Love Games that Insects Play

The Evolution of Sexual Behaviours in Insects

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Despite several differences, our two great epics Ramayana and Mahabharatha have at least one specific feature in common: the most important ladies of both the epics, Sita and Draupadi, were won by their respective heroes Rama and Arjuna in the contest termed 'Swayamvara'. A significant feature of this process of selecting the groom was that it did not lay restrictions on the wealth and social status of the contestant. In fact, when Arjuna entered the Swayamvara hall he had disguised himself as an ordinary man and was a stranger to the gathering. Yet, this did not in any way disqualify him from contesting and eventually marrying Draupadi. In other words, it appears that Janakaraja and Dhrupada did not bother to ensure the wealth and fame of the grooms-to-be for their daughters!

One wonders if there was any wisdom in such an apparently insecure way of selecting the groom. But the then social system had a different measure of the groom. It obviously valued the physical strength, fighting skill, valour and bravery of an individual more than anything else because these features automatically ensured to the possessor both wealth and fame. He who was valiant was not only likely to gain more wealth, but was also capable of guarding it, as well as his family. Whether or not this indeed was the reason for arranging the contests through 'Swayamvara', its striking similarity to many behaviours related to reproduction seen in insects and other animals is interesting. In fact, females in several species of insects exhibit varied patterns of behaviour (akin to 'Swayamvara') in order to ensure that the males they mate with are indeed physically fit and strong.

'Swayamvara' in Insects

In insects and, for that matter, in other animals as well, individuals

that are physically strong are also generally evolutionarily fit (evolutionary fitness is defined in terms of the number of offspring an individual leaves behind). A strong individual would fetch more food and can also survive better against the odds of nature. For this reason, evolution shaped females such that they give birth to strong offspring. And one sure way by which females can ensure this is by choosing a strong male to mate with. But how does a female ascertain that the male she selects is indeed strong and, therefore, presumably will sire sons that are also strong? Females are known to achieve this by inciting severe competition among males in a manner akin to 'Swayamvara'.

Females of several insect species exhibit various behaviours akin to the ancient 'Swayamvara' in order to ensure that they mate with only relatively stronger and fitter males.

Take the case of the black tipped hanging fly, so named because these predatory insects have black tipped wings and are found hanging upside down on the under surface of plant leaves. The females of this insect, in that position, emit a chemical (a sex pheromone) that can attract males from hundreds of metres away. The males thus attracted approach the females, invariably with a gift held between their forelegs. Generally this gift would be another insect or spider preyed upon exclusively for the purpose of presenting to the female.

But what happens when the male arrives at the female is a drama beyond belief. The female starts examining the gift brought by the male and if it is not appealing to her, she rejects the male and flies away to a different place to attract another male. Often the females even snatch away the prey brought by such unimpressive males before deserting them. On the other hand, if the gift is appealing enough she readily offers her abdomen to the male for copulation and starts eating the prey (*Figure 1*). Throughout the copulating period, the male holds on to the prey in its forelegs such that the female does not run away before he inseminates her. There are situations when, if the female manages to consume the prey much before copulation is over, she withdraws her abdomen, rejects the male and moves away to attract another male. In fact the time for which copulation proceeds, and the amount of sperm transferred, is known to be directly dependent

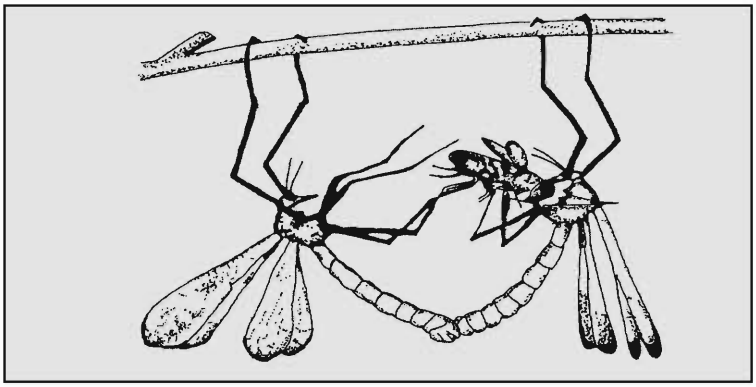

Figure 1. A mating pair of Black Tipped Hanging flies. The female, on the right, is eating the prey given to her as a nuptial gift by the male.

on the size of the prey offered to the female as a nuptial gift (*Figures 2a and b*). Clearly, the size of the prey brought by the male is an important parameter defining its success both in appeasing the female and also in successfully inseminating her. Consequently, only those males that bring relatively larger prey would gain access to a female, sire her offspring and, hence, attain reproductive success; other males down in the rank may suffer evolutionary death (i.e, they may be unable to sire any offspring and thereby do not pass on their genes to the next generation).

It is easy to see that this behaviour of the females creates an indirect yet severe competition among males to present her the biggest prey they can. Randy Thornhill (at University of Michigan), working on these black tipped hanging flies, showed

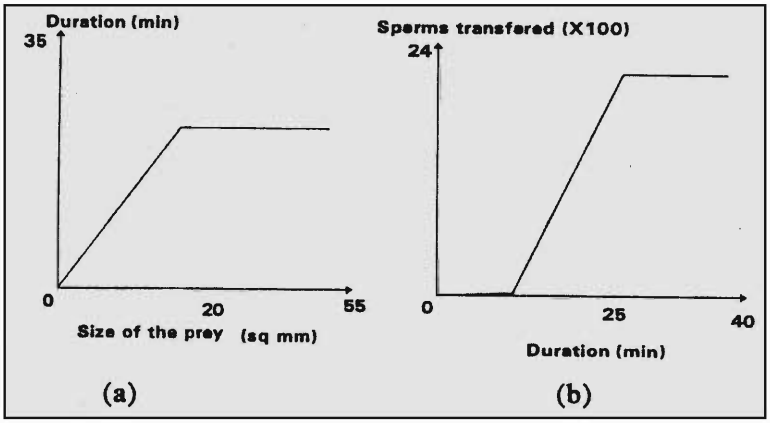

Figure 2. (a) Relation between the size of the prey presented as a nuptial gift and the duration of copulation in Black Tipped Hanging flies. (b) Relation between the duration of copulation and the number of sperms transferred in Beach Tipped Hanging flies.

that the size of the prey the males gather to offer to the females is, on average, larger than what they otherwise collect for their own consumption. Obviously males need to put in extra effort to hunt for these extra-large prey. Thornhill also showed that males need to travel relatively longer distances, quite likely risking their lives as they expose themselves to predators, while searching for such extra-large prey. Thus, the competition among males incited by females is akin to that of Swayamvara and results in females selecting the fittest (in this case fitness correlates with strength and foraging ability) male available to mate with.

Competition among males, incited by females, results in females being able to select the fittest male available to mate with.

Courtship Dance in Insects

Incitation of such male competition by females is a very common feature among insects (and many other animals) and the way males compete are also varied and often weird. The behaviour of males of the common fruit fly (*Drosophila*) is one such interesting case. These are small brown flies frequently found in houses flying around fruit baskets (and waste baskets), as they are generally attracted to rotting fruits. During mating, male flies gather around the female and compete among themselves to occupy the position in front of her. They then start dancing in front of her by vibrating their wings and body in a specific manner. Females evaluate males based on these dances and reject or choose them for mating. Clearly, the males have to be highly skilled and relatively physically stronger in order to win in their struggle with other males in gaining access to a female. Though insects exhibit a grand diversity of this phenomenon of female incited male competition, they all have one common biological basis: females ensure that they mate with a 'fit' male and therefore give birth to relatively 'fit' offspring.

Are the offspring born to females who choose their mating partner following such male competition really more 'fit' that those born to the females who cannot or do not choose? This question has been addressed by several workers in different ways. Among them the study on *Drosophila* flies by Linda

Fitness of offspring born to female fruit flies that exercised mate choice is higher than that of offspring born to females that did not have a chance to choose their mates.

Partridge (at University of Edinburgh) is probably the most celebrated, though not without controversies. Basically, she isolated virgin *Drosophila* females and offered them varied numbers of males. Obviously those females that were offered only one male had no choice and the male they mated with could be either very strong and fit or very weak. On the other hand, females that were offered more males enjoyed the benefit of the competition that ensued between the males and, thus, could mate with the more competent (fit) male. Linda Partridge then raised the offspring born to these two kinds of females in a common competitive background and compared their growth and performance. She found that the growth and survival of the offspring born to females that could exercise their choice on males were always higher (*Figure 3*). In other words, it does pay, in terms of enhanced fitness of offspring, for the female to be choosy while selecting a mate.

Swayamvara and Sexual Selection?

In fact, as early as 1860, Darwin noticed that such competition among males, (called male–male competition) and the selection by the female of the 'best' male (called female choice) could together lead to the evolution of certain traits. He called this process 'sexual selection' (it could well be Indianized as

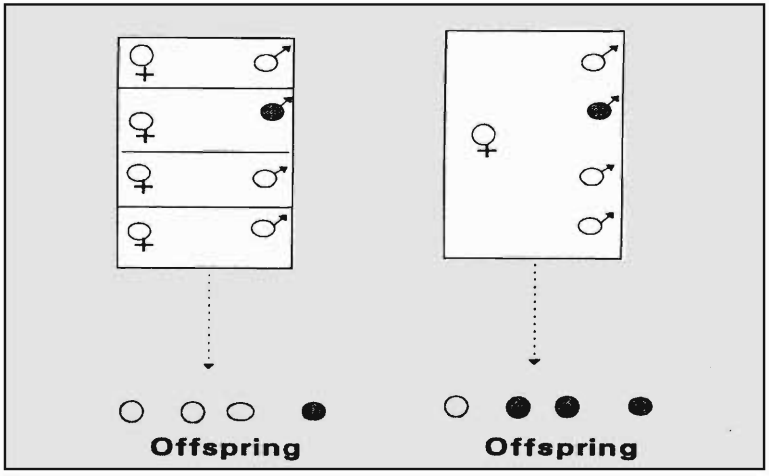

Figure 3. In Drosophila, the offspring born to the females offered randomly chosen single males to mate with were on an average weaker (open circles) compared to those born to females offered a set of males from among whom they could potentially choose a mate. This suggests that females do choose stronger males as mates.

Swayamvara) and suggested that it constituted an alternative form of natural selection. Natural selection typically explains how some traits that facilitate the survival of an individual in a particular environment become more common over generations because they help the bearer to leave behind more offspring. But it does not explain the evolution of some bizarre and maladaptive traits that are exclusive to only one sex. For example, males of some beetles develop long horns on their head which are either absent or less prominent in females. The horns of rhinoceros beetles – the black coloured, large almond sized beetles that are attracted to the light sources during the rainy season– are the best examples of such sexually dimorphic features. West Eberhardt from the Smithsonian Institute has worked extensively on these beetles and has shown that these horns are prominent in males and are used in bouts of combat with other males of the same species (*Figure 4*).

Some sex specific features do not seem to confer any survival advantage to the individuals that bear them.

Such sex specific features do not seem to confer any survival advantage to the individuals that bear them. In fact producing these bizarre features should be costly for the bearers in terms of energy invested in producing and maintaining them. Moreover, females without these features are equally capable of surviving as well as males; in certain situations (eg the bright coloured wings of male butterflies of some species), these features may even expose the bearer to predators. Darwin suggested that the extra cost to the males, owing to these sex specific features, is

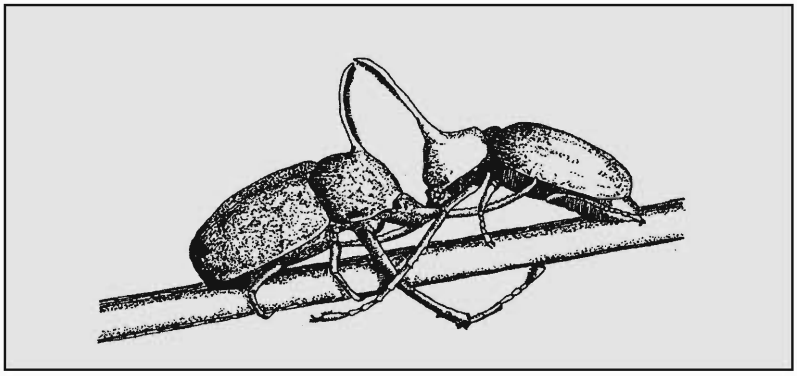

Figure 4. Male scarabs beetles (Golofa porteri) using their horns in competitive combat.

more than compensated for by the reproductive advantage they gain in terms of successfully gaining access to females for mating. Males endowed with relatively strong, well developed horns, for instance, defeat other males in the competition for females and thus enjoy greater success in reproduction. Consequently, they leave behind more sons that have strong horns; such competition can be expected to occur generation after generation, with selection favouring any genetic change that leads to the enhancement of the sex specific traits in males. However such indefinite 'run away' selection towards more and more or showy, gigantic features is not often observed because, after attaining a critical level, the cost of such enhanced traits may not be compensated for by the advantage to the male in gaining access to females.

Reproductive behaviours of males that enhance the likelihood of producing larger number of offspring often cost them their lives.

The Cost of Love

The love games insects play often cost them their lives. In one species of fire-fly, males are attracted by a specific pattern of light flashes produced by the females. A predatory insect copying this pattern lures and traps the males and thus attracts and eats them up. Death also strikes courting males in several other ways. Praying mantids are a group of insects, so called because these predatory insects sit waiting for their prey with folded forelegs looking as if they are praying. Mating in these insects often follows a long course of courtship and, during mating, the female starts devouring the copulating male as if it was eating any other prey. Eventually, she completely consumes the male. Surprisingly, the victims do not resist in the least this cannibalism by the females. In fact, it has been argued that, evolutionarily speaking, males are selected to concede themselves and not resist because the food or the energy thus gained by their female partners would help the latter to build up greater food reserves in eggs, thus benefiting offspring sired by the male. Indeed, scientists argue that, in an evolutionary sense, this is exactly the role of the males: to mate and fertilize as many eggs as possible, and to invest or contribute some resources to their offspring.

Once this is achieved, the male has no reason, evolutionarily speaking, to live, in that further life would not add to its fitness. The investment by the male in the offspring can be in any kind and form. In primitive human societies, males fetched food for the family by hunting. In black tipped hanging flies, they search out the food and present it to the females, whereas in the praying mantis they themselves serve as food for the females. In all these situations, the life of males is at risk to different degrees. In humans they might lose their life while hunting; in flies they risk being predated upon while searching for extra-large prey, and in the case of the praying mantis, their life is directly sacrificed for the sake of their progeny.

The Odd Lives of Males in Some Insects

The evolutionary role of males is to mate and fertilize as many eggs as possible and to invest or contribute some resources to their offspring.

In their role as mere fertilizers of the eggs of females (as described above), the life of males can be shaped by natural selection in weird ways. In one species of mite, *Acarophenax tribolii*, the impregnated mother attaches to its host, generally the egg of another small insect such as a thrip. The eggs inside the mother hatch, and the hatching larvae start devouring the mother. The mother sucks food from the host egg while her offspring eat her from within. Within a couple of days, the adults develop within her body and one among them is generally a male. He mates with all his sisters and dies within the mother's body. The mated females emerge out of their mother who is by now nothing but a carcass and a pool of dried exo-skeleton of the larval stages and faeces of her offspring. Thus the male in this species is never 'born' in some sense, but does his evolutionary job in the quickest and simplest way possible without ever leaving his mother's body.

There are several species of insects that are similarly destined, not to see the light of the day. In fig trees, the flowers are borne on the inner surface of the wall of a closed inflorescence which we call the fig fruit. Tiny females of certain wasp species that are known to pollinate these flowers enter the figs through a one

way channel called ostiole and pollinate some of the flowers with the pollen grains brought by them from another fig from where they have emerged. A proportion of the flowers in the new fig have eggs laid into them by these females and from them emerge the male and female offspring. The males that emerge mate with their sisters emerging in the same fig and die after boring an exit hole for their sisters. These sisters carry the pollen grains and enter another fig thus repeating the cycle. In the whole process, the males of the wasps have evolved just to fertilize their sisters and die. In fact, because males accomplish no other function than fertilizing their sisters, mothers economize even in producing them; males are produced almost always wingless and their numbers are as few as one per several hundred sisters that develop in each fig. Energy thus saved by the mothers is expended on producing more daughters to enhance her reproductive success.

While these are exceptional cases where a single male can inseminate a whole band of females, males in certain other insect species are at the other extreme. They invest considerably in guarding the chastity of their female partners. Once again, the parallels with human behaviour are interesting. In fact, excepting a few tribes, the human male, in general, insists that his female partner maintain loyalty to him. One wonders why this obsession with female fidelity has been such a prevalent feature or taboo in human societies through the ages. Scientists have found similar taboos in animals and offer adaptive reasons for this behaviour.

Ensuring Fidelity in Insects

Dragon flies and damsel flies are a group of insects that are generally found along small water pools and water bodies on rocky surfaces. Males of these species occupy and guard territories which are well defined areas in and around the water bodies. In fact, males invest a lot of energy and time in guarding these territories because the size and quality of such territories reflects the kind of food available to them. The females choose a male

based on the quality and the size of the territory he holds because this ensures an assured high quality food supply for herself and her offspring who are to be brought up in this territory. Besides, it also increases the likelihood that the sons born to her would be strong as well, guarding high quality territories in future for their own survival.

Male beetles incited for male–male competition ejaculate more sperm than other males not exposed to such competition.

Thus, males in dragon - and damsel - flies gain the females only after a lot of investment in guarding the territory. Therefore, in case the female later on mates with another male, it would mean a "reproductive loss" for the first male. Hence, males in some of these species ensure that this does not happen. Immediately following copulation, they seal up the reproductive opening of the females such that no other male can inseminate them later. This insect equivalent of the medieval "chastity belt" ensures that they are the sole contributors to the sperm pool to fertilize the eggs of the female with which they mate. The adaptive basis of such vaginal sealing seems merely the Darwinian argument that selection favours those traits, that increase the number of surviving offspring born to the bearer of the trait. A male who seals his mate's reproductive opening ensures that all the offspring born to her are sired only by him. A female mated by the male that does not seal may be mated again by different males and hence his sperm might face competition from those of other males. Thus the sealing tendency of males gets selected because it increases the chances of him leaving behind more offspring with similar sealing tendency than those males who do not seal. But if this be the argument, then males should also be able to evolve mechanisms to break this chastity lock, at least in principle. Indeed, in some species, males do break this chastity lock and scoop out the sperm of an earlier male and replace them with their own.

The common motive underlying diverse mating behaviours of males is to attain the evolutionarily important goal of maximising the number of their offspring.

That these 'sperm wars' of males are indeed a consequence of their competition to sire as many offspring as possible is evident from an interesting study in a group of teneubrid beetles. A group of scientists allowed females to be mated with two kinds of

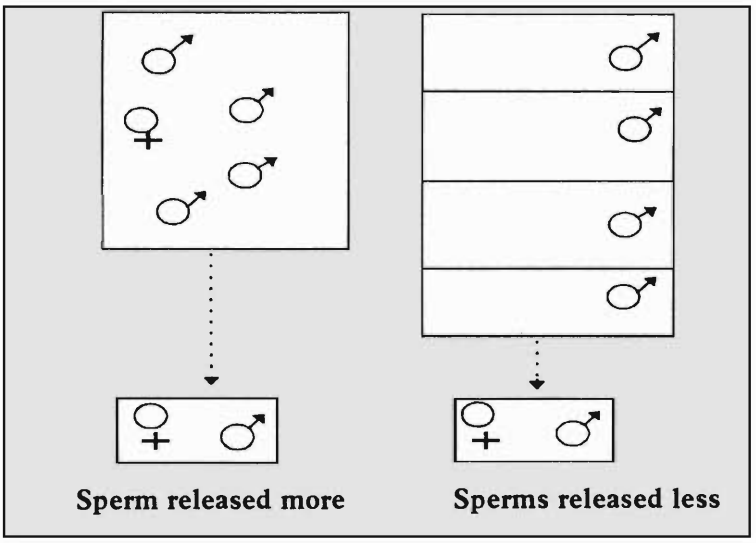

Figure 5. Sperm production in males of certain beetles changes in response to the extent of competition they experience. Those subjected to intense competition among males produce more sperm than those subjected to less competition.

males: those that had been exposed to other males and were therefore incited for severe male–male competition, and those that were isolated from other males and hence not been incited. The scientists then measured the number of sperm contributed to the female by these two kinds of males following mating. They found that the males incited for competition ejaculated three times more sperm than those who were not exposed to competition (*Figure* 5). How these insects adjust the amount of sperm released in response to the presence or absence of another male is yet to be understood.

Our understanding of the diversity of the mating systems and reproductive behaviours in the insect world has just begun. As more and more of the systems are investigated, we are exposed to an unbelievable spectrum of strategies that these tiny creatures employ, some of them even beyond our imagination. But it is satisfying to note that there is one common motive underlying this puzzling diversity of the love games they play, namely to achieve the evolutionarily meaningful goal of multiplying their own progeny.

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