

OBAFEMI AWOLOWO UNIVERSITY, ILE-IFE, NIGERIA.

Inaugural Lecture series 247.

ESSENCE OF INSECT PROMISCUITY

By

Wasiu Adesola Muse.

Professor of Insect Physiology and Biology



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**An Inaugural Lecture Delivered at Oduduwa Hall,
Obafemi Awolowo University, Ile-Ife, Nigeria
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Preamble

Mr. Vice Chancellor Sir, the topic of my Inaugural lecture titled "*Essence of Insect Promiscuity*" was chosen to present a discourse on paternity in insects. Mating in insects is synonymous to sex in human and if I have come up with a topic such as *Sexiology in Insects*, many of my colleagues would have felt offended because, for humans, sex is not a topic to be discussed in a gathering like this.

I started my Entomology career under Professor R. A. Balogun who supervised my Undergraduate and Masters degree projects in the area of Digestive physiology. He also supervised my Doctorate degree programme on an aspect of Insect Reproduction. I was able to pursue the study under Prof. Balogun, then Head of Zoology Department former Dean of Faculty of Science when I was appointed an Assistant Lecturer in the Department. I settled down for a successful career in this great University. The commitment of Prof. Balogun and myself was a thing of joy and that was what the academic environment was up till 1995. In the Obafemi Awolowo University, we have been grappling with how we can achieve the objectives of pre-1995 years when there was adequate funding and equipment to undertake meaningful research in Insect Physiology and Biology.

The Insect

Despite the remarkable diversity of form and habit, insect possesses several common features by which the group as a whole can be distinguished. They are generally small arthropods whose bodies are divisible into cephalic, thoracic and abdominal regions (Gillott, 1991).

The study of insect biology contributes to our knowledge of biology and physiology of other animals and humans. Some insects are easy to maintain in the laboratory as their short life cycles make them excellent subjects for research and teaching.

There are 26 orders of insects with up to 10 million species which translates to over 400 trillion insects at any point in time,

interacting with a world population of about seven (7) billion. Insects are found in gardens, schools and offices, in the jungles, desert, caves and bodies of water. They can also be found in the frigid North and South poles and the highest mountain tops. (www.entsoc.org/-20k). Insects are the largest group of animals in the world and have been in existence before man.

Insects are the chief competitors with man for domination of this planet. They destroy man's growing crops and defoliate his forests. They are responsible for the spread of nearly all the great epidemic fevers of the tropics and subtropics, and for infection of his livestock with some of their most fatal diseases. The structural timber of his buildings are weakened and destroyed by insect attack. His household goods are ravaged by moths and beetles and a heavy toll is levied on his stored reserves of food and grains (Wigglesworth, 1976). Insects, like other terrestrial animals, have to solve the major problems in connection with their reproductive biology, such as the bringing together of sperm and egg in the absence of surrounding water and the provision of a suitable watery environment in which embryo develops.

Mr. Vice Chancellor Sir, the main focus of this lecture is on reproductive tactics that have led to enormous multiplication of insects. However, without availability of food, mating can never be achieved.

The immediate activity of most insect species, post adult eclosion, is feeding. This is absolutely necessary for the organism to develop body parts, including its reproductive organs used for mating when sexually mature. Ingested food is digested and absorbed in the mid-gut (Fig. 1) which is endowed with structural characteristics that enable the region secretes various enzymes for the breakdown of macromolecules. Carbohydrate digesting enzymes such as lactase, fructase, mellibiase, sucrase and invertase were reported in the midgut of the cockroach, *Periplaneta americana* (Muse 1979, unpublished). The midgut extract of the bluish-green blowfly, *Chrysomya chloropyga* assayed at pH 3-11 and at temperatures 35^o, 45^o and 55^oC was shown to have optimum

activity at pH of 5 and 8 and at 40⁰C with the presence of trypsin and chymotrypsin (Muse and Balogun, 1986).

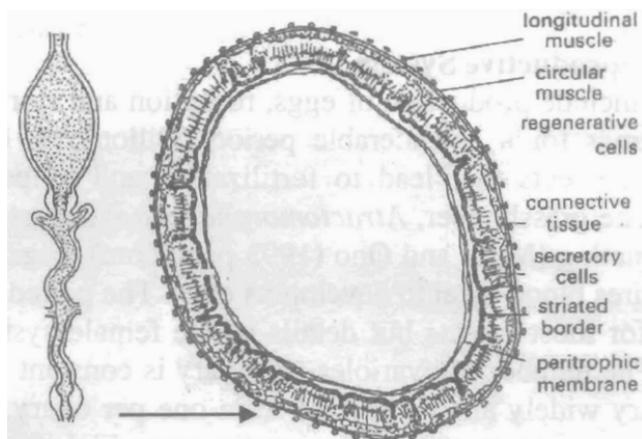


Fig. 1. Insect gut and the Transverse section of the midgut of the grasshopper, *Chorthippus brunneus* (Chapman, 1969; Wigglesworth, 1974)

The food ingested, digested and finally absorbed by insects is utilized in various ways, such as the development of the reproductive organs of several species of insects. The secretion accumulated in the accessory gland lumen of the male reproductive system contain several important amino acids, such as proline, glycine, glutamic acid and serine (Muse and Balogun, 1992), sugars, such as galactose, fructose, cellobiose, trehalose, and lactose (Muse and Balogun, 1993) and proteins (Muse, 1993). Among the amino acids detected, proline was the most quantitatively important. Proline is a non-essential amino acid synthesized by plant-feeding insects. It is essential for optimal growth when there is a good mixture of it in diet. It is present in

the flight muscles and also provides energy and motility for sperm (Aueswald *et al.*, 1998).

The Female Reproductive System

The functions include production of eggs, reception and storage of sperm, sometimes for a considerable period (Gillott, 1991) and coordination of events that lead to fertilization and oviposition (egg laying). The grasshopper, *Atractomorpha lata* will mature its eggs without mating (Muse and Ono (1993 pers. com) (Fig.2), but mosquito requires blood meal to develop its eggs. The paired ovary is a constant for most insects but details of the female system in insects vary. The number of ovarioles per ovary is constant within species but vary widely among species from one per ovary in the dung beetle to more than 2000 per ovary in some higher termite queen (Richards and Davies, 1977).



Fig. 2. Female system of *A. lata* (Muse and Ono, 1994 unpublished)

The Male Reproductive System

The male system of *Atractomorpha lata* (Muse, 2002) (Fig.3) and of most species of insects functions in the production, storage and finally, delivery of sperm to the female. In the pyrgomorphid grasshopper, the male system of *Zonocerus variegatus* produces

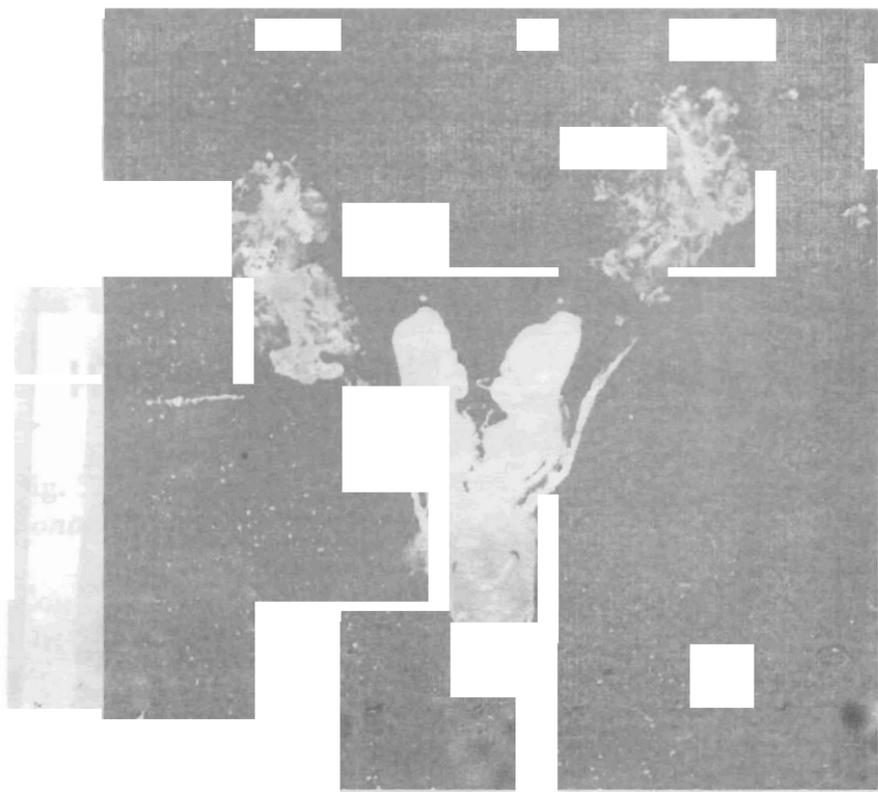


Fig.3. Light micrograph of male reproductive system of *A. lata* (Muse, 2002)

substance transferred during copulation that regulate female receptivity or fecundity (Gahan, 1902). It also supplies nutrients which can be incorporated in eggs for females. The male attention on

the sexual maturation in males compared to females insects has to some extent been attended to in my research endeavour. During sexual maturation in males, events such as synthesis and accumulation of accessory gland secretions for use in spermatophore or seminal fluid formation often occur. For instance, the male accessory glands of *Z. variegatus* become active with maturation and increase greatly in size as a result of synthesis and accumulation of materials (Figs. 4 and 5) (Muse and Balogun, 1991).

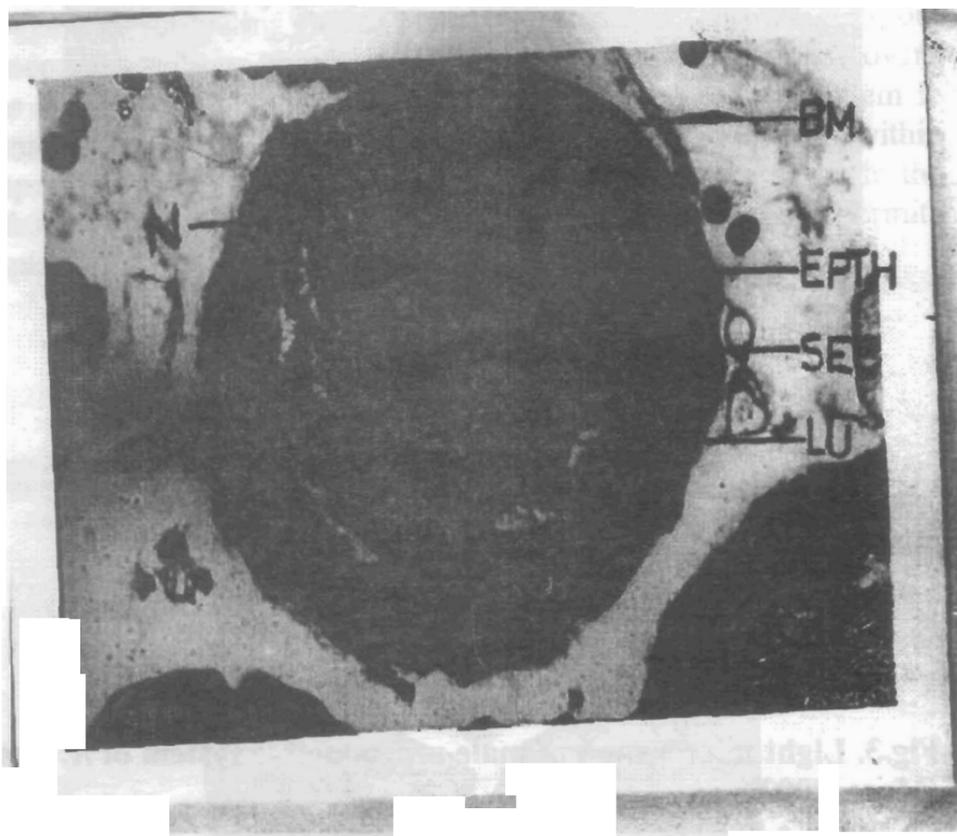


Fig. 4. Cross-section of an accessory reproductive gland of 14-day-old male *Zonocerus variegatus*

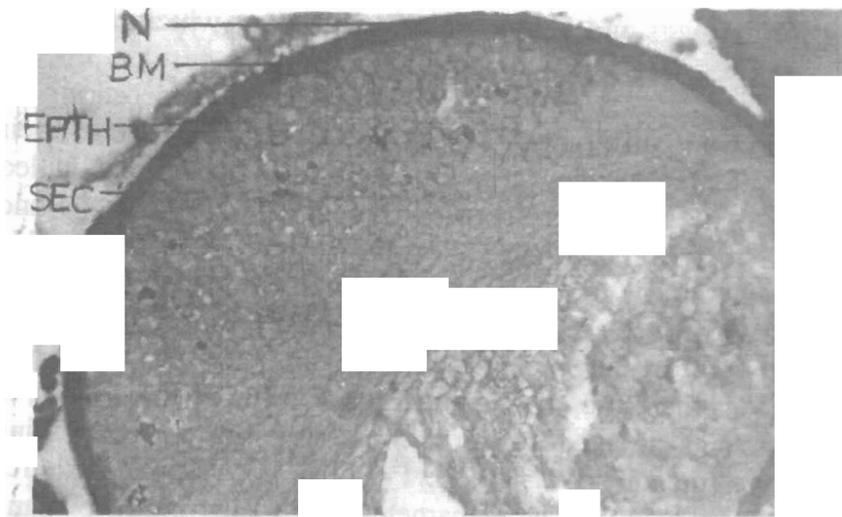


Fig. 5. Cross-section of an accessory gland of 42-day-old male *Zonocerus variegatus*

Courtship

The development and maturation of eggs and sperm in the reproductive organs often lead to commencement of courtship, which is a harmonious venture in which male and female cooperated to propagate their respective genes. There is no such cooperation in the Praying mantis because the female eats the male during mating, but generally, courtship serves common interest to male and female, particularly to synchronize the sexual arousal of the sexes and to establish the pair bond (Krebs and Davies, 1993). But during courtship, there are conflicts of interest between male and female. They form an uneasy alliance, as each attempt to maximize its own success at propagating genes. They cooperated

because both pass on their genes via the same progeny. But the choice of mating partner, provisioning of the zygote with food and caring for the eggs and young are all issues over which the sexes may disagree. The sexual conflict normally results in the exploitation by one sex of the other than to mutual cooperation.

The basic difference between the sexes is the size of their gametes. Female produces large immobile food-rich gamete called egg while male gamete or sperm is tiny, nutritionless, motile and consisting of little more than a piece of self-propelled DNA. This is the common pattern in sexually reproducing multicellular animals (Parker *et al.*, 1972). Females generally put most of their reproductive effort into parental effort while males put theirs into mating effort, therefore, male courtship and mating behaviour is, to a large extent, directed towards competing for and exploiting female investment (Trivers,1972). Females are a scarce resource since they produce few large gametes and males produce many small ones. Females are generally more selective than males during courtship. They often select males on the basis of material resources they can offer and perhaps sometimes to obtain genetic benefits for their offspring.

Food is a resource which often limits female's capacity to produce eggs and during courtship, females may choose whether or not to mate with a male on the basis of his ability to provide food. Female hanging flies, *Hylobittacus apicalis* (Mecoptera: Bittacidae) will mate with a male only if he provides a large insect for her to eat during copulation (Fig. 6). The larger the insect, the longer the male is allowed to copulate and the more eggs he fertilizes (Thornhill, 1976).

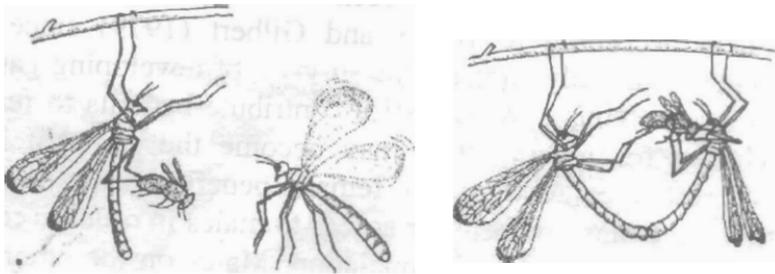


Fig. 6. Female hanging flies *Hylobitacus apicalis* mate with males longer if male brings a larger prey item to eat during copulation (Thornhill, 1976).

Reproductive Effort

Reproductive effort, as part of mate-guarding activities is, according to Williams (1966), the organism's total available energy that is used in reproduction and can be subdivided into mating and parental efforts.

- Mating effort is the component of reproductive effort expended in attempts to acquire mates.
- Parental effort is the sum of parental investments in offspring made by the individual.

A typical male provides nothing to a female and his progeny other than his sperm, although the nutritionless gene carriers are themselves a form of mating effort because the properties of sperm have evolved in the context of the rate to fertilize eggs. The male's time and energy are devoted to searching for or calling in females, fighting with other males for possession of sites likely to contain females and defending their actual or potential partners against rivals. All these activities are **energetically** demanding and also expose the actor to risk of death from exhaustion, predation or injuries sustained in male-to-male combat (Krebs and Davies, 1993).

Mating presents have been viewed as male parental investment according to Boggs and Gilbert (1979) since they potentially or actually enhance the survival of developing gametes carried by the female. When males contribute benefits to females in exchange for mating, they may become the sex that is the limiting resource. Also, when female benefits from the male donation, they may compete for access to males in order to receive the resource associated with copulation. Males on the other hand may become somewhat discriminating in an attempt to secure the greatest genetic return for their gifts by mating with relatively fecund females.

Mate choice and nuptial gifts

Some male species often provide their mates a material benefit, such as food or parental care in return for copulation. The females translate the gifts into fitness benefit for themselves, particularly increase in number and size of eggs. They prefer males whose offerings are better than average, creating sexual selection in favour of generous males. Males of black-tipped hanging flies *Hylobitacus apicalis* (Mecoptera: Bittacidae) handing over unpalatable ladybird beetles are quickly rejected. Even if the food item is edible and copulation begins, the duration of mating is dependent on the size of the prey. If the gift is small and the meal lasts less than 5 minutes, a female will leave without having accepted a single sperm; however, the female will depart with a full complement of the gift-giver's sperm, if the meal lasts up to 20 minutes (Thornhill, 1980) (Fig. 7).

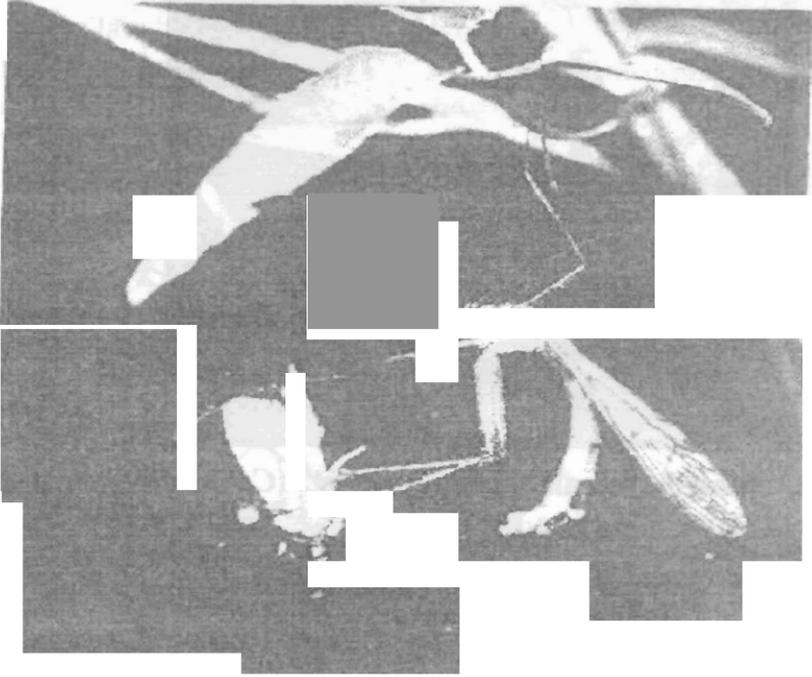


Fig. 7. Male *Hylobittacus australis* hanging from vegetation while holding a dead moth as a nuptial present for a female (*Hylobittacus apicalis* behaves similarly) (Thornhill, 1980).

Male bush cricket, *Conocephalus nigropleurum* transfers sperm along with an enormous spermatophore to their mate, which eats the nutritious spermatophore after sperm transfer is completed. The spermatophore constitutes 27% of the male's body mass and therefore cannot quickly produce new ones, making it difficult for a male to mate more than once in his lifetime (Figs. 8 and 9) (Gwynne, 1982).

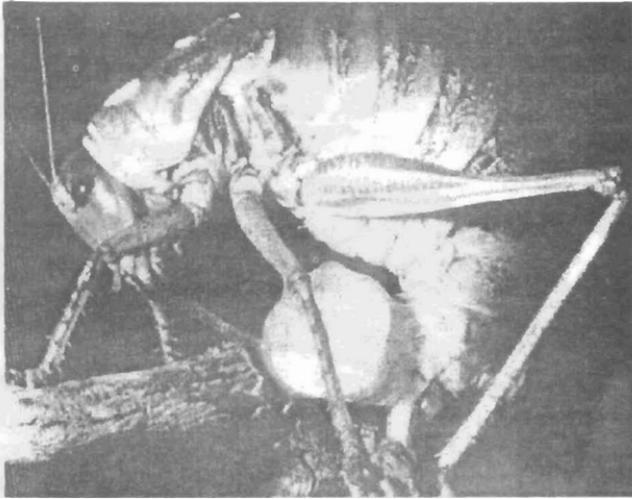


Fig. 8. Mated female bush cricket, *Conocephalus* with spermatophore (Gwynne,1982)

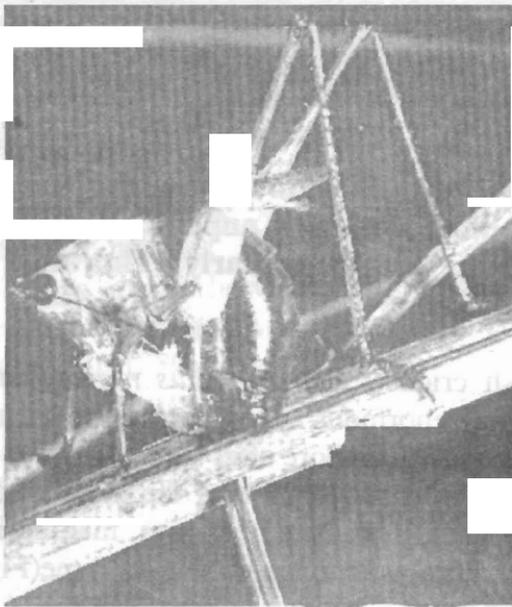


Fig. 9. Mated female bush cricket, *Conocephalus* eating spermatophore (Gwynne, 1982)

Females generally prefer males with larger prey as mating partners over males with small prey, since this affects the number of eggs laid by females and survivorship as well (Thornhill,1980).

In the lygaeid bug (Fig. 10), the sequence of nuptial giving, according to Carayon (1964) is shown below:

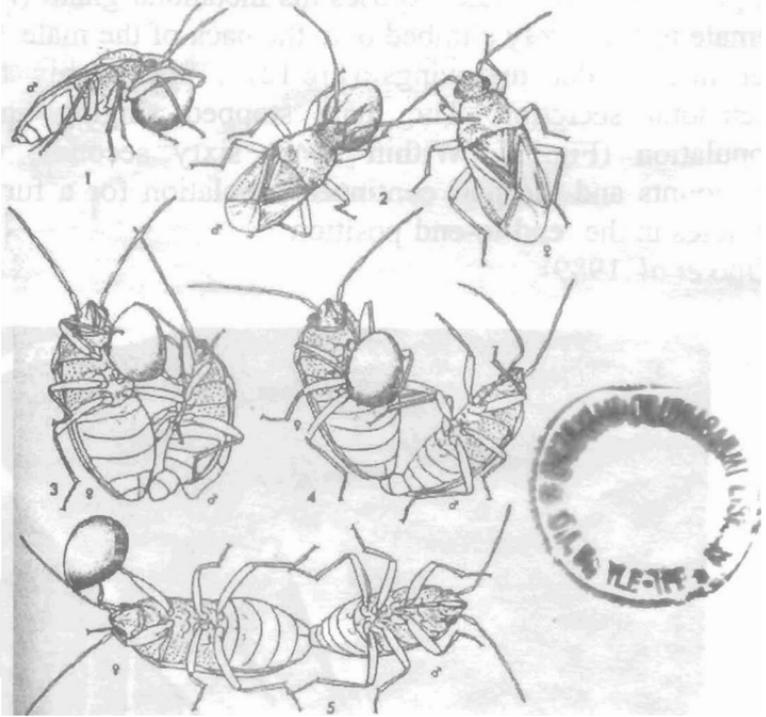


Fig. 10. Nuptial gift giving by the lygaeid bug. (1) male collects seed (2) pre-digests it (3) transfer seed to his partner (4) and (5) female permits copulation while she consumes the gift.

Some males may also have better genes than others. Females could therefore improve the success of her progeny by choosing males with good genes. This was proved by Partridge (1980) in his *Drosophila* experiment. He showed that females are able to increase the survival of their offspring by choosing good

genes in their mates or from a male that has been superior competitor against other males.

Under natural condition, males of the tree cricket *Truljalia hibernonis* (Orthoptera) begins singing from a variety of tree species from sunset to midnight. After attracting a female to a singing perch, the male exposes his metanotal gland (Fig.11). The female immediately climbed onto the back of the male. She pushed her head under his wings (Fig.12) , presumably to feed on metanotal secretion. The male stopped singing and initiated copulation (Fig.13). Within about sixty seconds, the female dismounts and the pair continues copulation for a further twelve minutes in the 'end-to-end' position (Ono *et al.*,1989).

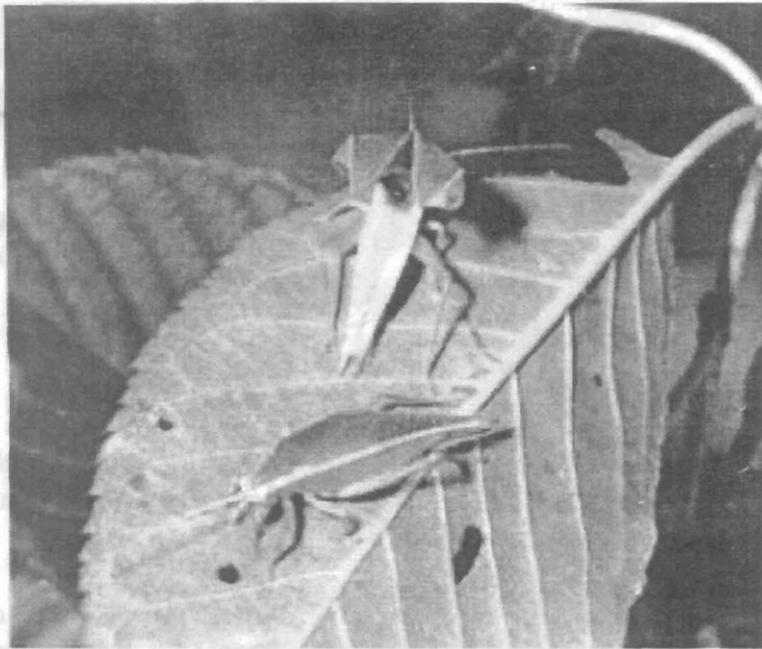


Fig. 11. Male *Truljalia* exposes metanotal gland to attract female (Ono *et al.*,1989).

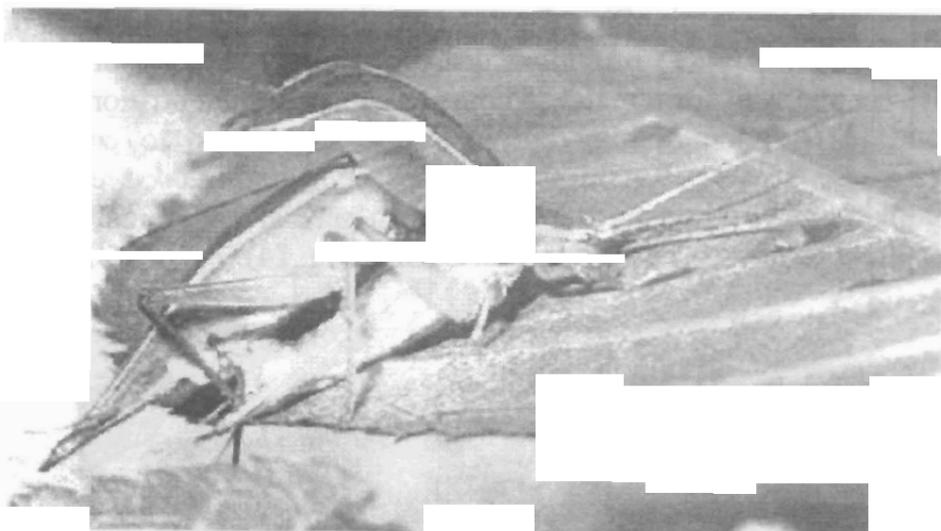


Fig. 12. Female feeds on metanotal secretion while male initiates copulation (Ono *et al.*,1989).

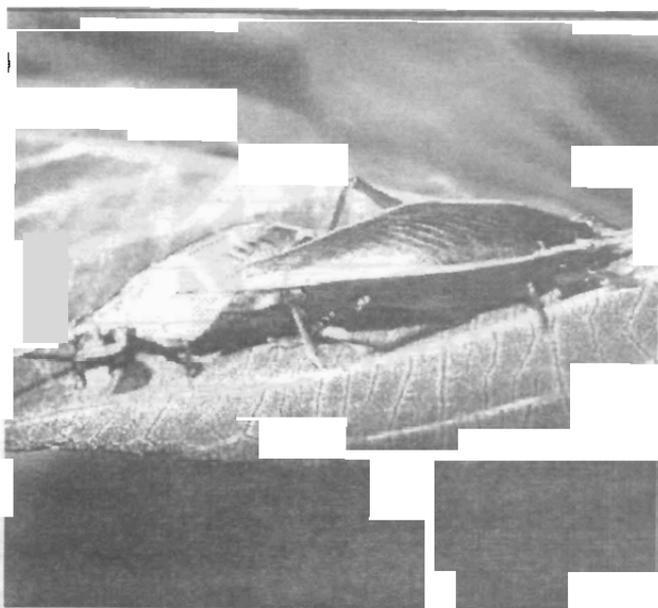


Fig. 13. Cotinuous mating in end-to-end position (Ono *et al.*, 1989).

Male scorpionflies, *Panorpa* exhibit three different ways of acquiring mates (1) providing dead insects (2) secrete saliva on leaves and wait for females to come to consume the nutritional gift and (3) provide nothing but instead force female to copulate (Alcock, 1993). Male scorpionflies, *Parnopa banksi* enforce copulation by grasping the female with special abdominal organ without offering a gift (Thornhill, 1980b) (Fig. 14).

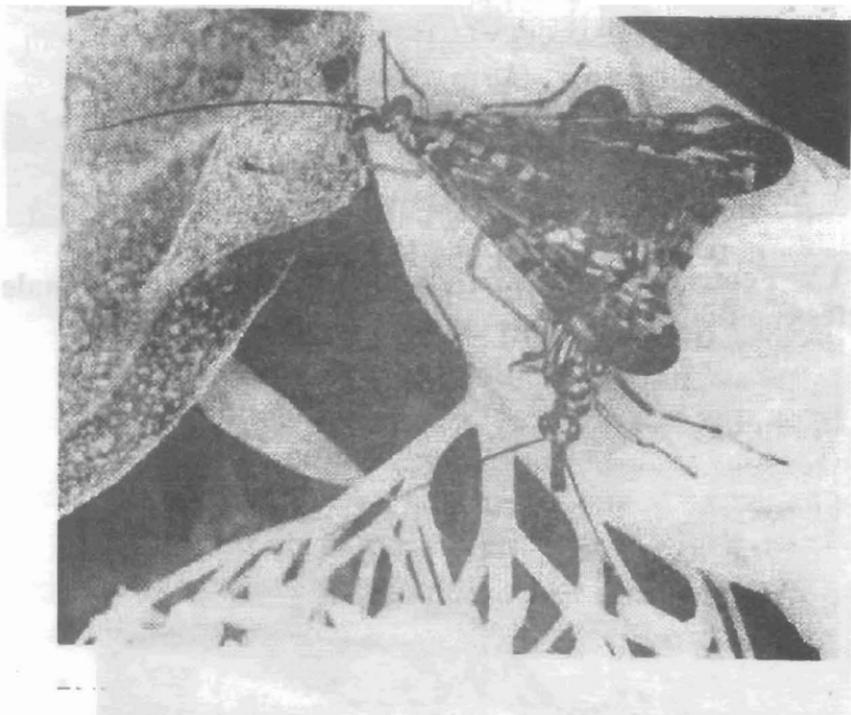


Fig. 14. Forced copulation in *Parnopa* scorpionflies (Thornhill, 1980b)

In enforced copulation, the female loses because she obtains no food for her eggs and has to search for food herself. For

example, in the pyrgomorphid grasshopper,

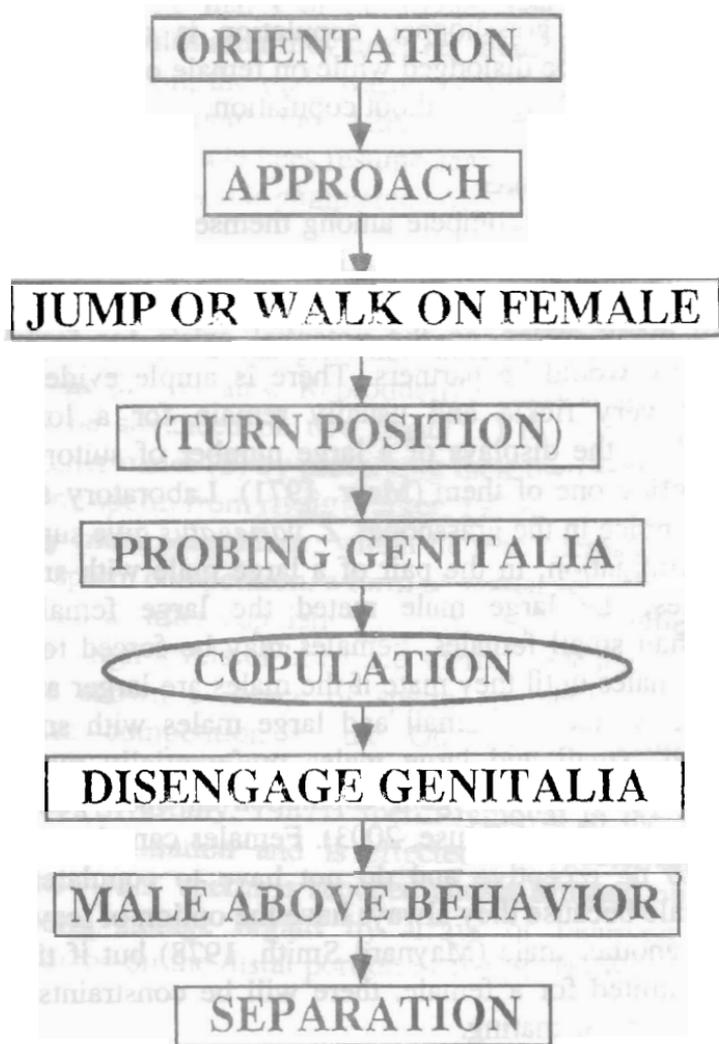


Fig. 15. Pattern of forced copulation in the grasshoppers, *A. lata* and *Z. variegatus* (Muse and Ono, 1996 ; Muse, 2003).

Z. variegatus, which I used extensively for my research, the period between mounting and copulation was 27.5 ± 3.67 min. (Muse, 2003) (Fig.15) and 5.9 ± 7.1 min. in *A. lata*. (Muse and Ono, 1996). In both species of grasshopper, copulation is not guaranteed because males may be dislodged while on female or probing of the genitalia may be prolonged without copulation.

Evidence of female choice

Males typically compete among themselves for possession of females because male reproductive success is limited by the number of eggs an individual fertilizes. Females are usually courted by many males, so the potential exists for females to choose among would be partners. There is ample evidence that females are very fickle and usually remain for a long time unimpressed by the displays of a large number of suitors before finally accepting one of them (Mayr, 1971). Laboratory studies of female choice in the grasshopper, *Z. variegatus* give support for female discrimination. In the pair of a large male with small and large females, the large male mated the large female more frequently than small females. Females may be forced to remain with certain males until they mate if the males are larger and more powerful. In the pairs of small and large males with small and large females, small and large males preferentially mate large females. Small males that gain copulation in such pairing are referred to as 'sneakers' (Muse, 2003). Females can choose where and when to be receptive and do not have to copulate with a particular male because they always have the option of leaving and looking for another male (Maynard Smith, 1978) but if time and energy are limited for a female, there will be constraints on her freedom to postpone mating.

Males are generally more strongly motivated than females to copulate. Males actively search for females in competition with other males and are prepared to copulate instantly should the opportunity arises. Males of the digger bee *Centris pallida* and the love bug, *Plecia nearctica* are typical male insects in their

eagerness to copulate. In both species, males, not females expend hours of time and considerable energy in flight, searching for potential mates. The males of the digger bee energetically dig down to reach females after they discover them. Having uncovered and captured a virgin, the male wastes no time in grasping her to begin courtship and copulation. After one mating, females are no longer receptive, but male bees resume search for additional mates as soon as one copulation is completed (Alcock *et al.*, 1976)

Sperm competition and mate guarding

The donation of benefits by the males to the females, including sperm and nuptial gifts demands that male guard their investments in the females. Reproductive success of individual males could be advanced on two fronts (1) by inseminating the partners of other males (2) by preventing their own sexual partners from acquiring sperm from rivals (Parker, 1970).

Many male adaptations, which help to increase paternity, results from sperm competition, a form of sexual selection that acts during, as well as after copulation (Parker, 1970). Studies which have revealed high levels of last-male sperm precedence in insect species have shown evidence of sperm competition (Gwynne, 1984). Sperm competition in the Odonata (Dragonflies and Damselflies) has resulted in the evolution of sperm removal (Waage, 1979; SivaJothy, 1987). Sperm removal in the Odonata occurs during copulation and is effected by specialized penis structure. The rivals' sperm is scooped and/or brushed out of the female's sperm storage organs by arrays of recurved spines, bristles and barbs on the distal portion of the penis (Waage, 1986) (Fig.16).

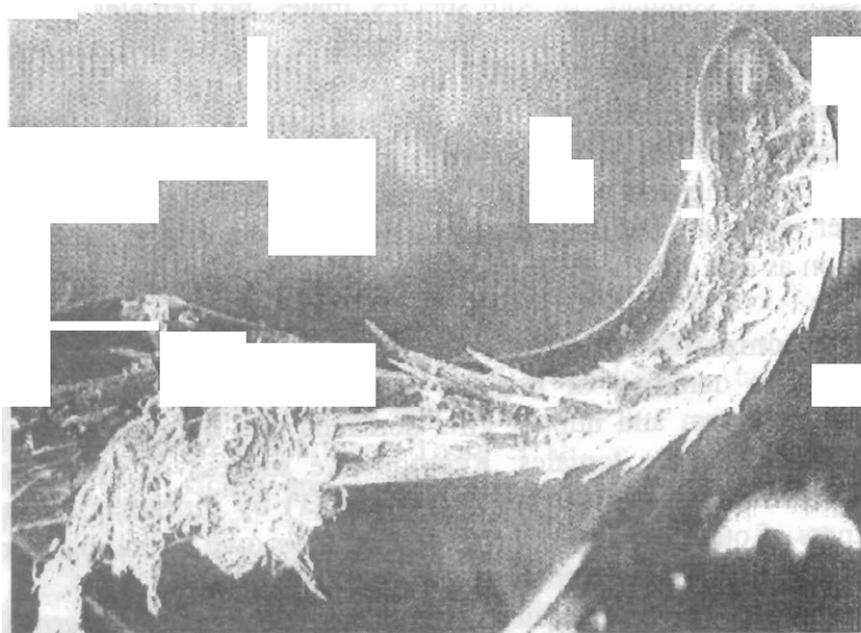


Fig. 16. Scooped sperm on the spiny penis of *Calopteryx maculata* (Waage,1979).

Multiple mating by male and female tree cricket and delayed fertilization results in high levels of sperm competition (Ono *et al.*, 1989). In the same paper, they proposed that sperm flushing in the tree cricket, *Truljalia hibinonis* occur as the copulating male introduces sperm directly into the anterior of the female's sperm storage. As the sperm fills up the sperm storage organ, rival's semen is displaced onto the copulating male's penis, which adheres to it because of its viscosity, and is removed on the genitalia at the end of copulation.

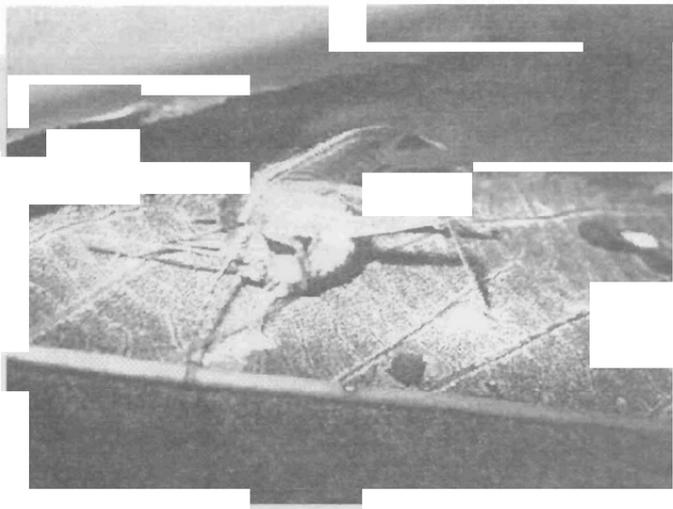


Fig. 17. Male post-copulatory oro-genital grooming in the tree cricket *T. hibinonis*.(Ono *et al.*, 1980).

The removed semen is ingested during post-copulatory oro-genital grooming (Gwynne, 1977) (Fig. 17) and may serve to recoup some of the mating effort males invest in females (Low, 1978). After multiple mating, the last male to mate in the desert locust, *Schistocerca gregaria* gains 99% of fertilization (Hunter and Jones, 1960). In *Locusta migratoria*, the last male fertilizes 88% of eggs after copulation. Parker and Smith (1975) proposed that this was achieved by a direct flushing out of previous sperm from the female's tube-like spermatheca.

The females of the black-winged damselfly, *Calopteryx maculata* often voluntarily mate with more than one male (Fig. 18) (Waage, 1973). When an egg-laden female flies down toward a stream to oviposit, she may be intercepted by a non-territorial satellite(sneaker) male waiting in streamside vegetation. But usually, male damselfly assumes contact guarding with his mate following copulation. The male stays in tandem with her while she lays her eggs, by clasping her thorax with the tip of his abdomen (Fig.19) (Alcock,1993).

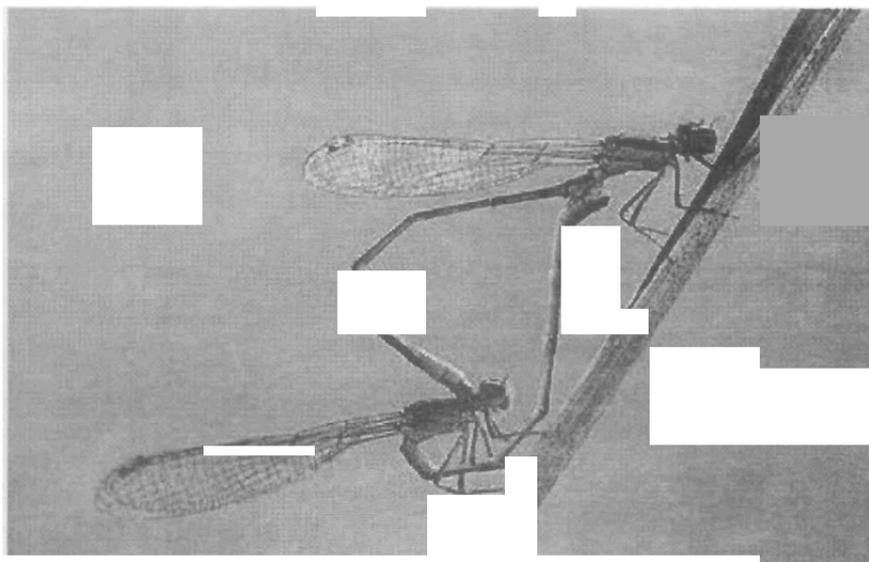


Fig. 18. Mating pair of the damselfly, *C. maculata*

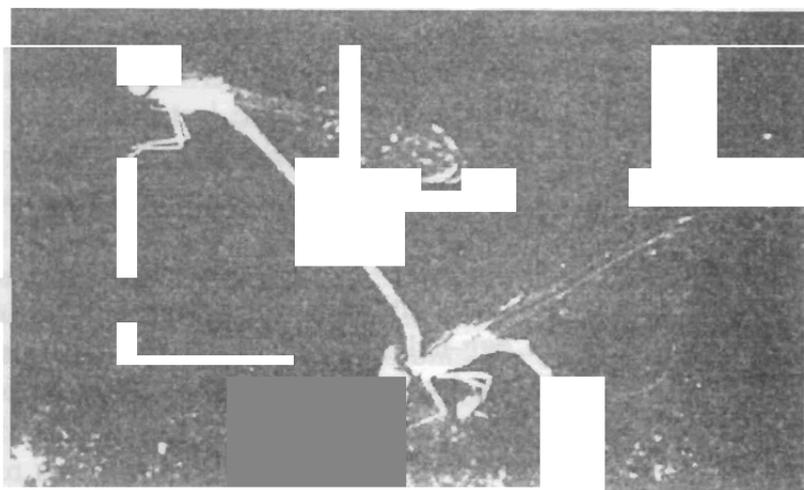


Fig. 19. Contact guarding by a damselfly male, which remains in tandem with his mate following copulation and stays with her while she oviposits (Alcock, 1993).

After male had disengaged his genitalia, guarding behaviour ensued. The male would stand close to the female (1cm away) and adopt either of the following positions: (a) facing the female with his antennae laid over the dorsum or (b) facing away from the female with his head directed toward her. If the guarding male lost contact with the female, he would move quickly and apparently at random around the mating cell until he resumed contact with her (Moc kam and Tjebek, 1987).

Following spermatophore transfer, the male maintains close contact with the female, behaves aggressively toward other males and makes movements toward the female (e.g. antennation, jerking the body backward and forward and in some cases head-butting) should she attempt to leave or removes the spermatophore (Mc Callum, 1992)

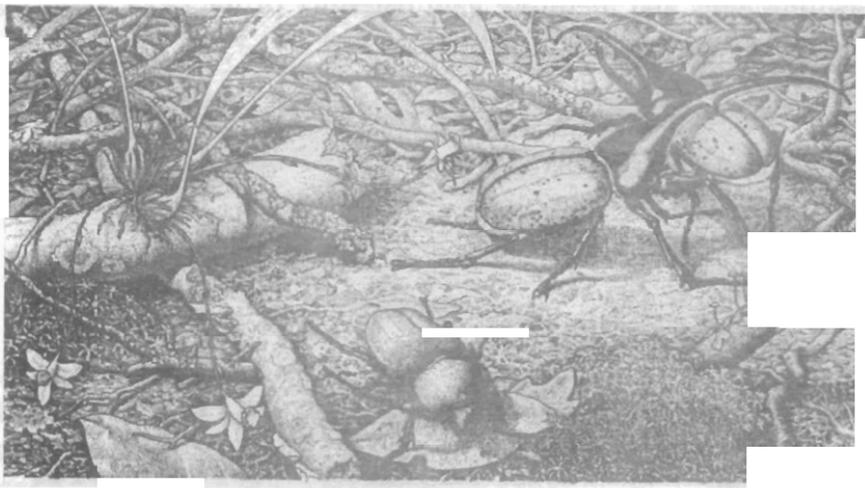


Fig. 20. Males of horned dragonfly, *Zygoptera*, competing for access to a female by engaging in fighting. (Thornhill and Alcock, 1983).

The most intense fights in many species occur when females are ready to be fertilized (Fig.20) and once a male finds a female, he often guards her. Males often compete in ways which are less conspicuous than fights but are no less effective and often more bizarre. Female dragonflies mate with a number of males and

store the sperm in a special sac (the spermatheca) in the body, for use at a later date. The male compete for fertilizations by trying to ensure that previous sperm is not used by the female. The penis of a male *Calopteryx maculata* (shown earlier), is equipped with a barbed whip at the end, which is used to scrape out of the female, any sperm left by previous males before he injects new sperm into the sperm sac. Another dragonfly, *Crocethemis erythraea*, uses an inflatable penis with a horn-like appendage to pack the sperm of previous male into corners of the spermatheca (Waage, 1979). Muse and Ono (1994 unpublished) proposed sperm displacement by flushing in the grasshopper, *A. lata*. The penis is devoid of recurved spines and fits the spermathecal tube (Fig.21). The penis of the mating male flushes previous sperm up and out of the spermathecal tube, deposits its own sperm so that it fertilizes depositing eggs and therefore gain paternity of the eggs, ensuring last male advantage.

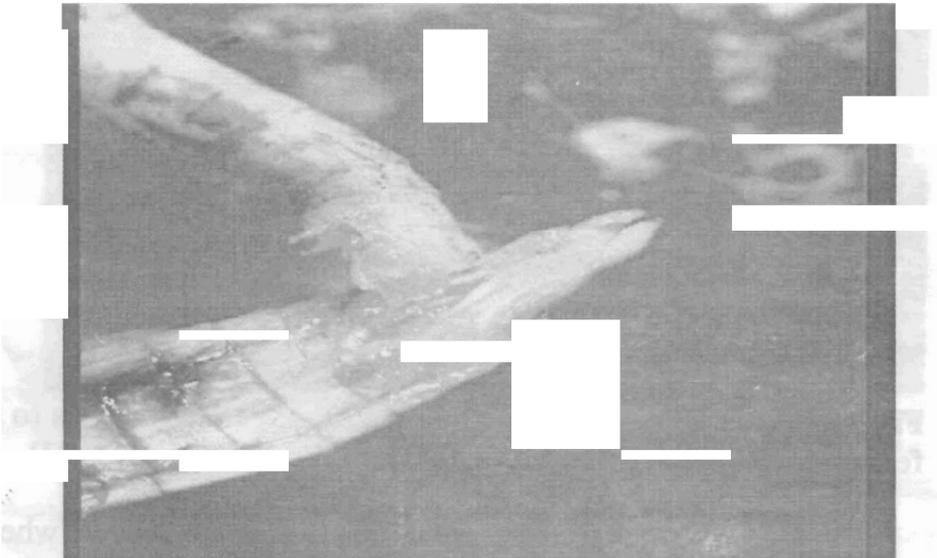


Fig. 21. Male and female *A.lata incopula* (freeze dried at -196°C and later dissected to reveal the structure of the penis). (Muse and Ono, 1994 unpublished).

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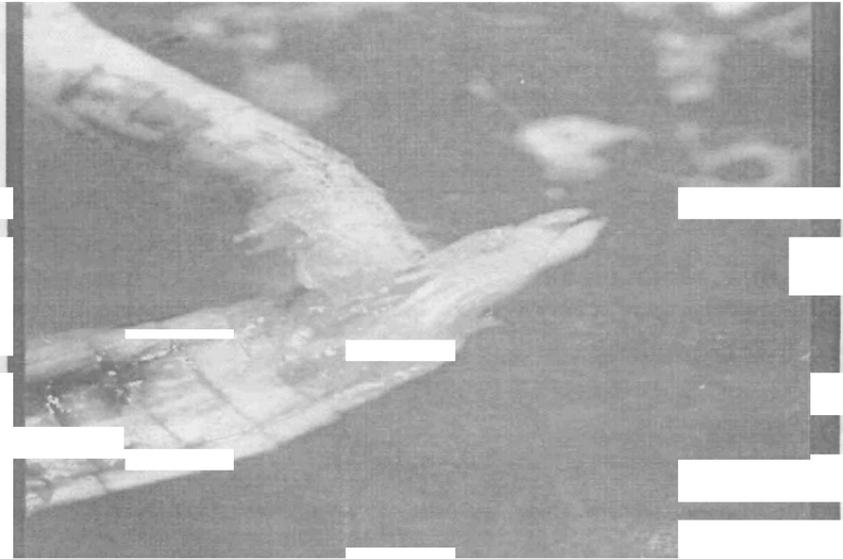


Fig. 21. Male and female *A.lata incopula* (freeze dried at -196°C and later dissected to reveal the structure of the penis). (Muse and Ono, 1994 unpublished).

The spermathecal proteins of once- and twice-mated females separated into the same number of protein fractions and with similar profiles, particularly with respect to prominence of fractions, indicating that sperm does not accumulate in the spermatheca of *A. lata* (Fig. 22) (Muse *et al.*, 1998).

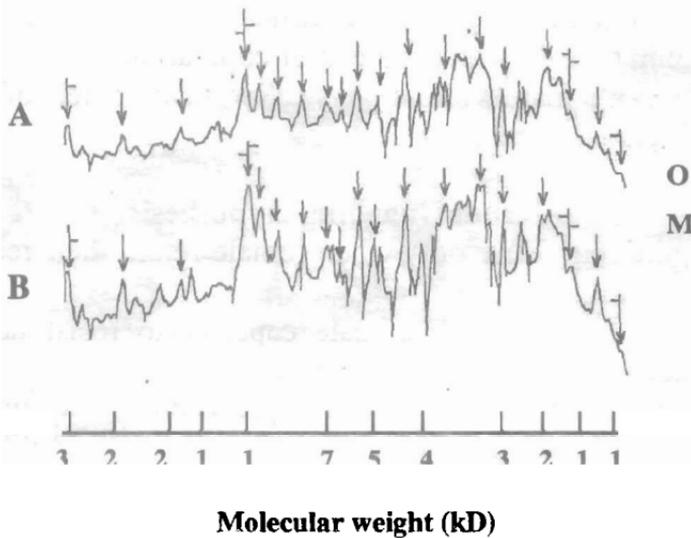


Fig. 22. Densitogram of SDS-PAGE of spermathecae of 20 day-old once- and twice-mated

Another secret and mysterious method of male-male competition for mates is the use of anti-aphrodisiac smells. Gilbert (1976) noticed that female butterfly, *Heliconius erato* always smell peculiar after mating. He showed experimentally that the scent does not emanate from the female but is deposited by the male at the end of mating. He also found that the scent discourages other males from mating with the female, perhaps because it resembles a scent used by males to repel one another in contexts.

The precise function of mate guarding also known as Post-Insemination Association (PIA) according to Alcock (1994) is to reduce sperm competition.

The four categories of PIA are :

- (a) Males prolong copulation after insemination.
- (b) Donate mating plug after insemination.
- (c) Retain contact with a mate after copulation.
- (d) Monitor a mate without physically grasping her following a completed copulation.

Testable Prediction from Guarding Hypothesis.

- 1. Mate guarding occur only when female retain their receptivity following insemination.
- 2. All things being equal, a male capacity to resist take-overs influence his readiness to mate guard.
- 3. The greater the degree of sperm precedence, the greater the likelihood of mate guarding.
- 4. Male-biased operational sex ratio is associated with intense guarding, female-biased ratio lead to little or no mate guarding.
- 5. The ease of access by rival males to mated females is correlated with the intensity of mate guarding.

Males maintain genital contact for beyond the time needed strictly for insemination of the female. This has been reported in several orders of insects (Thornhill and Alcock, 1983) and for *Zonocerus variegatus* (Orthoptera: Trogamorphidae) where male and female remain *in copula* for up to 6 hours (Muse, 2003). In a male-biased operational sex ratio experiment (Muse and Ono, 1996), the grasshopper *Atractomorpha lata* male holds the female on her back after insemination and disengages only after egg laying (Fig.23).

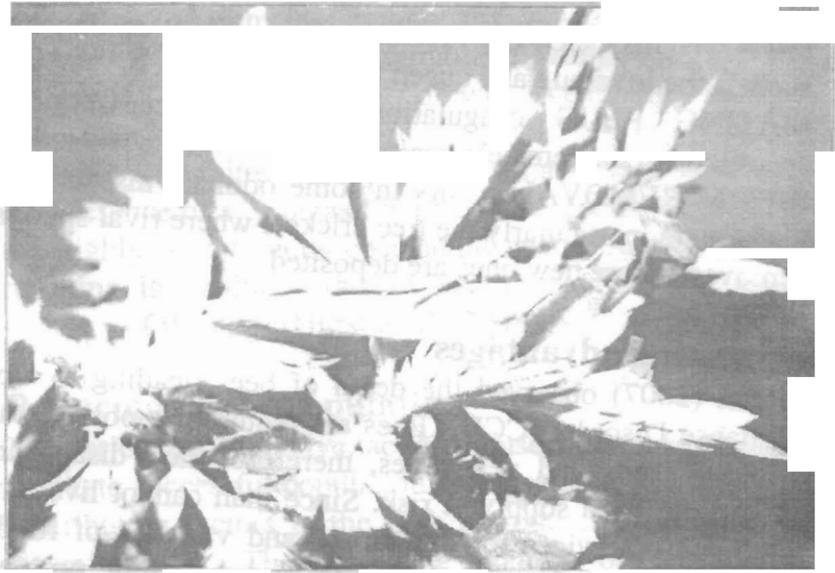


Fig. 23. Male *Atractomorpha lata* on the back of female (Muse and Ono, 1996).

The rival-repelling males gain egg-fertilization benefits from Post-Inseminating Association (PIA) with the female but the cost of the trait is sometimes enormous as follows:

1. Injury risk from repelling rivals
2. Danger from predators since males are more conspicuous, more distracted and less mobile while guarding.
3. Territorial species compromise their spatial defense in order to guard a mate.
4. Time required for the association

In summary, the following are types of male competition for female eggs :

1. **AGGRESSIVE EXCLUSION** as in Hercules beetle.
2. **LAST MALE ADVANTAGE** in cases where the last sperm is used for fertilization.
3. **MONOPOLISING FEMALE** staying in physical contact with a female without actual genital contact.

4. **PROLONGED COPULATION** occurs widely among insects such as the love bug and queen butterfly.
5. **MATING PLUG** coagulation of male accessory gland secretions in the female's genital tract.
6. **SPERM REMOVAL** occurs in some odonate insects and the Orthoptera, particularly the tree crickets where rival sperms are removed before new ones are deposited.

Some mating advantages

1. Caron (2007) observed the death of bees, leading to Colony Collapse Disorder (CCD). Bees are required to pollinate up to 80% of fruits and vegetables, therefore, their disappearance would put food supply at risk. Since man cannot live without pollination services for abundance and varieties of food, the researcher therefore used mating and breeding programme extensively to augment the shortage of bees in the field.
2. The whitefly, *Bemisia tabaci* (biotype B) owed its devastating effect on crops in China and Australia on its mating habits. The insect succeeded in displacing native populations of the same type in both countries. The marauding aphids damaged tomato and crops and caused spread of plant virus. De Barrow and Hart (2000) conducted regular field sampling of whitefly populations to monitor the insects behaviour as it spread and displaced native whitefly populations.

The invading and native populations interbred but cannot successfully reproduce. This resulted in a greater number of male offspring because the insect species is haplodiploid which means that males are produced from unfertilized eggs and females from fertilized eggs. The invasive females responded to the ensuing abundance of males in their environment, becoming more promiscuous and having more frequent sex with those males leading to an increase in female offspring. The invading male aphids courted the indigenous females and the females from their own "clan" reducing opportunities for copulation between native aphids. The upshot was that the

proportion of females among the invading population of biotype B insects keep climbing, while the number of indigenous females went down, eventually leading to extinction.

3. Sexually transmitted diseases (STD) have been reported with the presence of a parasitic mite of the genus *Coccipolipus* in the highly promiscuous coccinellid beetle, *Adalia bipunctata*, resulting in reduced rate of egg production and decreased viability of the eggs (Hurst *et al.*, 2008).

Reducing insect population

The various reproductive tactics in Insecta have been known to facilitate successful copulation and insemination which are the contributing factors to the high reproductive potential among insect species. Therefore, the control of insects in our environment, be it beneficial or non-beneficial, becomes a priority for entomologists.

I did collaborative research with colleagues using biodegradable insecticides of plant origin for the control of insects. The insects used were anopheles mosquito, *Anopheles gambiae*, yellow fever mosquito, *Aedes aegypti*, bluish-green blowfly, *Chrysomya chloropyga*, and maize weevil, *Sitophilus zeamais* (Muse *et al.*,1996; Lajide *et al.*,1998; Muse *et al.*,2002; Muse *et al.*,2003 and Ajileye and Muse, 2006). Our results were very promising for insect control and in agreement with the enormous work done by the few Applied Entomologists in Nigeria, including Professors Odebisi, Ogunwolu, Ewete, Ofuya, Lale, Adedire and Makanjuola.

Mr. Vice Chancellor Sir, Entomology is a profession that is highly neglected in Nigeria. This is in spite of the massiveness of the nation, its very large area of arable land, its livestock, game animals and its population of over 140 million. It is obvious that the Nigerian environment allows insects to thrive, hence diseases to our livestock, reduction in crop output, devastation of stored

products, including dry fish and the ubiquitous or perennial problem of malaria.

Therefore, the establishment of a National Centre for Insect Control is strongly recommended to the Federal Government of Nigeria, where professionals will be tasked to solve insect problems. There is also the need for the Federal Government of Nigeria to consider, as a matter of priority, the employment of an entomologist in each of the 774 local governments in the country. These trained men and women will coordinate, among others, malaria prevention by initiating mosquito control programme at the grassroot level as there is no Entomologist in any of the local governments in Nigeria at present.

Acknowledgement

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To my audience, I thank you all for your patience and attention.

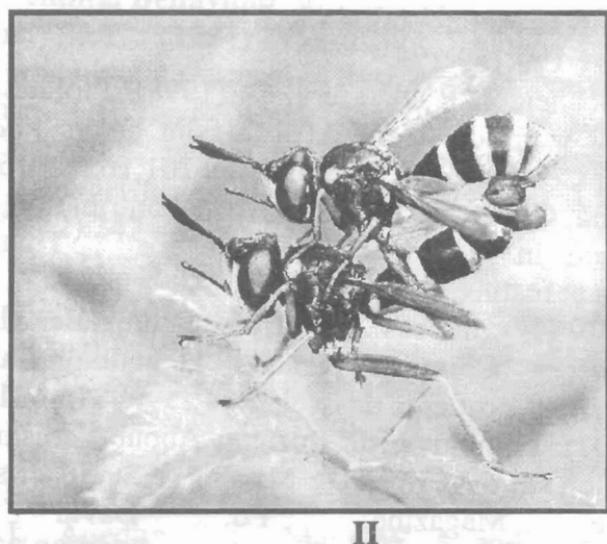
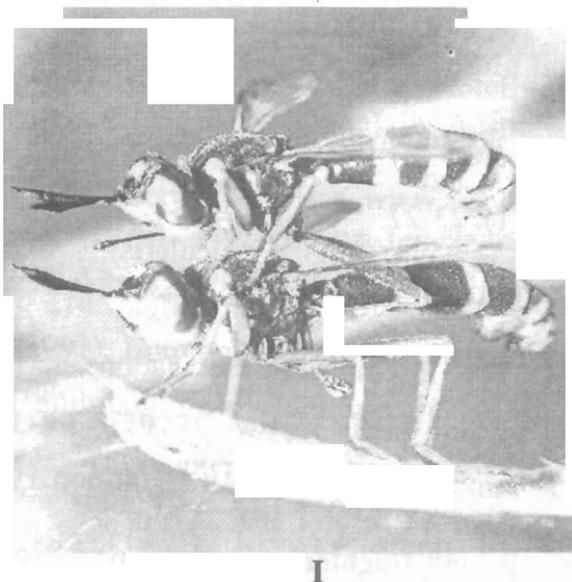


Fig. 24. Male and female *Conops vesicularis* (Diptera: Conopidae) before (I) and during (II) copulation (Photographs by Aivar Mikko, 2005).

REFERENCES

- Ajileye, A. Y. and Muse, W. A. (2006). Biological effect of some plant extracts on the reproductive development of the yellow fever mosquito, *Aedes aegypti* Linn. **Ife J. Sci.** 8(1): 23-27.
- Aivar Mikko (2005) Flylove (*Conops vesicularis*).
photo.net/photodb/photo?photo_id=3678606
- Alcock, J. (1994), Post insemination associations between males and females in insects: the mate - guarding hypothesis. **Ann. Rev. Entomol.** 39: 1-21.
- Alcock, J. (1993) *Animal Behaviour. An Evolutionary Approach* (5th Ed) Sinauer Associates, Inc. 217pp
- Alcock, J; Jones, E. and Buchinann, S.L.(1976) Location before emergence of the female bee, *Centris pallida* by its males (Hymenoptera: Anthrophoridae). **J. Zoology** 179:189-199.
- Aueswald L., Schneider, P and Gerd, G. (1998). Proline powers pre-flight warm-up in the African faint beetle, *Pachwoda Sinuata* (Cetonidae). **J. Exptal. Biol.** 201:1651 – 1657.
- Boggs, C.L. and Gilbert, L.E.(1979) Male contribution to egg production in butterflies: evidence for Transfer of nutrients at mating, **Science** 206:83-84.
- Carayon, J.L.(1964) Un cas d' offrande nuptiale chez les Heteropteres. **Comptes Rendus Hebedomadiars de Seances de l' academe des Sciences** 259: 4815-4818.
- Caron, D. (2007). Entomologists Buzzing About Vanishing Bee Population. In : *As Bees Go Missing, a \$9.3B crisis lurks* (Fortune Magazine). Ed. David Stipp. Money.cnn.com/magazine/fortunes/.../2007/09/03/100202647/index.html
- Chapman, R. F. (1969). *The Insects. Structure and Function.* The English University Press Ltd. London. 819pp.

- De Barrow, P. J. and Hart, N. J. (2000). Mating interactions between two biotypes of the whitefly, *Bemisia tabaci* (Hymenoptera: Aleyrodidae) in Australia. **Bulletin Ent. Res.** 90 (2): 103-112.
- Entomological Society of America, www.entsoc.org/-20k
- Gilbert, L.E. (1976). Post mating female odour in *Heliconius* butterflies: a male contributed antiaphrodisiac? **Science** 193: 419 – 420.
- Gillott, C.(1991). Entomology. 3rd ed. Plenum Press, New York, 728pp.
- Gwynne, D. T. (1977). Mating behaviour of *Neoconocephalus ensiger* (Orthoptera : Tettigoniidae) with notes on the calling song. **Can. Entomol.** 109 : 237-242.
- Gwynne, D.T. (1982). Mate selection by female Katydid (Orthoptera: Tettigoniidae, *Conocephalus nigroplenum*). **Animal Behaviour** 30:734-738
- Gwynne, D.T. (1984) Courtship feeding increases female reproductive success in bush crickets. **Nature** 307:361-363.
- Hockman, L.R. and Vahed, K. (1997) The function of mate-guarding in a field cricket (Orthoptera: Gryllidae; *Teleogryllus natalensis*. Otte and Cade). **J. Insect behavior** 10(2):247 – 255.
- Hurst, G.D.D., Sharpe R.S, Broomfield, A.E., Walker, L.E., Majerus, M.O., Sakharov A. and Majerus, M.E.N.(2008). Sexually transmitted disease in a promiscuous insect, *Adalia bipunctator*. **Ecol. Entom.** 20(3) 230 – 236
- Krebs, J.R and Davies, N.B. (1993). An Introduction to Behavioural Ecology (3rd.) Blackwell Scientific Publications Oxford 419pp.
- Lajide, L., Adedire, C. O., Muse, W. A. and Agele, S. O. (1998). Insecticidal activity of powders of some Nigerian plants against the maize weevil, *Sitophilus zeamais* Motsch. ESN Occasional Publication No. 31, pp 227-235.

- Low, P.T. (1978). Environmental uncertainties and the parental strategies of marsupials and placentals. **American Naturalist** 112: 197 – 213.
- Maynard Smith, J. (1978) The evolution of Sex. Cambridge University Press. Cambridge
- Mayr, E. (1971) Sexual selection and natural selection. In: Sexual selection and the descent of man, ed.B.Campbell. Chicago: Aldine.
- Muse, W. A. (1979) Carbohydrases in the midgut homogenate of the American cockroach, *Periplaneta americana* (Linnaeus). B. Sc. Dissertation. 28pp.
- Muse, W. A. and Balogun, R. A. (1986). Studies on the proteolytic activity in the midgut homogenate of the blowfly, *Chrysomya chloropyga* (Wied.) (Diptera: Calliphoridae). **Nig. J. Entomol.** 7: 42-51.
- Muse, W. A. and Balogun, R. A. (1991). Histology of the accessory gland of male variegated grasshopper, *Zonocerus variegatus* L. (Orthoptera: Acridoidea, Pyrgomorphidae) at different ages of the adult. **Nig. J. Entomol.** 12: 35-45.
- Muse, W. A. and Balogun, R. A. (1992). Free amino acid concentrations in the male accessory gland during development of adult variegated grasshopper, *Zonocerus variegatus* L. (Orthoptera: Acridoidea, Pyrgomorphidae). **Insect Sci. And its Appl.** 13: 35-45.
- Muse, W.A. (1992). Fecundity-enhancing-substance in the accessory gland of adult male variegated grasshoppers, *Zonocerus variegatus*. L. (Orthoptera: Acridoidea, Pyrgomorphidae). **J. Agric. Sc. and Tech.** 2(1) 92 – 94.
- Muse, W. A. (1993). Size and protein content of the accessory gland in the variegated grasshopper, *Zonocerus variegatus* L. (Orthoptera:Pyrgomorphidae). **Eur. J. Entomol.** 90: 365-367.
- Muse, W. A. and Balogun, R. A. (1993). Carbohydrates in the accessory reproductive gland of adult male variegated

- grasshopper, *Zonocerus variegatus* L. (Orthoptera: Acridoidea, Pyrgomorphidae). **Entomon** 17: 155-158.
- Muse, W. A. and Ono, T. (1994) Gross morphology of the female reproductive system *Atractomorpha lata* Motschulsky (Orthoptera; Tetrigidae) (unpublished).
- Muse, W. A. , Balogun, R. A. and Oluyole, O. O. (1996). Effect of Aqueous neem leaf extract on growth and development of larvae of *Anopheles gambiae* (Gills). **Pakistan J. Entomol. Karachi** 11(1&2): 5-8.
- Muse, W.A. and Ono, T. (1996). Copulatory behavior and post-copulatory male guarding in a grasshopper, *Atractomorpha lata*. Motschulsky (Orthoptera:Tetrigidae) under laboratory condition. **Appl. Entomol. and Zoology** 31(2): 233 – 241.
- Muse, W. A., Ono. T. and Tanaka, T. (1998). Electrophoresis and molecular weight estimation of spermathecal proteins of female *Atractomorpha lata* Motschulsky (Orthoptera : Tetrigidae) **J. Orthoptera Res.** 7: 179-184.
- Muse, W. A., Kehinde, T. O., Oloidi, A. O. Sosan, M. B. and Obuotor, E. M. (2002). Effect of some pulverised plant extracts on oviposition, hatching and development of larvae of *Aedes aegypti* (L). **Environ. And Ecol.** 20(4):810-817.
- Muse, W.A. (2002). Morphology of the male reproductive system and the nature of secretions of the accessory glands and seminal vesicles of adult, *Atractomorpha lata*. Motschulsky (Orthoptera: Acrididea). **Formosan Entomol.** 22: 249-259.
- Muse, W. A. (2003). Copulatory behaviour and mating frequency of pyrgomorphid grasshopper, *Zonocerus variegatus* L. (Orthoptera : Pyrgomorphidae) under laboratory conditions. **Fig. J. Exptl. Appl. Biol.** 4(2):257-263.
- Muse, W. A., Lajide, L. and Adedire, C. O. (2003). Effect of some Nigerian plants on survival, oviposition and emergence of adult blowfly, *Chrysomya chloropyga* (Wied.) (Diptera: Calliphoridae). **J. Asia-Pacific Entomol.** 6(1): 249-259.

- Ono, T., Siva-Jotty, M.T. and Kato, A (1989). Removal and subsequent ingestion of rivals' sperm during copulation in a tree cricket. **Physiological Entomology**. 14:195 – 202.
- Parker, G.A.(1970) Sperm competition and its evolutionary effects on copula duration in the fly *Scatophaga stecoraria*. **J. Insect Physiol** 16:1301-1328
- Parker,G.A ; Baker, R.R. and Smith V.G.F.(1972). The origin and evolution of gamete dimorphism and the male-female phenomenon . **J. Theoretical Biology**, 36; 529-553.
- Parker, G.E. and Smith, J.L. (1975) Sperm competition and the precopulatory passive phase behavior in *Locusta migratorioides* . **J. Entomol. Ser. A**. 49: 155 – 171
- Patridge, L.(1980). Mate choice increases competence of offspring fitness in fruit flies. **Nature** 283:290-291.
- Richards, O. W. And Davies, R. G. (1977) Imms' General Textbook of Entomology. Tenth Edition. Vol. 2. Classification and Biology. 1354 pp
- Siva-Jothy, M.T. (1987). Deviation in copulation duration and resultant degree of sperm removal in *Orthetrum cancellatum* (L.), (Libellulidae : Odonata). **Behavioral Ecology and Sociobiology**, 20:147 – 151.
- Trivers, R.L.(1972). Parental investment and Sexual Selection. In: Sexual and the descent of Man, R.Campbell (ed.). Aldine, Chicago.
- Thornhill, R. and Alcock, J. (1983). The Evolution of Insect Mating Systems. Harvard University Press, Cambridge, Massachusetts, 547pp.
- Thornhill, R.(1976). Sexual selection and nuptial feeding behaviour in *Bittacus apicalis* (Insecta :Mecoptera). **American Naturalist** 110:529-548.
- Thornhill, R.(1980) Mate choice in *Hyalobittacus apicalis* (Insecta:Mecoptera) and its selection to Some models of female choice. *Evolution* 34:514-538.
- Thornhill, R.(1980b). Rape in *Panorpa* Scorpionflies and a general rape hypothesis. **Animal Behaviour** 28:52-59

- Waage, J.K. (1973). Reproductive behaviour and its selection to territoriality in *Calopteryx maculata* (Beaveis)(odomata: Calopterygidae). **Behaviour** 47:240-256.
- Waage, J.K. (1986). Sperm displacement by two libellulid dragonflies with disparate copulation duration (Anisoptera). **Odonatologia**, 15,429 – 444
- Waage, J.K.(1979) Dual function of the damselfly penis :sperm removal and transfer. **Science** 203:916-918.
- Wigglesworth, V. B. (1974). Insect Physiology. 7th Ed. Chapman and Hall, London. 166 pp.
- Wigglesworth ,V.B (1976). Insect and the life of man. Collected Essay on Pure Science and Applied Biology. Chapman and Hall, Lond. 267pp.
- Williams,G.C. (1966) Adaptation and natural selection, Princeton University Press, Princeton, New Jersey.

