm within a female's reproductive tract. Examples about post-copulatory competition are provided from both insects and vertebrates. What is also discussed is that such competition between males takes place in view to the passing on of genes that carry traits able to bring upon reproductive success to future generations via sexually-selected strategies towards the ultimate goal of fertilisation of females' reproductive tracts.

Keywords- Post-Copulation; Genital Morphology; Scrambling; Mate Guarding; Cryptic Female Choice; Double Mating

I. INTRODUCTION

Sperm competition is explained as an important selective force that led to the evolution of key male traits [1]. Males compete with each other during and after insemination - post-copulatory competition - as to whose sperm would remain in a female's reproductive tract to fertilise her eggs [2].

Key male traits refer to mate fertilisation strategies subject to species' fulfilment of reproduction needs. Body size, the amount and frequency of ejaculation, vas deferens sensitivity, early sexual maturation, careful strategic or prudent allocation of sperm, mate guarding, mating plugs are some of the traits evolved to meet sperm competition needs [3]. Post-copulatory competition is the intra-sperm rivalry occurring within a female's reproductive tract. Females can influence post-copulatory mating outcomes in their reproductive morphology in terms of choosing males the traits of which can be passed on to their offspring, and the way to do that is to mate with those whose sperm could remain in their tracts so as to fertilise their gametes successfully [4].

The purpose of the topic in question in this paper is twofold:

1. To inform us about reproduction fulfilment needs the way these are satisfied in insects' and vertebrates' environments
2. To consider, how the knowledge we acquire could be useful and/or applicable to discuss human reproduction needs and mating strategies

II. MAIN PART

Post-copulatory competition takes place when males inseminate many females over a single reproductive period during which sperm can be located in females' reproductive tracts [5]. Sperm competition is a risky business for males because even the mere presence of a rival can increase or decrease fertilisation chances [6]. Key male traits that evolved due to sperm competition may refer to the amount of sperm ejaculated and the body size of potential competitors. Body size, whether large or small, including secondary sexual traits, displays (leks) and ornamentation, is an important mating factor for males to sire more offspring [7]. Species observed in that category are groups of insects where larger males can father greater number of offspring compared to small-sized competitors [8]. A trait associated to body size is genital morphology [9]. Dual penis function refers to such morphology where species like damselflies (*Calopteryx maculata*) can displace rival sperm by the utility of extension barbs on their penises while copulating with a female [10]. In this way, males by removing rival sperm can enhance fertilisation and paternity chances [11]. The amount of sperm ejaculated has also been found to correlate with larger testes [12]. In invertebrate species, such as the hermaphroditic leech *Helobdella papillornata*, larger testis size is associated with increased risk of sperm competition and greater sperm release [13]. A similar finding is being argued by [14], where larger testes males of the *Tettigoniidae* bushcricket family are preferred as mates compared to those with smaller testes. However, in that species, larger testes correlate negatively to the amount of ejaculates delivered due to varied female receptivity as to the number of males available for mating. Species, like sticklebacks (*Gasterosteus aculeatus*), inseminate more sperm in the presence of a larger body competitor indicating that one's size can arouse greater amount of sperm from a mating rival [15]. Body size and the size of the ejaculates correlate also in the case of larger males who inseminate more sperm compared to smaller males [16].

In multi-mating taxa¹, the quality of sperm ejaculated can be connected to vas deferens sensitivity. Vas deferens sensitivity is an important trait whereby quick contractility of sperm emission into a female's vagina may ensure successful fertilisation. Species from the *Peromyscus* genus have been reported for vas deferens sensitivity with polyandrous females during a single reproductive bout [18]. In that understanding, quick emission of sperm from vas deferens, during increased mating opportunities, is subject to sperm competition risk in social environments [19].

A model that explains fertilisation chances when males frequently copulate with more than one female is the 'raffle' or 'lottery' principle. By this it is meant that the more the ejaculates the more the possibility of fertilisation and therefore sperm competition succeeds [20]. A species in that category is the bulb mite *Rhizoglyphus robini* which by producing more sperm during copulations achieves higher fertilisation rates [21]. According to this principle, the trade-off between effort spent on ejaculates and effort spent on acquiring more mates may outcome to fitness maximization as to efforts spent between insemination tactics and mating success [22]. In such a sense, the chances a male has to fertilise a number of females could be analogous to the sperm inseminated to females' reproductive tracts and the success of fertilisation compared to another male's fertilization successes to same females [23].

Scrambling is another key situation explaining that quickly finding a mate before rivals do can have a successful outcome to the sperm competition arms race. Successful sperm competition can be achieved either by reproductive readiness, such as early maturation—sometimes called protandry—or by well-developed sensory organs, such as spatial memory [24]. Scramble competition has been noted in the *Stegodyphus lineatus* spider, where smaller males were able to inseminate larger females due to early sexual maturation [25]. Early sexual maturation provides fitness advantages to smaller-sized males, for females they mate with are likely to be virgin; something that increases fertilisation chances [26]. Well-developed sensory organs are also a characteristic of scrambling strategy whereby males can rapidly locate partners to copulate with [27]. A species with such trait is *Pseudomantis albofimbriata* where males use visual contact to locate and mate with females. [28].

Males competing with each other are also involved in post-copulatory intrasexual conflict whereby traits such as mate guarding and copulatory plugs may monopolise fertilisation of female gametes [29]. Mate guarding examples can be found in *Phocoenoides dalli* porpoises which stay closer to females to reduce extra-pair copulations from rival suitors [30]. Copulatory plug examples can be found in guinea pigs that place chastity enforcements on females to secure fertilisation success [31].

Sperm that is ejaculated according to females' availability for mating has led to a phenomenon called prudent sperm allocation [32]. Due to that phenomenon, and given the fact that continuous sperm allocation to females' reproductive tracts may lead to sperm depletion, species tend to reserve enough sperm in view to future matings [33-35]. In this way, by adjusting the amount of sperm prudently, inseminations can become more efficient in terms of sperm competition risk [25]. Increased risk of sperm competition increases the amount of sperm delivered, whereas sperm is conserved when no rivals are at sight [32]. Due to sperm competition risk, there has been observed a parallel phenomenon to prudent sperm allocation which does only indicate that species reserve sperm for future matings, but also that they ejaculate as more sperm as possible when mating in the presence of a rival male. Evolutionarily, this is explained as a necessary consequence of adaptive changes in copulatory behaviour, so that the sperm ejaculated to succeed in inseminating a female's reproductive tract. This is the case of the male house mouse (*Mus musculus domesticus*), which succeeds higher sperm transfers due to the fact that chance in mating with the same female is scarce [36].

In parallel to copulatory behaviour and prudent sperm allocation, as to the amount of sperm ejaculated, there is also the understanding of sperm intensity which postulates that species, like meadow voles (*Microtus pennsylvanicus*), invest higher or lower sperm amounts in females' reproductive tracts subject to the presence of rivals during copulations [37]. That means that sperm is allocated optimally so that reproduction chances to be prudently increased subject to the sperm competition intensity that is experienced [38-40]. However, there has also been observed [15] that prudent sperm investment depends also on the number of other males present during copulation, that is to say that the increase or decrease of ejaculation is analogous to the number of rivals wishing to inseminate a female: i.e. the more the number of rivals present the more the amount of sperm ejaculated, whereas the opposite is true when rival males are less [41]. To that, there is still no clear explanation why it takes place, though there has been suggested that such evolutionary phenomenon takes place due to the idea that maximal investment of sperm allocation may depend on the intensity that sperm needs to be allocated in relevance to saliently equal strong competitors [38]. Among species modulating the amount of sperm ejaculated are the Norway rat, *Rattus norvegicus* [5], and *Drosophila pachea* [42]. Norway rats ejaculate more sperm when in polyandrous settings, whilst reserve it in monandrous environments and *Drosophila* partition it in analogy to the number of females they are coupled with. A physiological mechanism supporting prudent sperm allocation is vas deferens contractility as to the distribution and balance of semen volume [23].

Post-copulatory competition is related to female promiscuity. In species, like the mouse house (*Mus musculus*), promiscuous females mate both with dominant and subordinate males [43]. Males' gametic investment in ejaculations is reflected by female promiscuity and the presence of rivals [44]. Female promiscuity enhances post-copulatory competition.

¹Namely, species that have more traits in common so to mate to each other -assortative mating-, compared to species the taxa of which differ to the extent mating between them to be dependent on random chance [17].

Females' morphological, physiological, and behavioural traits influence post-copulatory competition between males as to whose sperm would be preferred to win successful fertilisation [13].

Females can influence the outcome of post-copulatory competition in their reproductive morphology by preventing inseminated sperm from reaching their eggs directly [44]. Issues of morphology in females' reproductive tracts indicate that females choose which male's sperm will be retained. Females, by favouring and biasing fertilisation success, influence the outcome of post-copulatory competition [45]. Post-copulatory female choice has evolved either because of limited number of mates, or because mating was costly to females [46]. A species which can influence post-copulatory competition between rivals in her reproductive morphology is *Drosophila melanogaster* [47]. Females promote post-copulatory competition between rivals by cryptically favouring post-insemination preference to a particular male's sperm in their reproductive tracts [46].

Post-copulatory female choice can also be called cryptic female choice. By 'cryptic female choice' it is meant that females are able to manipulate paternity by choosing whose male's sperm to be stored to fertilise their eggs [48]. Cryptic female choice is related to female sperm choice as to which male would be accepted to fertilise a set of eggs [49]. An evolutionary explanation to cryptic female choice can be that females eject a male's sperm if his phenotype does not match dominance status [50]. Females through cryptic choice discriminate between the semen of rival males, introducing thus a conflict between partners [47]. Discriminative female mating behaviour has been observed in the *Lasiopodomys brandti* vole, where male social status and dominance account for sperm acceptance in females' reproductive tracts [51]. In parallel, sperm removal in the female *feral fowl* can be explained as rejection of a male's subdominant ranking status [52]. The same applies in species like the fowl *Gallus gallus*, where males succeed in fertilising females by terms of status-dependent sperm investment [53, 54]. A biological explanation might be argued to such status-dependent sperm investment, versus not, is the presence of less stress in hormone levels, more brain serotonergic activity, as well as efficiency in metabolic and growth rates, which offer sperm allocation dominance compared to subordinate and subdominant conspecifics [55].

In cryptic female choice, fertilisation success and post-copulatory competition can be biased when females look for direct and indirect fitness benefits from partners [56]. Through direct fitness benefits females look to obtain fertility gains through adequate sperm supply, better resources in terms of food and nestlings, protection from dangers, and a good parental care for their offspring [57]. Indirect fitness benefits are genetically-based and can influence female partner choice by mating with a male in order attractiveness and viability traits to be passed on to offspring [47]. A species that receives both types of benefits is the freshwater crustacean *Hyallela* amphipod [58]. Cryptic female choice can also be directional or non-directional. Directional is when females choose to retain sperm because of a male's phenotypes, whereas non-directional when one's sperm is preferred because of genotypic compatibility to the female [47]. Categories of species as such are the *Drosophila* [4] and the comb jelly *Beroë ovata* [59].

In such a way, females look for mates able to pass on traits to male offspring that can inherit their fathers' mating success. The higher the mating success of their offspring, the higher the chances females' genes could also have to spread across future generations [24]. Females seek for males able to provide indirect fitness gains to them, even if males' mating success may result to reduced viability or increased risk of life expectancy.

Search for the appropriate mate explains females' double mating attitude whereby competition between ejaculations from different males is ensured [60]. Double mating indicates re-mating, whereby females by engaging different males copulating with them, they seek to influence the outcome of post-copulatory rivalry in their reproductive tracts [61]. Double mating is risky for males, because it increases the trade-off between nontrivial costs and semen production during post-insemination competition [62]. Post-copulatory competition is increased between males if the balance between nontrivial costs and sperm production is unclear regarding success of a female's fertilisation [19]. A species engaged in double mating is the land snail *Helix aspersa* which influences the outcome of post-copulatory competition in its reproductive tract by inducing intra-sperm conflict between males [62].

III. CONCLUSION

Sperm competition is an arms race intrasexual conflict between males as to who can fertilise a female and father her offspring [63]. Selective pressures during sperm competition have led males to evolve particular traits allowing them to succeed in insemination efforts. Large testes, prudent sperm allocation, scrambling strategies, the raffle principle, or vas deferens sensitivity are among the key male traits associated with sperm competition [64].

Females can influence the outcome of such competition by favouring sperm of particular mates, whilst rejecting that of others, if it does not match their preference of a male's phenotypes and genotypes. Post-copulatory competition is mainly influenced by cryptic female choice because females choose to mate with more than one male. In this way, post-copulatory competition is increased because males inseminate more sperm in their effort to successfully fertilise a female.

The knowledge we have acquired by studying insects' and vertebrates' copulatory/post-copulatory behaviours may introduce the understanding that human sexual strategies could also be subject to similar kinds of male traits, such as body and/or testicular size, sexual maturation and mate guarding, leading to successful fertilisation in view to healthy offspring [65,

66]. These traits have also been found to generate similar male jealous behaviours inter-culturally, so that rival others to be kept at bay [67]. Human jealousy over mating processes doesn't affect only males but females as well: Males are affected by jealous behaviour when their partners are flirted by other males; females are affected by the same emotion when their partners are courted by rival females [68, 69]. In both sexes, jealousy can be activated both as a defence as well as an attacking mechanism against rivals of the same sex [70]. The evolutionary explanation to the use of jealousy is that it has been selected for to minimise losses with regards to accumulation and ownership of resources, care for offspring and prosperity of the family in social milieus [71]. In this way, jealousy is regarded as the driving emotional force not only against potential rivals, but also as one of the chief mating characteristics that could lead to successful fertilisation outcomes [72]. Probably, a paper to be attempted in the future could be an empirical study on male-female reproduction strategies and the establishment of intimate relationships in the light of the emotion of jealousy.

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