SEXUAL SELECTION IN INSECTS

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ABSTRACT

Sexual selection is an evolutionary process, that increases the direct and indirect fitness of an organism by non-random preference of mates, based on their differential ability. Sexual selection may be in the form of intrasexual selection and intersexual selection. The former involves competition between the males (usually), while females are passive acceptors of winners as mates. The latter involves display of abilities by the males (usually), while the female inspects and assesses them prior to selection of mate. Traditionally both these mechanisms are believed to take place prior to copulation. However, studies indicate that these also take place, post copulation. The post copulatory displays of sexual selection involve sperm competition and cryptic female choice. Not only are all these displays fascinating, understanding their evolution and their ecological modulations make this field an interesting one. This review deals with these aspects of sexual selection in insects, as they encase some of the most diverse mechanisms of sexual selection.

Key words: Intrasexual selection, intersexual selection, sperm competition, cryptic female choice, direct and indirect fitness, sperm precedence

Charles Darwin during his long duration of observations of natural forms and analysis came up with the concept of natural selection. While this theory seemed to explain most animal diversity and the economics of form and structure across the animal world, it failed at explaining the aberrations in male and female form and behaviour that he saw time and again. It was his observation that largely males tended to exhibit form and behaviour that seemed to show no direct apparent survival benefits. In fact, these seemed to be energetically expensive and attracting attention of predators thereby increasing the incidence of attacks and mortality significantly. In an attempt to explain these observations, Darwin in 1859 proposed a phenomenon called "sexual selection". He suggested that the seemingly non-survival adaptations were aimed at increasing the chances of passing on their genes successfully to the next generation even at the cost of reducing their immediate survival. In this phenomenon, he suggested the inclusion of certain types of non-survival adaptations that seemed misfits under the parasol of natural selection (Darwin, 1871).

Alcock (2001) defines sexual selection as, *"A form of natural selection that occurs when individuals differ in their ability to compete with others for mates or to attract members of the opposite sex"*. Sexual selection, simply owing to its beautiful representation in nature through complex structures, colouration, patterns, songs and behaviours, has fascinated common man as well as scientists. The allure to the scientists is largely to understand the strength with which sexual selection drives the evolution of characters that impact the direct and indirect fitness of organisms (Andersson and Simmons, 2006) and may also influence speciation via non-random selection leading to varying rates of gene flow (Coyne and Orr, 2004).

Sexual selection can broadly be clubbed into intrasexual and intersexual selection. Intrasexual selection is based on competition between the members of one sex, usually males, with the females opting to mate with the "winners" while the other males usually remain without mates. Locking of horns, territorial competition, all come under the purview of intrasexual selection. Intersexual competition on the other hands involves female active choice; males are prone to displays of morphological, physiological and behavioural abilities. Females showing intersexual selection usually take their time in inspecting males

and choose the one that meets their requirements. In such a scenario, the males tend to have a rather more even playing field than the males of species indulging in intrasexual selection. Both intra and intersexual selection can occur at pre- and post-copulatory sexual selection. While initial and much evident studies on a large number of organisms concentrated on the visible form of sexual selection (pre-copulatory sexual selection; Wheeler et al., 2012), the current era of researchers is fascinated by the sexual selection that is hidden, that occurs in the female genital tract (post-copulatory sexual selection; Pischedda and Rice, 2012).

A lot of work on sexual selection has been done in insects, birds, fishes and mammals. Insects provide a wide variety of evidences of both pre- and post-copulatory mechanisms. Some aspects of sexual selection in insects are discussed below.

CAUSES OF SEXUAL SELECTION

The underlying cause of sexual selection is the competition for the rarer resource, in this case a suitable mate resulting in the increase of direct and indirect fitness. The number of mates that an individual has gained access to, also influences sexual selection, thus by extension, the limited sex causes greater selection pressure in the non-limited sex. Traditionally, competition and mate selection were considered the hallmarks of sexual selection, with males largely competing and females largely selecting; however, this was too simplistic a version of sexual selection and failed to explain the complexities of myriad incidences observed in the natural world across different taxa. Several hypotheses have thus been proposed to explain sexual selection, such as parental investment (Lehtonen et al., 2016), mating system (Darwin, 1871), sex ratio/ operational sex ratio (Emlen and Orring, 1977) *etc.* The parental investment theory simply states that the parent investing more per offspring is likely to be the more discerning one during mate selection. The mating system approach to sexual selection also indirectly talks about how many individuals can successfully rear an offspring, thus dictating the limiting and non-limiting sex.

PRE-COPULATORY SEXUAL SELECTION

Precopulatory sexual selection is usually associated with assessment of phenotypic characters prior to copulation (Pizzari and Parker, 2009). These phenotypic characters are considered indicators of fitness levels of the nonlimiting sex, thereby indicating the probability of their being selected as mates by the rarer sex.

Some of the phenotypic characters that help in selecting mates are: (1) size: often relevant in competitive assessments involving fighting, endurance, productivity, etc. (2) colour: indicates health, immunity, etc. via morphological appearances, (3) age: is again indicative of reproductive status, health, etc., (4) mating history: is indicative of the viability of a mate in terms of sperm and ova quantity as well as quality, paternity determination and offspring share, (5) nutritional plasticity: indicative of adaptability to varying nutritional conditions, (6) chemical signals: as an honest signal of health, mating status of an individual.

Body size: Size is usually a reliable indicator or physiological state of an organism and whether the individual is in possession of "good genes" and strong immune system (Pech-May et al*.,* 2012). In some taxa, the larger size of the females gives them higher fecundity and healthier fast developing offspring (Dixon, 2007; Salavert et al*.,* 2011) while larger males other than the likelihood of having greater quantity of sperms and better ejaculate (Bissoondath and Wiklund, 1996; Avila et al*.,* 2011) are also likely to outcompete other males during any competition designed for their selection as mates (Filin and Ovadia, 2007; Anjos-Duarte et al*.,* 2011). However, there are reports that smaller males perform better in nutrient restricted scenarios (Gotthard et al*.,* 1994; Blanckenhorn, 1998) and are also preferred as mates. Large individuals are also more likely to be parasitized (Zuk and Kolluru, 1998) and attacked upon (Blanckenhorn, 2000). The gain incurred by the adults of both sizes across the taxa is nothing but the outcome of "who fits better with respect to time and space."

A number of studies ranging from mayflies, dragonflies, crickets, beetles, butterflies; moths, etc show the preference of larger male as adults (Crespi, 1988; Brown, 1990a, b; Omkar and Afaq, 2013; Dubey et al., 2016a). However, the choice is not absolute and smaller sized adults are also selected resulting in stabilizing sexual selection (Moore, 1990). Small females are known to utilize more resources in reproduction (Wiley, 1974), breed earlier in case of unreliable and ephemeral food resources (Grant and Grant, 1989). Smaller males mature and breed earlier (Wallace, 1987) and are more likely to succeed in cases of scramble competition or where manipulation and agility are more important than brute strength.

Body colour: Differential colourism usually in the form of melanism is known to confer thermoregulation, UV resistance, desiccation tolerance, resistance to abrasion, advantage during predator attack and are less tolerant to desiccation than typicals (Safranek and Riddiford, 1975; Majerus, 1998). Degree and frequency of melanism displayed is usually governed by genetic and environmental interactions (Wang et al., 2009; Michie et al., 2010, 2011). Non-random morph preference is reported from a large number of insects. However, the preference for a particular morph is dependent on a number of abiotic conditions. In ladybird beetles, melanics are more preferred as mates during colder season, while typicals are preferred during warmer season (Wang et al., 2009; Dubey et al., 2016b). In *Drosophila biarmipes* (author), males bearing an apical dark wing patch achieved higher mating success as compared to males lacking the wing patch (Singh and Chatterjee, 1987).

Age: Increase in age is known to have a negative impact on mating and fertilization success across a large number of insects (Jones et al., 2000; Bonduriansky and Brassil, 2002; Bista and Omkar, 2015). Older parents are also known to produce offspring of poorer quality (Hercus and Hoffmann, 2000).

The preference of females for older males is suggested by the good genes model owing to their higher survival being indicative of good genes (Kokko and Lindstrom, 1996); many insects have supported this model (Hasselquist et al., 1996; Sundberg and Dixon, 1996). However, another model talks about younger males being preferred over older males due to poorer sperm quality and quantity in the latter (Hansen and Price, 1995; Price and Hansen, 1998). Studies in insects have shown age preference in almost all studies; however, the direction of preference is species specific (Jones and Elgar, 2004; Avent et al., 2008; Xu and Wang, 2009; Perez-Staples et al., 2010). Studies show that age affects the degree of choosiness displayed, with older individuals being less choosy (Atwell and Wagner, 2014).

Mating history/pattern: When and with whom mating took place can be a game changer in affecting both direct and indirect fitness. The recency of mating can in the case of females cause lack of fertilizable eggs and even increased chances of sperm competition leading to reduced paternity share. In case of males, the recency of mating may cause reduction in both quantity and quality of ejaculate. However, in certain cases, mated mates are preferred as they indicate vitality and acceptability.

Mate choice in relation to mating history has been reported in several insects. *Tribolium castaneum* (Herbst) males prefer to mate with previously mated females (Arnaud and Haubruge, 1999), while fruit fly females do not prefer previously mated males (Markow et al., 1978; Nakatsuru and Kramer, 1982). Other than these major factors, multiple factors play a role in assessing suitability of mates during precopulatory sexual selection.

POSTCOPULATORY SEXUAL SELECTION

While the phenomenon of pre-copulatory sexual selection is often engaging, enamouring and awe inspiring, there are many mechanisms at play hidden from the naked eye that determine the selection of mates and allocation of paternity share. It is these hidden mechanisms that occur within the female genital tract that mayeither signify male-male competition or female choice, which form post copulatory sexual selection.

Post-copulatory processes are grouped into sperm competition (direct male-male competition) (Eberhard, 2009; Manier et al., 2010) and cryptic female choice (female modulation of paternity share) (Aquiloni and Gherardi, 2008; Eberhard, 2009).

Sperm competition: The competition between sperms of different males to fertilize the ova of female is known as sperm competition. In females with sperm storage organs, an intense selection pressure can be generated which might pave the way for adaptations in males designed to improve paternity share.

Modulation of sperm ejaculate is easiest way to indulge in sperm competition. Male ejaculate expenditure in terms of sperm production and sperm allocation is likely to increase with higher sperm competition risk (Engqvist and Reinhold, 2005; Kelly and Jennions, 2011; Parker et al., 1997). Table 1 shows some examples of various constraints on the male ejaculates of various insects.

For sperm competition to occur, there has to be spatial and temporal overlap amongst ejaculates of multiple males. Studies have revealed various kinds of sperm competition as described below.

Sperm mixing: As the name suggests, sperms of different males are mixed together in the female storage organs rapidly and randomly. The sperms with greater competitive ability are predicted to win the fertilization race (Parker, 1990a, b).

Sperm precedence: This competition involves non-random utilization of sperm of a particular male when multiple males are present. This may be in the form of first male or last male sperm precedence. It can also be short or long term, with the former resulting from slow random mixing and the latter involving (a) Sperm stratification, (b) sperm incapacitation, and (c) sperm displacement. Sperm displacement can be owing to sperm removal or sperm flushing (Saxena et al., 2022).

Several morphological, behavioural and physiological mechanisms have evolved to avoid sperm competition. Primary amongst these mechanisms is mate guarding behaviour. This behaviour involves the guarding of females post copulation till the eggs are fertilized. This may involve prolonged genital contact or carrying the female for a long time after copulation has ended. The former behaviour has been observed in ladybird beetles (Chaudhary and Mishra, 2017) and the latter is very common in dragonflies (Johansson et al., 2009) and *Heliconius* butterflies, where females mate only once, the mate guarding of pupa has been observed, with mating occurring just after eclosion (Estrada and Gilbert, 2010).

Table 1. Some example of major insects with male constraint on ejaculate production (from Saxena et al., 2022)

Species	Constraint	Evidence	Reference
Gryllus veletis, *G.pennsylvanicus,* *Gryllodes sigillatus*	Gut parasites	Decreased spermatophores production	Zuk, 1987
Diploptera punctata	Male age, duration of larval development	Increased sperm number	Woodhead, 1984
Gerris lateralis	Remating interval	Increased sperm number, decreased oviposition stimulation	Arnqvist and Danielsson, 1999
Lucilia cuprina	Multiple matings	Decreased sperm numbersand decreased inhibition of female remating,	Smith et al., 1990
Drosophila melanogaster	Multiple mating	decreased fertility and lifespan	Prowse and Partridge, 1997
Drosophila nigrospiracula	Ectoparasites	Decreased testes mass	Polak, 1998
Plodia interpunctella	Diet Viral infection, Rearing condition	Decreased sperm numbers, fertility and fecundity	Lum and Flaherty, 1970; Gage and Cook, 1994
Pieris rape	Mating	Decreased spermatophore mass	Bissoondath and Wiklund, 1996; Cook and Wedell, 1996
Pieris napi	Mating	Decreased spermatophores mass	Kaitala and Wiklund. 1995; Bissoondath and Wiklund, 1996
Jalmenus evagoras	Mating	Decreased spermatophores mass	Hughes et al., 2000

In many insects, mate guarding via reduction of female receptivity chemically using receptivity or ovulation suppressants in ejaculates or anti-aphrodisiac pheromones is also reported (Fricke et al*.,* 2009).

Other than mate guarding, females can also be prevented from mating with other males either by blocking their genital tract using mating plugs or by completely damaging the female genital tract (Simmons, 2001; Calabrese et al*.,*2008). Table 2 shows examples of different pre- and post-copulatory mate guarding behaviour in different insects.

CRYPTIC FEMALE CHOICE

Cryptic female choice is primarily female choice happening non-apparently. In many cases females have evolved mechanisms to avoid energetically expensive precopulatory sexual selection. Instead of wending off male advances and inspecting and assessing male prowess, females may subject themselves to mating with eager males, and cryptically select the best male sperm within her genital tract.

This is however a very difficult trait to assess experimentally. Studies across taxa have indicated female control over timing and order of insemination (Xu and Wang, 2010). While size of ejaculate falls under the regulatory purview of the males and is part of sperm competition, the acceptance or rejection of the ejaculate falls under the purview of the females, i.e. cryptic female choice. The rejection of the ejaculate can be achieved via improper sperm storage, sperm digestion, ejection, and incapacitation (Saxena et al., 2022).

Table 2. Pre- and Post -copulation mate guarding behaviour in different insects (from Saxena et al., 2022)

Species	Type of mate guarding	Duration	Reference
Locusta migratoria	Pre-copulatory	10 hours	Zhu and Tanaka, 2002
Sphenarium purpurascens Charpentier	Post-copulatory	17 days	Del Castillo, 2003
Anomala albopilosa sakishimana	Pre-copulatory	Highly variable	Arakaki et al*.,* 2004
Papillia japonica	Post-copulatory	<400 minutes	Saeki et al*.,* 2005
Tenebrio molitor	Post-copulatory	Highly variable	Carazo et al*.,*2007; 2012
Hypopnera opacior	Pre-copulatory	<800 minutes	Kureck et al*.,* 2011

CONCLUSIONS

This paper provides a brief introduction about sexual selection in insects. The mechanisms of pre- and post-copulatory sexual selection and the flexibility of these choices based on environmental cues. Sexual selection is responsible for a whole lot of anatomical, physiological and behavioural complexities observed across the insect world. In insects, owing to their massive diversity, it attains a great variety, making these very good models for exploring and understanding the mechanisms of sexual selection.

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