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Sexual Selection

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ABSTRACT: Selection in evolution of sexual features, including sexual behaviour, has been referred to as sexual selection, of which three modes are: (a) Sperm Competition, (b) Cryptic Female Choice, and (c) Sexual Conflict. Examples of the three modes have been included. Difference between sexual selection and natural selection has been made out, but it has been inferred that it is difficult to draw a firm line between the two types of selection. West-Eberhard's concept of social selection, evolution of female ornaments, and mechanism of exaggerated development of male ornaments and weaponry have been briefly reviewed.

Keywords: sexual conflict; social selection; sperm competition

INTRODUCTION

Selection, involving sexual features, including sexual behaviour, has been referred to as sexual selection. As has been pointed out by Padian and Horner (2010), the phenomenon was given this name by Charles Darwin. Sexual selection is Darwinian selection among sexual traits; but this statement may cause some confusion. Generally by Darwinian selection is meant Natural Selection. While, as is the common impression, Natural Selection leads to taxonomic diversity, sexual selection operates within the limits of a population or a species. However, this difference between the two sorts of selection, is not a firm one, as in some cases sexual selection too may result in speciation in sympatry (Mank. 2009; Kraaijeveld et al., 2011).

Among the various definitions of sexual selection, the most comprehensive is the one suggested by Emlen and Oring (1977), who say that sexual selection is concerned with evolution of "the ability of a portion of a population to control the access of others to potential mates". As Wenninger and Averill (2006) have pointed out, evidences, pointing to the role of sexual selection in shaping sexual features, are "mounting". These authors have mentioned three modes of sexual selection, viz.:

(i) Sperm competition, i.e. sperms, received from different males, compete in the female genital tract to fertilize eggs.

(ii) Cryptic female choice, i.e. the female accepting or rejecting the sperms from a particular male.

(iii) Sexual conflict, i.e. conflict between sexes over control of reproduction. An instance of sexual conflict is, for example when a female shows resistance to the male attempting to achieve intromission.

SPERM COMPETITION

Recently some well planned and well executed studies on sperm competition have been published. Fisher and Hoekstra (2010) have noted cooperation among sperms of the same or similar origin to achieve precedence in effecting fertilization. They have experimented with the deer mice (*Peromyscus maniculatus*). A female of this species is highly promiscuous, mating with several males in a very short period, a few minutes. As a result sperms of different males are simultaneously present in the female genital tract. These sperms form aggregates, either by heads of a number of sperms getting glued together, or by the head of a sperm joining the middle piece of another sperm, and several sperms, joining in a series this way, form a train-like aggregate (Fig. 1). Such aggregates have the advantage of swimming with greater velocity to reach an ovum than single sperms.

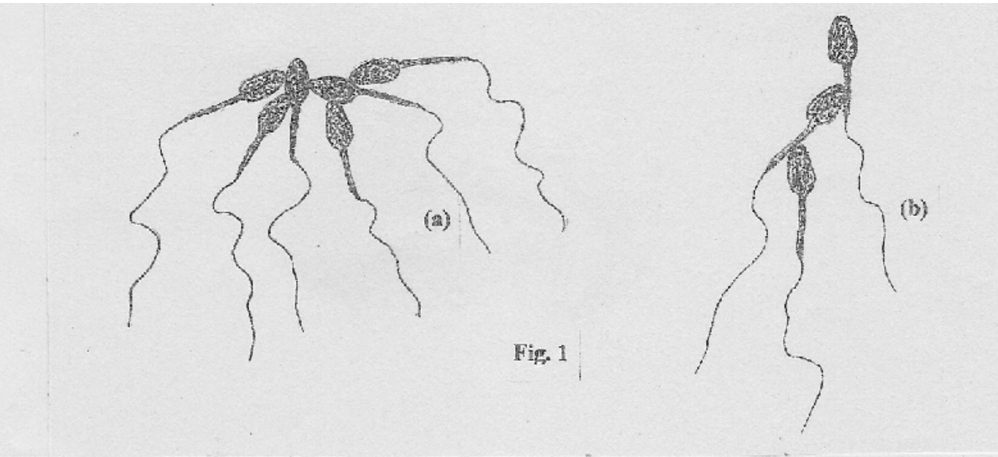

Fig. 1

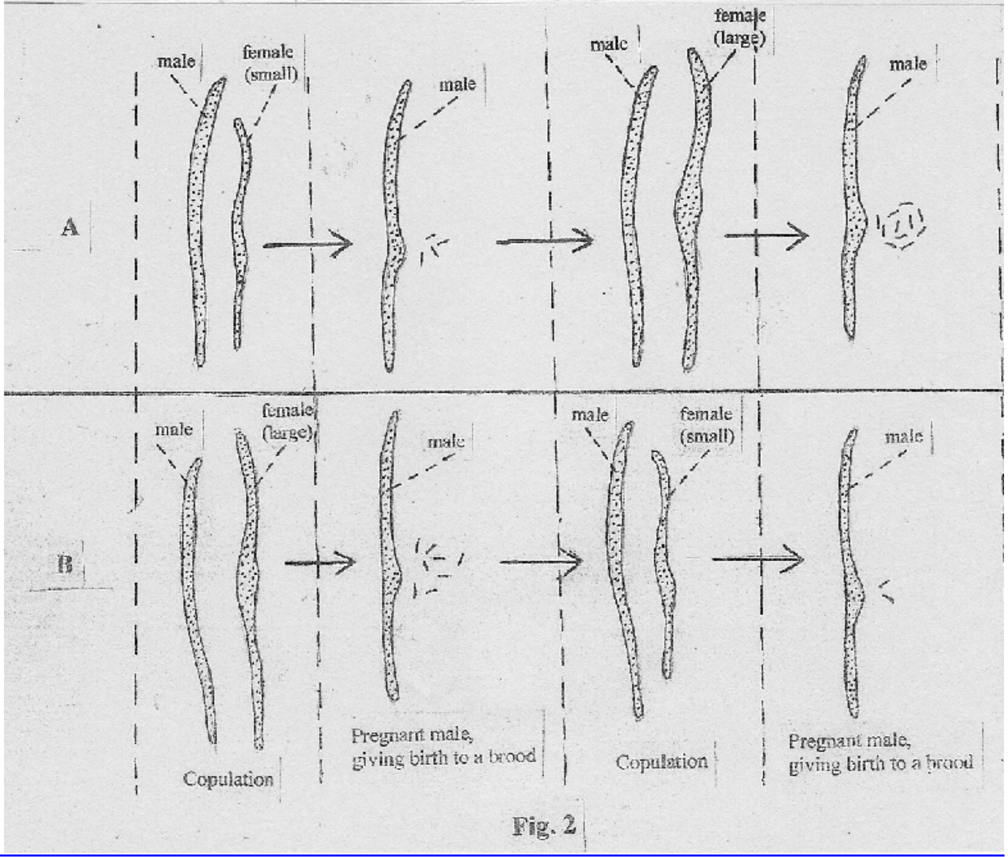

Fig. 2

Fig. 1 – Cooperative aggregate formation by sperms of similar origin in deer mice in the female genital tract..

[(a) Aggregate formation by heads of several sperms getting glued.

(b) Head of a sperm gets glued to the middle piece of another, and in this way a chain like aggregate is formed. (The figure is based on description and photographs in Fisher and Hoekstra, 2010)]

Fig. 2 – Diagram to illustrate a subtle sexual conflict in the pipe fish *Syngnathus scovelli.* (Based on observations of Paczolt and Jones, 2010).
[**A** – A male, copulating with a small bodied female, receives only a small brood, as the small female has transferred only a small number of eggs to the brood pouch of the male. Next the male copulates with a large female. As during the previous pregnancy there has been only a small energy input for rearing a small brood, the male has more energy to invest in the current pregnancy; hence a large brood is delivered, larger than what it could have delivered, if the previous mating were with a large female.
B – A male, mating with a large female, delivers a fairly large brood. Next it may mate with a small female. Due to a large energy investment in rearing the brood resulting from the previous mating, the male has available only a small amount of energy for the next brood. Moreover, the energy starved male, during development of the second brood, may absorb some nutrients from the developing embryos in its brood pouch; as a result there may be some "filial annibalism", and only a tiny brood may eventually be delivered. Thus in either situation (A or B) small females are negatively Selected.]

Fisher and Hoekstra (*loc. cit.*) have studied sperm behaviour in interspecific matings by bringing together *in vitro* live sperms, obtained from *P. maniculatus* male and those from male of another species of *Peromyscus* , *P. polionotus*. The sperms from the two species had been dyed with different fluorescent markers. Among the aggregates, formed by the sperms, in 83% aggregates sperms of both the species were present, but most aggregates were constituted by significantly more conspecific sperms. In intraspecific matings, with some conspecific sibling/littermate males, it was noted that a greater proportion of sperms from the same male/litter group aggregated together. From such observations the authors have inferred that the sperms were able to recognize relatives and that genetically similar sperms have the tendency of grouping in the aggregate formation

This cooperation strategy has the advantage of genetically similar sperms moving faster to reach an egg. But out of the sperms in an aggregate only one is able to fertilize the egg, while other sperms in the group may undergo premature acrosome reaction , and thus get wasted. The sperm, successfully fertilizing the egg, gets the advantage of positive selection (direct fitness), and other sperms in the group, with the same genetic constitution, get the advantage of aiding a genetically related sperm passing its genome to the next generation (indirect fitness).

In another species of *Peromyscus*, *P. polionotus* the female is strictly monoandrous. But in this species too there is tendency of sperm aggregate formation in the female genital tract. The significance of sperm grouping in this case, as per Fisher and Hoekstra (*loc. cit.*), is to make the sperms move faster in a "potentially hostile female tract".

Parker (1998) has inferred, on basis of theoretical considerations, that males achieve fertilization in proportion to the number of sperms in their ejaculate. Simmons et al. (2007) have interpreted their results on basis of this principle. They have studied 16 species of the scarabaeid *Onthophagus* with dimorphic males. The two male morphs are: (i) 'major males' or 'guards', which are large bodied and provided with weapon-like sclerotic growths for fighting rival males and for guarding their females, and (ii) 'minor males' or 'sneakers', which are small bodied, without the 'weapons', and which sneak copulation with females , while the females are being guarded by major males. It has been noted by the authors that sneakers have bigger testes than guards. This difference in testis size has been ascribed to resource allocation trade off. As a major male develops into a large body with offensive/defensive devices, it has only a small resource availability for sexual development, while a minor male, with its small body and lack of 'weapons', can afford more resource use for development of sex organs. Presumably the larger testis size of the sneakers enables a larger ejaculate with higher sperm count, and thus gets a selective advantage over major males. These presumptions need to be supported by empirical studies.

The selective advantage to the minor males should lead the *Onthophagus* species, with dimorphic males, to evolve towards having monomorphic males, i.e. with all males 'minors' or 'sneakers'. Agreeing with this suggestion is the situation that *Onthophagus taurus* populations in western Australia and those in North America show genetic divergence. The *O. taurus* populations in western Australia have high density, and those in N. America are low density populations. Coupled with his fact is that west Australian populations have a significantly higher proportion of sneakers than N. American populations.

den Boer et al. (2010) have studied sperm survival in some eusocial insects. They have chosen two species of bees and three species of fungus growing ants. In all eusocial insects the queen mates early in life, soon after eclosion, and then has a life time supply of sperms stored in her spermatheca. Among the species chosen, two (*Bombus terrestris*, a bumble bee, and *Trachymyrmex zeteki,* an ant) with the queen monoandrous, i.e. mating with a single male, while three species (*Apis mellifera, Atta colombica,* and *Acromyrmex echinatior*, the last two leaf cutting ants) are polyandrous, i.e. the queen mates with several males in a quick succession. The authors have assayed in these species sperm survival in ejaculates under different conditions *in vitro*. The main inferences, arrived at by the authors in these studies:

(1) The male AG (= accessory gland secretion), present in the ejaculate, has the effect of reducing the level of survival of the sperms from another male, already present in the queen's genital tract in a polyandrous species, but has no such effect in a monoandrous species.
(2) The AG secretion, from a brother or an unrelated male, has no differential effect on sperm survival.
(3) AG secretion contains compounds, which are favourable for survival of sperms from the same male, and may contain also compounds which "incapacitate sperm of competing males".

den Boer et al. (*loc. cit.*) have collected some virgin queens of *Atta colombica*, which were artificially inseminated. They removed fresh sperms from the testis of the donor male, and mixed them with AG secretion from the same male. Such treated sperms showed a high level of survival. But, when the sperms were mixed with AG secretion of an alien male, the survival value of the sperms was significantly reduced. If, however the alien AG secretion was mixed with the spermathecal secretion of the artificially inseminated female, the sperm survival was almost as high as when mixed with the AG secretion of the sperm donor male.

In brief, as per the findings of den Boer (*loc. cit.*), in a polyandrous queen of an eusocial insect species, after mating , the AG secretion , received with the ejaculate, tends to incapacitate the sperms from an alien male, but her spermathecal secretion tends to counter this effect of the AG secretion, seemingly to ensure a life time supply of sperms.

Pennisi (2010), studying movement of red and green fluorescent sperms, from two different males, in the female genital tract of a fruit fly, has also recorded competition from the sperms from the two donors for reaching an ovum.

Pizzari (2010) has also pointed out that, as noted in recent researches, related sperms form a cooperative team in their run for the egg.

SEXUAL CONFLICT

There is a recent review on sexual conflict by Bonduriansky (2009). The author says that the first mention of sexual conflict is in Bateman (1948), who has pointed out that among sexually reproducing organisms nearly always there is undiscriminating eagerness in males and "discriminating passivity" in females. In the later half of the last century empirical evidences, supporting the notion of sexual conflict between eager males and resisting females appeared in good numbers. Formally the concept of sexual conflict was launched by Parker (1979), based on his observations on mating behaviour in dung flies. Typically in sexual conflict an eager male, trying to achieve intromission, may force copulation with a resisting female, and in this 'he' may cause harassment and even injury to the female. The forced mating may reduce life expectancy and life-time fecundity in the female. Hence sexual conflict is expected to be weak and even lacking in monogamous species, and may be seen in species, the males of which or both the sexes of which mate with multiple partners. Sexual conflict may lead to "antagonistic coevolution" of those morphological/behavioural features, which in the male help in holding on to the female firmly and in forcing intromission, and which in females help resisting the male's efforts for a forced mating. This may set what may be called an "arms race" between the two sexes.

Though empirical observations keep on accumulating, our understanding of evolutionary implications of sexual conflict is far from adequate (Bonduriansky, 2009).

As has been said above, sexual conflict is obvious when a female is resisting a male aiming at a forced mating. But in some cases sexual conflict is a subtle phenomenon. Cited here are two examples of subtle sexual conflict among non-arthropods. Similar observations among insects are needed, as that may help us in appreciating their evolutionary significance.

A subtle case of sexual conflict has been studied by Paczolt and Jones (2010). They have made observations on male pregnancy in *Syngnathus scovelli*, a pipe fish, belonging to the family Syngnathidae, the family of pipe fishes and sea horses. In many members of this family copulation is followed by eggs being deposited in a brood pouch, developing on the abdomen of the male. The brood pouch is not just a bag for holding developing eggs, but plays the role of a uterus in viviparity. The eggs develop in the brood pouch for several weeks, and the pouch provides "aeration, protection, osmoregulation, and nutrition". Recent studies have shown that nutrients move both from the father to the developing brood and from the brood to the father. Referring to the work of Sagebakken et al. (2009), Paczolt and Jones (*loc. cit.*) point out that amino acids, formed in the developing eggs, pass through the walls of the brood pouch to be incorporated in the liver and muscles of the father.

Some of the observations, made by Paczolt and Jones (*loc. cit*.) on *Syngnathus scovelli* are:

(i) Embryo survivorship in a current male pregnancy is negatively related to the survivorship in the prior pregnancy. Thus there is energy trade-off between the two broods.

(ii) Males prefer to mate with larger females. Male's reluctance time to mate is significantly shorter for a larger female.

(iii) The number of eggs, transferred to the male brood pouch, is significantly larger during mating with a larger female.

(iv) If a mating is with a smaller female, only a small brood has to be reared by the male; hence energy investment is small. In the rearing of the next brood the male may invest more energy. On the other hand, if after mating with a large female, the next copulation is with a smaller female, after the prior copulation so much energy has been invested in rearing a large brood that in the following mating there will be paucity of energy and the smaller female's offer of a reduced brood size will suffer from energy need in the brooding male, as a result of which there may be absorption of nutrients from the developing embryos, and this may be resulting in "infanticide or filial cannibalism". Thus smaller females are discriminated against or negatively selected both in the pre- and in the post-copulatory phases (Fig. 2). In the pre-copulatory phase because of the smaller female's capacity to deliver only a small number of eggs during copulation, and in post-copulatory phase because of energy expenditure by the male in brood rearing following the previous copulation, specially if the previous copulation has been with a larger female. Thus a subtle sexual conflict is going on in this fish.

Ryan et al. (2010) have studied mating calls in the tungara frogs (*Physalaemus pustulosus*), and have noted that the mating sound signal, emitted by males, may be a simple whine or a whine ornamented with other sounds (whine chucks). Through experiments, using recorded conspecific, heterospecific, predator produced and human made sounds, the authors have inferred that females of the species show a strong preference for ornamented whines or whine chucks to simple whines, and that males are evolving towards production of ornamented whines as mating calls.

Yet another example of sexual conflict is sexual cannibalism by female known in some spiders. Female spiders are polyandrous, which tendency is countered by the mating male by taking to mate guarding, genital mutilation, or by application of a mating plug. In some highly sexually cannibalistic species the mating plug is provided by the intromittent 'palpal' organ, getting severed from the male body and left in the copulatory position beneath the epigynum of the female. The palpal organ is an appendage carried on the tarsus of the pedipalp. It represents a modified tarsal claw (Marshall & Williams, 1972), which has become adapted to sperm storage and intromission. The organ is differentiated into a basal 'bulb' and a distal spine-like 'embolus' (Fig. 3) The bulb is hollow, and stores sperms, and its cavity continues as a fine lumen into the embolus, ending in an opening at its tip. The male deposits sperms on a special part of the web, from where the sperms get sucked into the bulb. During copulation the embolus enters the vagina, and delivers sperms into it. From the vagina the sperms move into the spermathecae (Marshall & Williams, 1972).

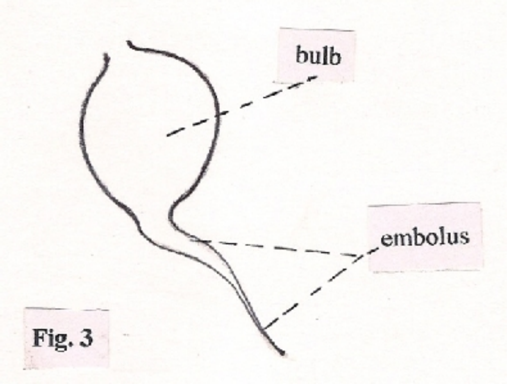

Fig. 3. Palpal organ of a spider.
(Based on a figure in Marshall and Williams, 1972)

In some highly sexually cannibalistic spider species, as has been said above, during copulation the palpal organ gets detached from the male, and remains in the copulatory position in the female. Li et al. (2012) have observed that sperm transfer from the detached palpal organ into the female genital tract continues in the spider *Nephilengys malabarensi.* In fact they have noted that the sperm transfer is faster from the severed intromittent organ than when it was a part of the male body. This sperm transfer after detachment of the palpal organ has been referred to by Li et al. (loc. cit.) as “remote copulation”. In this the detached palpal organ acts both as a mating plug and as a means to improve the quantity of sperms transferred, though the male in this act sacrifices its own reproductive capacity.

Perry and Rowe (2012) have comparatively studied intraspecific divergence in the copulatory apparatus of the water strider *Gerris incognitus*, and also mating behaviour in this species. In a male of this insect the genital apparatus include a grasping mechanism to grasp a resisting female, while in the female there are abdominal structures to help in warding off an approaching male. The armaments, involved, show considerable variation in the extent of exaggeration. If the armaments in the female are large in size, the frequency of successful mating is low. But, if a male has large armaments, successful mating depends upon which mating partner has relatively larger armaments. From this study the authors have inferred sexually antagonistic coevolution going on in this species.

Judson (2010), in her recent popular article, says, <…the traits that make a “good” male are often different from those that make a “good” female (….talking about “good” in evolutionary terms. That means a trait that improves your chance of having surviving offspring) ….and this is the source of tension…>

CRYPTIC FEMALE CHOICE

During copulation the female may obstruct insemination by contracting some muscles in her genital complex, so that intromission is incomplete or sperms fail to enter the spermatheca, or the female may emit sperm droplets through her genital pore. The rejection or acceptance of the male in copula has been referred to as ‘cryptic female choice’ (Eberhard, 1996). An illustrative example of cryptic female choice is in the work of Rodriguez et al. (2004). These authors have studied the flagellar length and the length of the spermathecal duct in 56 Neotropical leaf beetle species belonging to the subfamily Cassidinae. They have noted a high correlation between the length of the two genital tubes among the species. The authors have experimentally studied the sperm transfer role of the flagellum in the cassidine species *Chelymorpha alternans*. In this species the average length of the spermathecal duct is 5.9 +/- 1.2 mm, and the average flagellum length 21.45 +/- 2.67 mm, the latter more than three times the average body length. The hinder part of the median ejaculatory duct extends into the flagellum, which gets inserted into the spermathecal duct during copulation, and helps depositing a spermatophore close to the spermathecal capsule. The flagellum length varies significantly in the three colour morphs of *Chelymorpha alternans*. When Rodriguez et al. (*loc. cit.*) arranged matings with virgin females, it was noted that, if the male in copula has a long flagellum, either no or only a few sperm droplets were emitted through female genital opening during the copulation, but, if the male was with a shorter flagellum, sperm emission was more. The sperm emission was found negatively correlated with the number of sperms getting stored in the spermatheca.

Rodriguez et al. (2004) arranged copulation with virgin females also with males with flagellum artificially shortened, and observed that the sperm emission by the female was more and sperm storage in the spermatheca was less as compared to mating with an unoperated male.

SPECIATION THROUGH SEXUAL SELECTION

Mank (2009), referring to the study by Varn Doon et al. (2009) (not cited under “References” in this review), have pointed to the occurrence of “sympatric speciation via condition-dependent sexual selection”.

Kraaijeveld et al. (2011) have tested the hypothesis, that sexual selection contributes to speciation, by extensively reviewing the published data for different groups, and have statistically and phylogenetically analyzed the data. They have inferred :

(1) that there is a small but significantly positive support for the hypothesis; and
(2) that the frequency of the correlation between sexual selection and speciation varies considerably among different taxa, e.g. :
    (a) Among the available data for birds in 38 studies, 24 showed positive correlation,
    (b) Among the available data for insects in 6 studies, in 4 studies the hypothesis was supported, and
    (c) Among 14 studies on mammals, none was found supportive.

From these studies it may be inferred that in some cases sexual selection may result in speciation.

SOCIAL SELECTION

West-Eberhard (1983) formulated the theory of social selection, which refers to differential success in social interactions. Among social interactions is included the sexual process. In the original description it has been clarified by the author that sexual selection is a part of social selection. Thus social selection includes ‘sexual social selection’ and ‘non-sexual social selection’; the two components may overlap.

The advantage of social selection concept is that it has a broad coverage of the social or group living phenomenon, including pre-mating and post-mating behaviour.

The significance of considering sexual selection as a component of social selection has been pointed out by Tobias et al. (2012), Rubenstein (2012) Lyon and Montgomerie (2012), and Roughgarden (2012). Pizzari and Gardner (2012) suggest a sociobiology approach to problems of sexual interactions; this suggestion comes close to social selection.

MECHANISM OF EXAGGERATED DEVELOPMENT OF SEXUAL ORNAMENTS AND WEAPONS IN THE MALE

Studies on the rhinoceros beetle, the male of which has a long and apically bifurcated horn, have shown that males with bigger horns succeed in access to the female (Meeting briefs, 2012).

Emlen et al. (2012), from their studies, have inferred that exaggerated development of the male horns and other ornaments is due to increased cellular sensitivity of the rudiments of these structures to insulin and insulin-like growth factor (IGP). This situation has obviously resulted from selection in favour of increasing cellular sensitivity to these hormonal factors in the developing male weapons and ornaments.

Emlen et al. (*loc. cit*.) further point out that increasing level of secretion of these hormonal factors affect growth of other organs, in addition to that of sexual ornaments and weapons, including mating signal producing structures. Thus the hormones provide several ranges of variation for selection, including sexual selection.

Besides IGP, another hormone, involved in growth of sexual ornaments and weaponry in insects is JH (Juvenile Hormone), as inferred by Gotoh et al. (2011), which groups has included Emlen. Gotoh et al. (*loc. cit.*) have experimentally studied the development and growth of the extremely long mandibles in the male of the stag beetle, *Cyclommatus metallifer*. They have found that the extent of the growth is proportional to the amount of JH made available (through application of JH analog) to the last larva and the prepupa.

It may be added that JH is known to have a role in inducing polyphenism in insects (Verma, 2007).

ORIGIN OF FEMALE ORNAMENTAL FEATURES

Ornaments and weaponry in males have been briefly referred to as ornaments by Tobias et al. (2012). Females too may too have such ornamental features. A prevalent view is that males have such structures to fight and drive away rival males. How have females evolved such structures? Tobias et al. (*loc. cit.*) have pointed out three possible answers to this question:

(i) About half of the genome in a female is similar to that in a conspecific male. Due to this genetic correlation females may also have ornamental traits.

(ii) Like males, females may also compete for a mate.

(iii) Females strongly compete among them for ecological resources.

Tobias et al. (*loc. cit.*) say that each of these possibilities has theoretical and empirical support.

HYPOALLOMETRY OF INSECT MALE GENTALIA

Insect male external genitalia present rich structural details, which are remarkably uniform within a species, presenting only a small range of variation. Reviews on the hypoallometry have been done by Verma (2008, 2011).

In the 2011 review it has been said that to attribute evolution of the hypoallometry to sexual selection does not appear reasonable, and that Natural Selection can explain it. But the hypoallometry in a species differs considerably from that in a related species; hence it should have evolved in the evolutionary history of the species. Thus evolution of the hypoallometry shares one point of resemblance with sexual selection, which happens within the limits of a population or a species, as has been said under the section “Introduction” of this review.

Rowe and Amqvist (2011) have comparatively and quantitatively studied many genitalic and non-genitalic traits in a clade of 15 water strider species. From their quantitative approach in this study they find a support for the hypothesis that sexual selection is involved in the evolution of the complexity in the genital traits.

It may be added here that female genitalic features too show low intrapopulation variability (Eberhard, 2008).

CONCLUDING REMARKS

From the foregoing account it may be inferred that Natural Selection and Sexual Selection are two modes of the Darwinian Selection, but it is difficult to draw a firm line of distinction separating the two modes.

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