Age related mating behaviour and bioassay of the synthetic sex pheromone of the spotted stem borer, *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae).

By
Florence Njeri Njogu
B.Ed. (Science) (Hons)
Kenyatta University

Thesis submitted in Partial Fulfillment of the Requirement for the Award of a Master of Science (MSc.) Degree in Agricultural Entomology.

Zoology Department
Kenyatta University
P.O. Box 43844
Nairobi, Kenya.

December, 1995

DECLARATIONS

This thesis is my original work and has not been presented for a degree in any other University.

Florence N. Njogu
Candidate

This thesis has been submitted for examination with our approval as supervisors.

Prof. Jones M. Mueke
Zoology Department
Kenyatta University
P.O. Box 43844
Nairobi, Kenya

J.M. Mueke

Dr. Slawomir A. Lux
The International Centre of
Insect Physiology and Ecology (ICIPE)
P.O. Box 30772, Nairobi

S.A. Lux

DEDICATION

To my mother Mrs. Esther Wamwirua Njogu and to the memory of my late father, James Njogu Mabu.

ACKNOWLEDGEMENTS

I wish to sincerely thank my supervisors, Prof. J.M. Mueke from Kenyatta University and Dr. S.A. Lux from ICIPE for their guidance and counsel during the period of this research project.

It is also a great pleasure to express my appreciation and thanks to the following: Kenyatta University for offering me a scholarship, Dr. Hans Herren, the Director General, ICIPE and Prof. A. Hassanali, the Head of Behavioural and Chemical Ecology Research Unit (BCERU) for allowing me to use their facilities and all the provisions that I enjoyed during the course of this study. P. Njoroge and M. Onyango for constant supply of laboratory reared and field collected insects. Dr. W. Lwande and N. Gikonyo whose wealth of experience I shared and Mrs. B. Opiyo for the secretarial assistance in putting this thesis to its final format. Lastly, a special word of thanks to my mother, sisters, brothers and friends for their love, patience and moral support when hard times came by.

TABLE OF CONTENTS

CHAPTER FIVE

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

The influence of age on the mating behaviour of *Chilo partellus* (Swinhoe) was investigated. The observations on the behaviour of 0-, 1-, and 3-day-old moths were carried out to ascertain if any changes occurred relative to age in attractiveness of the females and in the responsiveness of the males. The results showed that males were more attracted to 0-day old females than to 3-day old ones. No difference in attractiveness was found between 0- and 1-day old females. 0-day old males were found to have a significantly lower responsiveness to the females than both 1- and 3-day old ones. However, although 3-day old males were more responsive than 1-day old ones, this difference was not found to be significant.

Observations of the mating behaviour of the moths showed that there were quantitative differences in the behaviour of 0-day old males and 3-day old ones. 0-day old males were found to spend the largest proportion of the time passive and only very few of them copulated by the end of the observation period. On the other hand, 3-day old males spent a relatively smaller proportion of the time passive and most of them had mated by the end of the observation period. No significant differences were detected between the behaviour of the laboratory reared and the field collected insects.

The effect of proximity of release points of the two pheromone components (Z)-11-hexadecenal and (Z)-11-hexadecen-1-ol of the female moth were investigated. Separating the dispensers of the two components by a mere 3cm resulted in a significant change in the male behaviour and a decrease in the bait performance as compared to the dispensers with the two components dispensed close to each other.

A study to establish the effect of polyvinyl chloride (PVC) on the response of the male *C. partellus* to the synthetic blend of the sex pheromone of the female showed that PVC does not inhibit male response to the pheromone. It was found, however, that the PVC dispenser loaded with the alcohol was inferior in its performance to the filter paper dispenser loaded with the same and this could possibly be attributed to a lower release rate of the alcohol by PVC.

CHAPTER ONE

1:0 INTRODUCTION AND LITERATURE REVIEW

1:1 Pheromones

A pheromone is a substance that is secreted by an organism to the outside and causes a specific reaction in a receiving organism of the same species. Sex pheromones are the most widely documented types of pheromones and they may be produced by females or by males or both sexes according to species. Thus both sexes may contribute to the chemical communication involved in mating. In many cases different pheromone components are responsible for the principle behavioural phases of mate location and courtship (Carde' et al., 1975).

1:1:1 Sex pheromone perception in moths

The perception of most of the sex pheromones studied to date is mainly by means of olfaction (Kaissling ,1971). The main site of olfactory receptors in Lepidoptera is on the antennae and the sensilla responsive to pheromones are the sensilla trichodea (olfactory hairs) (Waldow, 1970). Most moths are extremely sensitive to olfactory stimuli as has been demonstrated in the silk moth (Kaissling and Priesner, 1970; Schneider, 1970; Steinbrecht, 1970).

However, a mere knowledge of the potential capacities of sense organs cannot guarantee the actual complex of stimuli responsible for the release of a reaction. This is because an animal does not react to all the changes in the environment which its sense organs can receive, but only to a small part of them (Tinbergen, 1936c; Tinbergen, 1942; Lack, 1943) and is a basic property of instinctive behaviour. Instinctive behaviour is caused by the fact that an animal responds "blindly" to only part of the total environmental situation and neglects other parts, although its sense organs would be perfectly able to receive them (Tinbergen,1969). The female sex pheromone is often such an important stimulus for premating behaviour that the remainder of the female's body is not necessary at all as in the case of the male cabbage looper moth (Ignoffo et al., 1963). This illustrates a classical example of an instinctive reaction whereby the moth responds to only a few stimuli (in this case chemical stimuli) and the greater part of the environment has little or no influence to the insect although it may have the sensory equipment for receiving numerous details (Tinbergen , 1969).

1:1:2 Hierarchies of sex pheromone behaviour

The release of sex pheromone by females of many species elicits in the conspecific male a hierarchic sequence of behavioural steps. These include activation of the resting males, orientation of males in locating the source of pheromone and an often complicated series of behavioural responses at short range in the presence of the female which usually lead to copulation (Colwell et al., 1978; Ostaff et al., 1974; Hirai, 1977; Bartell, 1977; Bartell and Shorey, 1969; Daterman, 1972; Fatzinger, 1973; Shorey, 1974; Hegdekar and Dondale, 1969).

Studies on the dependence of behaviour on sensory stimuli have revealed that many behavioural reactions are in reality a chain of separate reactions, each of which is dependent on a special set of sign stimuli (von Frish , 1927; Tinbergen, 1935; 1942). According to Tinbergen (1969), this scenario is characteristic of most mating behaviour. Such a chain character of a response is susceptible to a sudden break during its progress and this could only be prevented by presenting a new stimulus situation of the special kind required at the right instant (Tinbergen, 1969).

Therefore the behavioural reactions displayed must occur in such a way that the sequence correctly culminates in a male locating and copulating with a female. These behavioural steps have been found to follow a fixed succession (Ignofo et al., 1963; Shorey, 1964; Shorey and Gaston, 1970; Gothif and Shorey, 1975), and it is possible that the completion of one step serves in part as a stimulus for initiation of the next. Each step may require a higher pheromone concentration for its release than did the previous one (Bartell and Shorey, 1969; Shorey and Gaston, 1970; Daterman, 1972; Farkas and Shorey, 1974) and since some of the steps occur while the male is moving towards the female, he automatically becomes exposed to a higher pheromone concentration and thus becomes primed for the next step (Bartell and Shorey, 1969).

1:1:3 Sex pheromone mediated orientation behaviour in moths

Male moths have been observed to vibrate their wings when exposed to sex pheromone and this behaviour has been highly associated with attraction (Islam & Alam, 1979; Baker & Carde', 1979). This behaviour probably aids in gradient detection. For a moth to locate a pheromone odour source found many metres or kilometres away it must be stimulated by the odour to orient its body into the air and thus approach the odour source (Shorey, 1973; Farkas and Shorey, 1972; Kennedy and Marsh, 1974; Marsh et al., 1978). Such an orientation made with respect to the direction of air flow is known as anemotaxis.

When moving air sweeps past a source of pheromone , an elongate cloud or plume of odour molecules is produced on the downwind side. The pheromone plume is not uniform and linear but is disrupted and filamentous consisting of pulses of high and low pheromone densities (Murlis and Jones, 1981). Due to the disrupted nature of the aerial odour trail, flying moths easily lose contact with the trail from time to time (Shorey, 1976). A flying moth must therefore be in a position to make corrective steering movements along the aerial pheromone plume if it is going to arrive at the source of the odour (Kennedy and Marsh, 1974; Kennedy, 1983).

The movement of moths flying along aerial trials of pheromone often consists of a sequence of sinusoidal or zigzag oscillations in a lateral plane (Marsh et al. 1978; Berisford and Brady, 1972; Brown 1972; Farkas and Shorey, 1972; Hidaka, 1972; Hendry et al., 1973). It is proposed that the moth senses when it is diverging laterally from the highest average pheromone concentration found near the central axis of the trail and is entering the lower concentrations near the boundaries of the active space and therefore turns back towards the higher concentration. This is a chemotactic mechanism which might continuously reorient the moth towards the trail`s central axis (Farkas and Shorey, 1972; 1973; Kennedy, 1983).

Apart from triggering anemotaxis and probably chemotaxis , sex pheromones have been found to directly influence the movements of flying moths by altering the frequency and angular magnitude of zigzags (Kennedy, 1982; Kennedy et al., 1980; Baker and Kuenen, 1982; Kuenen and Baker, 1983). Unlike Farkas and Shorey (1972) who proposed that all turns were steered with respect to pheromone gradients (a type of direct reaction to odour gradient), Baker and Kuenen (1982 ; Kuenen and Baker , 1983) invoked the concept of self steering (Kennedy 1978; 1983). These authors proposed that pheromone stimulation initiates and maintains a programme of movements, which may be regular "zigags" or counter-turns (Bell and Tobin, 1982; Kennedy, 1983). These movements are self-steered because they are a part of a "programme" originating from within the moth (Kennedy, 1978;

1983) and are described as indirect reactions to odour (Kennedy, 1978; Bell and Tobin, 1982).

1:1:4 Sex pheromone mediated short-range behaviour in moths

As a moth approaches the pheromone source , it encounters a progressively higher average molecular concentration. It has been proposed that at a very short range (probably within a few centimetres of pheromone emitting female), the high pheromone concentration may stimulate a male moth to visually orient to the female's image (Hutt and White, 1977; Castrovillo and Carde', 1979; Carde, 1981; Elkinton and Carde', 1984; Farkas and Shorey 1972; Shorey and Gaston, 1970; Hidaka , 1972 ; Daterman , 1972). The pheromone is often essential for this behaviour, and males of some species do not appear to observe a nearby female at all if they are not stimulated by the appropriate odour (Farkas et al., 1974).

As the moving moth approaches a pheromone source it decreases the rate of forward locomotion in relation to the increasing concentration of pheromone perceived (Farkas and Shorey, 1974; Farkas et al., 1974). This has been explained as being due to the fact that the Central Nervous System (CNS) receives less action potential stimulation from the receptors even though the pheromone concentration has increased (Baker, 1985; Bakers and Haynes, 1989). It appears that although the pheromone at low concentration may act as an initial stimulus to cause the moth to start moving along the odour trail, at high concentrations it acts as a stimulus to inhibit locomotion (Bell et al., 1972; Borden, 1967; Farkas et al., 1974). In some species certain chemicals ("aphrodisiacs") act at short range to cause courtship and copulatory reactions (Birch , 1974 ; Butler , 1970).

1:2 Pheromones as tools for insect pest control

The interest in pheromones has greatly intensified, not only because of public pressure for more selective methods of pest control, but also because advances in the analytical techniques have enabled structural assignment to be made to many pheromones. However, progress towards widespread practical use of these compounds has been slower than expected mainly due to the difficulties encountered in relation to understanding the biology of the insects and the use of the pheromones in the field.

1:2:1 Monitoring and survey work

The most extensive use of pheromones has been associated with the development of pest monitoring systems. The number of insects caught in pheromone baited traps is used as an indicator of the presence of the pest or more rarely as an estimate of population density (Arn, 1990). This has a major disadvantage in that the trap catches of males must usually be interpreted in terms of females, thus adding to the complexity of the interpretation. For those insects in which aggregation pheromones play an important role, traps containing synthetic pheromones can be used to catch both sexes (Hardee et al., 1969; Levinson and Levinson, 1973; Blight et al., 1984), thus providing a better opportunity for successful monitoring. Such aggregation pheromones are mainly found in Coleoptera. This technique can be used to detect early infestations of an insect pest, monitor established populations and assist in the timing of pesticide applications in relation to the build up of populations to economic damaging levels. Traps baited with sex pheromones have been used successfully for monitoring certain lepidopterous pests (Klassen et al., 1982; Campion, 1984). The efficiency of pheromone traps for monitoring populations of a few species of pyralid stem borers have been investigated (Campion and Nesbitt, 1983; Durant et al. , 1986; Tatzuki, 1990). Pheromone traps have been reported to be more sensitive than light traps for monitoring the rice stem borer *Chilo suppressalis* Walker (Tatzuki, 1990).

Monitoring populations of *C. partellus* has been based on destructive sampling of the crop to determine the population density of the immature stages of the pest (Warui and Kuria, 1983). This method is not suitable because it can be used only after the occurrence of the pest damage. Therefore, pheromonal monitoring method would be an ideal alternative. Trials with pheromone traps baited with virgin females indicate that such traps can be useful tools for detecting the presence of *C. partellus* and monitoring flight phenology (Unnithan and Saxena, 1990). There is need to establish the mating behaviour of the moths in order to obtain basic knowledge for designing and developing a durable slow-release pheromone dispensing system for monitoring *C. partellus* populations in the field.

1:2:2 Mass trapping

Mass trapping involves using large numbers of pheromone traps to catch a large proportion of the pest population. Insect pests are lured into an area of active surface which could be a sticky trap, a surface treated with a toxicant, sterilant, or pathogenic organism where they can be easily killed. Mass trapping has been used successfully in controlling certain pests of stored products (Levinson and Levinson, 1979; Trematerra and Battami, 1987). In a moderate insect population it may suppress the population below the economic damage level over some time. In this way, it is possible to reduce the use of insecticides and thus the probability of development of resistant strains of insects.

Mass trapping, however, has proved unsuccessful for a whole range of lepidopteran and coleopteran pests (Campion, 1989). This method would be ineffective where *C. partellus* occurs at high densities (Beever et al., 1990; Unnithan and Saxena, 1990) and also at low densities since males may mate up to six times (Unnithan and Paye, 1991). Mass trapping of stem-borers has been ruled out as a practical control method (Campion and Nesbitt, 1983).

1:2:3 Mating disruption

The use of pheromones for mating disruption is potentially a very powerful tool in insect pest management. The technique is based on the premise that male insects would be unable to locate females if the environment around the female is permeated with sex pheromone (Jackson and Lewis, 1981; Cardé, 1990). This would reduce the number of successful matings and thereby the subsequent number of damaging larvae in the next generation and perhaps the number of adults in future generations.

A univoltine pest with a limited mating period is particularly susceptible to this type of control as the population has less time to recover and treatment is necessary only for a limited period within the season. Mating disruption technique would be best suited to low-density pest problems, since the likelihood of chance encounters leading to mating is low. Since *C. partellus* is short lived, and fecundity and egg viability are both reduced by a delay in mating (Unnithan and Paye, 1991), this technique might be effective. However, the technique would fail to reduce pest damage if mated females immigrated into the treated area as was observed in *Ostrinia nubilalis* (Hubner) (Buchi et al., 1981; Cordillot and Duelli, 1989) and *Chilo suppressalis* Walker (Tanaka et al., 1987). In such situations, pheromones would have to be applied at the mating site which for *C. partellus* appears to be the eclosion areas (field where the previous crop was maize and sorghum or wild grass areas) (Pats, 1990; 1992). However, for effective control by mating disruption to be achieved, large areas would have to be treated because of the moth's great dispersal ability (Pats and Wiktelius, 1989) and large areas covered with wild grasses acting as environmental reservoir for the pest and this is quite expensive. The mating disruption of *C. suppressalis (Walker)* is so far the only instance of successful commercial application of the technique to a pest of a cereal crop (Casagrade, 1993).

1:3 Status of *Chilo partellus* as a pest

Among the forty one species of the genus *Chilo* known, twenty five of them, including eighteen species which occur in Africa, infest cereals (Beever et al., 1990). Larvae of all *Chilo* species are stem borers of graminaceous plants and most species are oligophagus.

The spotted stem borer, *Chilo partellus* Swinhoe is a major pest of sorghum and maize in both Southern Asia (Neupane, 1990) and Africa (Sithole, 1990). Essentially, *C. partellus* is a pest in hot lowland areas and is seldom found above an altitude of 1500m (Hill, 1983). *C. partellus* is widely spread in Asia and is probably indigenous to these areas. The pest has been recorded in Malawi (Jepson, 1954), Uganda (Ingram, 1958) South Africa (van Hamburg ,1979), Ethiopia, Kenya, Mozambique, Somalia, Central Africa (C.A.B. , 1977a), Bostwana, Swaziland and Zimbabwe (Sithole, 1989b) as well as in West Africa (IAPSC, 1985), indicating a further Western extension in its distribution.

The main hosts of *C. partellus* are maize (Mohyuddin and Attique, 1978), sugar cane, rice, wheat foxtail and finger millet. The wild grass species *Sorghum halepense* (L.), *S.verticilliflorum* (Stend.), *Panicum maximum* (Jacq.) and *Pennisetum purpuneum* (K.) Schumach can act as alternative hosts (Ingram , 1958). The survival of *Chilo* spp. in the dry season depends upon these grasses (Wheatly, 1961).

Larvae feed actively on tender leaves but later bore into the stems. In young plants, larvae attack the growing point and cause dead hearts (Leuschner, 1990). In older plants they bore into the main stems which subsequently are hollowed out over a considerable length. Consequently, infested plants have stunted growth, reduced yield and are more susceptible to wind damage and secondary infections. An estimated loss of up to 50% of the harvest has been reported in both maize and sorghum (reviewed in Seshu Reddy and Walker, 1990).

Chilo species are particularly difficult to control by the use of insecticides largely because of the cryptic nocturnal habits of the adult moths, and the protection afforded by the stem or cob of the host crop to the larvae (Singh and Rana, 1989).

In addition insecticides are prohibitively expensive to the resource poor farmers and cause serious pollution problems in the environment. Thus alternative control methods that would overcome the drawbacks of insecticides are required.

Recent work at the International Center of Insect Physiology and Ecology (ICIPE) has demonstrated the potential of pathogens, *Bacillus thuringiensis* and *Nosema* spp., for controlling *C. partellus* (Brownbridge, 1991; Odindo, 1991). However, these management options are not currently available to the farmer. ICIPE and the Department of Entomology, Wageningen Agricultural University (WAU) have jointly imported the larval parasitoid *Cotesia flavipes* Cameron from Pakistan and its potential for regulating *C. partellus* is being evaluated.

C. partellus breeds continuously in the dry season on stubble and volunteer tillers of sorghum (Ingram , 1958; Adeyemi, 1969). Intercropping of appropriate crop combination of host and non-host plants and the destruction of crop residues after harvest may decrease the abundance of *Chilo* (Ongwaro, 1983; Omolo and Seshu Reddy, 1985b; Minja, 1990). Cultivars of maize and sorghum with partial resistance to *C. partellus* have been identified (Dabrowski and Kidiavai, 1983; Omolo, 1983; Seshu Reddy, 1983; 1985c; Ampofo et al., 1986).

It is unlikely that any of these various methods will be effective in reducing stem borer populations to levels acceptable to man. However, success may ultimately be achieved by combining several tactics in an integrated approach. Pheromones unlike insecticides are generally species specific and therefore harmless to non-target organisms. However, lack of information on insect behaviour, particularly the mating process has tended to be a major limiting factor impairing the inclusion of pheromones into an Integrated Pest Management (IPM) package. Therefore the need to study the nature of the mating behaviour of this pest to establish how sex pheromones can be manipulated as part of an IPM system is justified.

1:4 Reproductive behaviour of *C. partellus*

Majority of *C. partellus* males emerge within the first two hours of scotophase (2000 to 0800 hrs.). The females emerge about five hours later (Kanaujia et al., 1981; Pats, 1992). The asynchrony of eclosion times facilitates mating during the first five hours of scotophase on the night of eclosion since the moths are ready to mate soon after eclosion. Most mating occurs between the night of eclosion and the second night after eclosion (Bughio et al., 1977; Kurmar and Saxena, 1985; Unnithan, 1988; Pats, 1992).

There is evidence that parental age of moths influence the reproductive potential and certain biological characteristics of the offspring (Unnitham and Paye, 1991). In *C. partellus*, oviposition is delayed or prevented in the absence of mating while female longevity and preoviposition period are increased with delayed mating

(Unnithan and Paye, 1991). However, longer lifespan in late mated females is not accompanied by extended reproductive period. These authors observed that the oviposition period , fecundity and egg fertility were significantly reduced with delayed mating. Mating activity was high 1-2 days after eclosion, after then it was inversely correlated to the moth's age.

It has been found that *C. partellus* females of different age categories emit different amounts and ratios of pheromones (Lwande, ICIPE, pers. comm., 1993). This implies that the signals emitted by the calling female are age dependent and different in quality. Consequently, males of different age categories might respond differently to these signals. Studies need to be conducted to verify these hypotheses.

Availability of such knowledge will be of great value to researchers designing and developing a pheromone dispenser for monitoring *C. partellus* populations. Such knowledge will help establish the age of the female that the dispenser shall mimick. The female age category that is most attractive to the males in terms of behavioural signals will be the most desirable for mimicking. The knowledge of the male age group that is most responsive to the females will be of great value in making correct interpretation of catches since this would be the age group the developed bait would trap. This knowledge would also be important to researchers testing the response of male *C. partellus* to the dispensers of the female synthetic sex pheromone since this would be the most desirable age to use.

In *C. suppressalis*, Kanno and Sato (1975) reported decreased fecundity, percentage of fertile eggs, hatching rate and survival rate of newly hatched larvae with increasing maternal age. Decreased fecundity due to delayed mating has also been found in *Ephestia kuehniella* (Z.) (Norris, 1933), *E. cautella* (W.) (Barrer, 1976), *Heliothis virecens* (F.) (Proshold et al., 1982), *Pectinophora gossypiella* (Sounders) (Lingren et al., 1988) and *Panolis flammea* (Schiff.) where it also resulted in reduced egg fertility (Leather et al., 1985). The marked reduction in the reproductive potential as a result of delayed mating of the females suggests that late mated females contribute least to the population of the next generation as compared with earlier mated ones. This suggests a favourable outcome for control techniques that reduce the chances of females being mated (Ellis and Steele, 1982).

According to Thornhill and Alcock (1983), the most common form of mating system in all animals including insects is polygyny. These authors defined polygyny as the mating system that results when some males copulate with more than one female in a breeding season. Several workers have proposed that in the course of evolution, there have been two conflicting extreme options for males; to allocate limited supplies of time, energy and risk taking to: mating or parental effort (Trivers, 1972; Low, 1978; Alexander and Borgia, 1979). Mate acquisition has greater yields than parental behaviour because males have vast supply of sperm for fertilizing many females each of which has a relatively small number of eggs. Since females typically make a large parental investment per offspring, it is acceptable that a male can rely on his mate`s investments in nutrients for the eggs and other parental activities to produce viable offspring. Copulatory success then is likely to be an accurate measure of genetic success for a male (Thornhill and Alcock, 1983) and this possibly explains why males are generally more strongly motivated than females to copulate.

The males of *C. partellus* are able to mate once per night for several nights and the spermatophores transferred are all equally effective in producing fertile eggs (Unnithan and Paye, 1991). According to these authors, a single spermatophore, if received at the right age, is enough to fertilize eggs throughout the female`s lifespan and females rarely mate more than once. Such females are said to be monogamous. Monogamy occurs when a male and a female have only a single partner per breeding season (Thornhill and Alcock, 1983). These authors postulate that there is generally nothing to be gained from mating more than once from the female`s perspective because her limited number of eggs can often be fertilized by sperms received from a single male (Alcock et al., 1978; Walker, 1980). Since males rarely offer anything other than sperm in return for the copulation, females may mate simply to acquire sufficient gametes to fertilize their eggs, and one mating usually suffices. For *C. partellus*, mated females are less attractive to males in the field and therefore males are likely to mate with only unmated females (Unnithan and Saxena, 1990; Unnithan and Paye, 1991).

1:5 OBJECTIVES

The objectives of this study were:

1. To investigate the influence of age on the mating behaviour of *C. partellus*.
2. To compare the mating behaviour of *C. partellus* reared in the laboratory with those collected from the field.
3. To investigate the effect of proximity of release points of a synthetic blend of the female sex pheromone on the behaviour of male *C. partellus*.
4. To test for any inhibitory effect of polyvinyl chloride on the response of the male *C. partellus* to the synthetic blend of the female sex pheromone.

CHAPTER TWO

2.0 General materials and methods

2:1 Rearing of the insects

Insects were obtained from ICIPE mass-reared colonies. Larvae were reared on an artificial diet based on Roscoco bean powder (a variety of *Phaseolus vulgaris* L.) and sorghum leaf powder (Ochieng et al., 1985). They were kept under natural illumination (Light : Day = 12 : 12 hours) and held in a rearing room with temperatures between 22-30° C and 55-80% relative humidity until they developed to pupae. The colony was constantly renewed with insects collected from the field.

2:2 Field collection of pupae

Pupae were collected from growing maize stems in the Mtwapa area on the Kenya Coast and brought to the laboratory. They were separated by sex and held in different cages, 15 by 15 by 20 cm, with a mosquito net fitting at the top to allow free air circulation. Separation of the sexes was carried out at this stage in order to prevent mating after moth emergence. The photoperiod was reversed (12 hrs light, 12 hrs dark) and the pupae were allowed to adjust to the reversed photoperiod for a few days. On emergence, the moths were supplied with a vial containing cotton wool moistened with 5% sucrose solution. The moistened cotton wool was changed daily.

2:3 Experimental conditions

All experiments were conducted in a dark room with temperatures ranging between 20-22° C and a relative humidity of 50-60%. A red lamp of about 1.0 lux intensity was used to allow observation of insects without interfering with their normal behaviour.

2:4 Determination of moth age

The moths which emerged within a period less than 24 hours were designated as day 0. Those which emerged within 24 hours (6.00-6.00) as day 1 and within the subsequent 6.00-6.00 period as day 2 and so forth.

CHAPTER THREE

3:0 The influence of age on reproductive behaviour

3:1 The influence of age on the attractancy of the female and the responsiveness of the male *C. partellus* moths.

3:1:1 Introduction

Studies show that the attractancy of the female to a male and the responsiveness of a male to a calling female vary with age in some species of moths. Shorey et al. (1968b) reported that the production of sex pheromone in the pheromonal gland of the female moths of seven species of Noctuidae and its subsequent release during calling depends upon age. Little information is available on the effect of age on the mating behaviour in *C. partellus*. This study investigated the effect of age on the sexual behaviour of both sexes of *C. partellus*.

3:1:2 Materials and methods

One-day- and three-day-old virgin calling female moths were each confined in small cylindrical wire cages 8 cm long and 3 cm in diameter. The cages were placed parallel to each other 20 cm apart at the upwind end of an observation chamber, 1 x 0.6 x 0.6 m. A one-day-old virgin male was released at the downwind end of the chamber and its behaviour towards the two calling females observed for one hour. A three-day-old male was similarly treated. For the control experiment, two empty wire mesh cages 3 cm in diameter and 8 cm long were placed 20 cm apart but parallel to each other at the upwind end of the chamber. One-and three-day-old males were each released separately at the downwind end and their behaviour observed for one hour.

In another experiment a 0-day and a 1-day-old virgin calling females were each confined to small cylindrical wire cages of the same size as described earlier. 0-, 1-, and 3-day-old males were each released separately at the downwind end of the chamber. The behaviour of each male was observed for one hour. For the control experiment, empty cages of the size described earlier were presented at the upwind end of the chamber to the three different age categories of the males separately. The behaviour of the male of each age category was observed for one hour . The observations were carried out between the 8th and the 11th hour of the scotophase because sexual activity peaks at this time (Pats, 1992). The position of the caged females and the order of release of the males into the chamber were systematically rotated. The observation of the male's behaviour towards the caged females was repeated 20 times.

In each experiment the following parameters of the male's behaviour were quantified:

a. the number of times the male landed on each source;

b. time spent walking while wing fanning round the source;

c. time spent in flight round the source;

d. the number of times each source was located first.

3:1:3 Data analysis

95% confidence limits for the means was calculated. Chi-square test was done to determine whether there was any difference in the number of times each female of the given age category was located first by the male of the given age category.

3:1:4 Results

Tables 1 and 2 show the response of various age categories of males to various age categories of females. One-day-old males were more attracted to 1-day-old females than to 3-day-old ones. Similarly, 3-day-old males were more attracted to 1-day old than 3-day old females (Table 1). One- and 3-day-old males landed 11.55 ± 1.35 and 13.25 ± 1.69 times respectively on cages in which1-day old females were kept and this was a significantly higher number of times than on 3-day-old females (3.00 ± 0.41 and 3.65 ± 0.70 respectively). These males spent a significantly longer time fanning wings while walking and in flight round 1-day old female cages than 3-day old ones (Table 1). However there was no significant difference in response due to male age (χ^2 = 0.78, df = 1 N.S.).

Table 1: Effect of age on the attractiveness of the female and responsiveness of the male (One- and three-day-old) *Chilo partellus* moths

AGE		Number of times male landed on the source. Mean ± S.E	Time in seconds spent fanning wings. Mean ± S.E	Time in seconds spent in flight. Mean ± S.E.	Number of times the source located first*
Male	Female				
1	1	11.55 ± 1.35b	656.76 ± 72.28b	140.90 ± 15.81b	15
1	3	3.00 ± 0.41a	85.85 ± 17.39a	34.05 ± 5.38a	5
3	1	13.25 ± 1.69b	583.60 ± 53.62b	145.35 ± 17.42b	19
3	3	3.65 ± 0.70a	107.25 ± 20.26a	43.00 ± 7.67a	1

* This data represent the actual number of times and not the averages (χ^2 = 0.78, df = 1, N.S.)

Means within the same column followed by the same letter are not significantly different at 5% significance level.

No difference in attractiveness was observed between 0- and 1-day old females (Table 2). Three-day-old males had a higher responsiveness to all the age categories of females tested than 1-day old ones. When 3-day old males were paired with 1-day-old female they fanned wings round the female for 278.55 ± 19.34 sec. and when 1-day-old male was used, it fanned wings for 250.30 ± 14.65 sec. Similarly, 3-day-old males flew round 1-day old females for 105.65 ± 8.19 sec while 1-day old males took 99.5 ± 10.43 sec. These differences, however, were not found to be significant (Table 2).

In contrast, there was a significant difference in response between 0-day old males and both 1- and 3-day old ones (Table 2). O-day-old males landed on the source for significantly fewer times (6.90 ± 0.52) compared to both 1- and 3-day-old males (11.15 ± 0.96 and 12.90 ± 0.95 respectively) when paired with 0-day old females. Similarly, these males spent less time fanning wings while walking and in flight round the source (Table 2).

Table 2: Effect of age on the attractiveness of the female and responsiveness of the male of (zero-, one- and three-day old) *Chilo partellus* moths

AGE		Number of times male landed on the source. Mean ± S.E	Time in seconds spent fanning wings. Mean ± S.E	Time in seconds spent in flight. Mean ± S.E.	Number of times the source located first*
Male	Female				
0	0	6.90 ± 0.52a	186.40 ± 18.49a	64.95 ± 6.13a	11
0	1	6.75 ± 0.51a	179.30 ± 18.49a	72.30 ± 11.26ab	9
1	0	11.15 ± 0.96b	284.45 ± 15.77bc	167.75 ± 9.57b	9
1	1	10.60 ± 1.10b	250.30 ± 14.65b	99.50 ± 10.43b	1 1
3	0	12.90 ± 0.95b	342 ± 26.54c	108.25 ± 7.11b	13
3	1	11.80 ± 0.71b	278.55 ± 19.34bc	105.65 ± 8.19b	7

* The data represent the actual number of times and not the averages (χ^2 = 1.62, df = 2, N.S.)

Means within the same column followed by the same letter are not significantly different at 5% significance level.

3:1:5 Discussion

The results strongly support the hypothesis that males are able to distinguish between 1-and 3-day-old females. All the three age categories of males tested were not able to distinguish between 0-and 1-day-old females. This implies that both 0-and 1-day-old females may have been equally attractive to these males. Newly emerged males showed a lower responsiveness to females than older ones. This observation implies that newly emerged males would be the least attracted to the lure of the pheromone trap. The observation that 0-and 1-day-old females were more attractive than 3-day-old ones implies that the developed trap should sufficiently resemble or mimic 0-and 1-day-old females in the composition and the release rate of the pheromone.

Age specific responsiveness has been observed in other species of Lepidoptera. In the true armyworm *Pseudalentia unipunta* (Haw.), the responsiveness to different concentrations of the sex pheromone was lowest on the day of emergence increasing up to day 5 and then declining on day 7 (Mcnell et al., 1983). In *Trichoplusia ni* (Hbn.), newly emerged males are essentially non-responsive and responsiveness increases rapidly through the age of 2.5 days (Shorey et al., 1968b). In another species *Epiphyas postvittana* Walker, peak response to the sex pheromone was not attained until the 2nd night after moth emergence then it remained at this plateau to the 10th night (Bartell and Shorey, 1969). In another species *Zeadiatrea gradiosella* (Dyar), the attractancy of females was high on the night of emergence then dropped sharply after the fourth day. No males were attracted to virgin females over 8 days old (Davis and Henderson, 1967). Banerjee (1969) reported that *Crubus trisectus* Walker and *C. teterrellus* Zinken females were most attractive during the first 2-3 days of their life but their attractiveness decreased with age.

Struble and Jacobson (1970) reported that virgin males of the red-backed cutworm *Euxoa ochrogaster* Guene'e, were not responsive to the pheromone until they were 5-9 days old. Perez and Long (1964) also reported that the females of the sugar cane borer, *Diatraea saccharalis* (F.) were most attractive during their first 3 days of life after which attractiveness decreased with age. Outram (1971) reported that males of *Choritoneura fumiferana* (Clem.) were least responsive to females soon after emergence and most responsive when 2-4 days old while females were most attractive when less than 0.5 day old then became progressively less attractive with age.

Since in this study only three age categories of moths were used, further investigations should be conducted using 4-day old moths and above to verify if similar results could be obtained.

3:2 The influence of age on the mating success in *C. partellus*

3:2:1 Introduction

Quantitative analysis of behaviour can be carried out in many different ways. A set of discrete behavioural categories is usually formulated before the behaviour is recorded on the computer compatible event recorder. This study investigated the quantitative differences in mating behaviour of different combinations of females and males of *C. partellus* of different age categories reared in the laboratory and those newly collected from their natural environment.

3:2:2 Materials and methods

A female of the appropriate age category in calling position was selected and placed in an observation chamber made of clear perspex measuring 50 x 50 x 50 cm. The chamber had mosquito net fittings at two opposite ends to allow free air circulation. A petri-dish containing moist cotton wool was placed inside the chamber to maintain humidity. A passive male of the appropriate age category was released in the chamber and its behaviour observed and recorded on the computer event recorder for thirty minutes at most. The following behavioural categories were registrated:

A: PASSIVE

This category covers the following male behaviours:

- sitting doing nothing
- cleaning antennae

B: ACTIVE

The category covers the following male behaviours:

- any movements greater than one centimetre
- all walking without fanning wings.

C: FANNING

The category covers:

- wing fanning while stationary with vigorous antennal movements.

D: PRE-FLIGHT WALK

The category covers:

Walking while wing fanning before any flight has been undertaken.

E: FLIGHT

The category covers all forms of flight .

F: POST-FLIGHT WALK

The category covers:

All walking while fanning wings and touching the substratum with the antennae after a flight period.

G: WALK ALONGSIDE FEMALE

The category covers:

Male walking while wing fanning alongside the female touching her with his antennae.

H: CLASPING

The category covers:

The male bending his genitals towards the female ovipositor.

I: COPULATION

The category covers the act of coupling when the male turns 180°.

Observations were performed for four different combinations of age categories 0-day-old male x 0-day-old female (0m-0f); 0-day-old male x three-day-old female (0m-3f); three-day-old female x three-day-old male (3m-3f); three-day-old male x 0-day-old female (3m-0f). All the 0-day-old moths are hereafter referred to as young adults while the 3-day-old moths are referred to as mature or old adults. A set of observations was made for both insects reared in the laboratory and those collected from the field (Mtwapa region of the Kenya Coast). The order of these observations was systematically rotated. Every day, four observations were recorded, one for each combination of age category.

3:2:3 Recording of behaviour

A program for automated observation of insect behaviour (event recorder program) (Lux, 1989; 1990) was used for recording of behaviour (data collection).

3:2:4 Data analysis

The data collected by the event recorder program was analyzed by a program for ethological analysis [Quant Etho program] (Lux, 1989; 1990). This program selects a specified part of each observation and calculates: duration of each activity (it`s variability and histogram), number of it's occurrences and total time spent for it, relation to others -probability of passing from other activities to the given one (input chances) and passing from the given activity to others (output chances), diagram of the "time budget" -ratio of time spent for each activity during the selected part of observation. Statistical comparison was performed using 95% confidence limits to attach confidence to the means of the behavioural activities of moths of different age categories and from either the laboratory colony or from the field.

3:2:5 Results

3:2:5:1 Time budget

Figures 1-8 show the behaviour (time budget) of various combinations of ages of *C. partellus* male and female moths from the laboratory and from the field within a period of 30 minutes (1800 seconds). The results show that young males spent the largest proportion of the time passive in the 30 minutes of observations. This observation is consistent for both field and laboratory insects (Figs. 1, 2, 5 and 6). In the 1st, 3rd, 16th and 26th minutes of observation, the field and the laboratory insects spent 78-95%, 68-93%, 64-90% and 76-100% (lower and upper limits of the proportion) of the time passive, respectively. By the end of the observation period 56-90% of the time they were passive. Young males spent a very small proportion of the time (22%≤) copulating and in one combination, 0m-0f (Field), no copulation occurred. In contrast, mature males spent a relatively smaller percentage of their time passively but a larger percentage of the time in copulation (Figures 3,4,7 and 8). This observation is consistent for both field and laboratory insects . In the 1st, 3rd, 16th and 26th minutes of observation, the field and the laboratory males spent 58-73%, 30-68%, 5-18% and 8-22% of the time (lower and upper limits of the proportion) passively, respectively. By the end of the observation period only 9-27% of the time was spent passive. These males spent the largest percentage of the time copulating. For instance by the 12th and 20th minutes, 50-64% and 50-84% of the time respectively, they were in copulation. By the end of the observation period 70-84% of the time was spent in copulation.

3:2:5:2 Mean duration of a single act

Young adult males when paired with old females were passive for a longer duration than the mature males (Table 3). The results from the field mature males showed some degree of overlap in the duration of this behavioural activity. The same trend was reflected in the results obtained when young adult males were paired with old females (Table 4). Mature males walked longer after a flight period than did immature ones irrespective of whether they were paired with young or old females (Tables 3 and 4). Mature males flew for a longer duration when paired with females than did immature ones. The behaviour of the laboratory and the field insects did not differ statistically. No statistical difference was detected when either immature adult or mature males were paired with young or old females.

Fig. 1 Time budget for Om-Of laboratory insects.

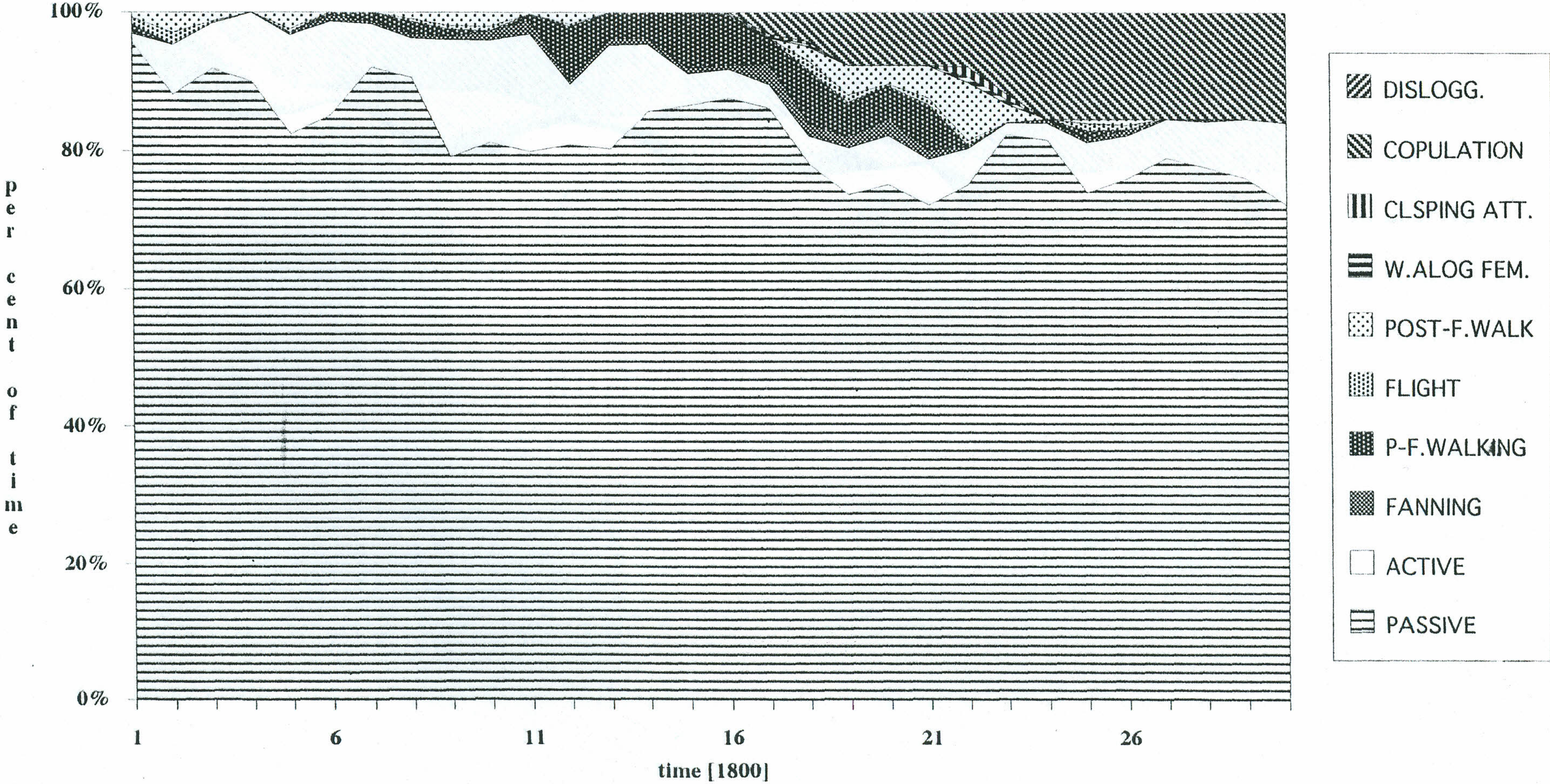

Fig. 3 Time budget for 3m-Of laboratory insects.

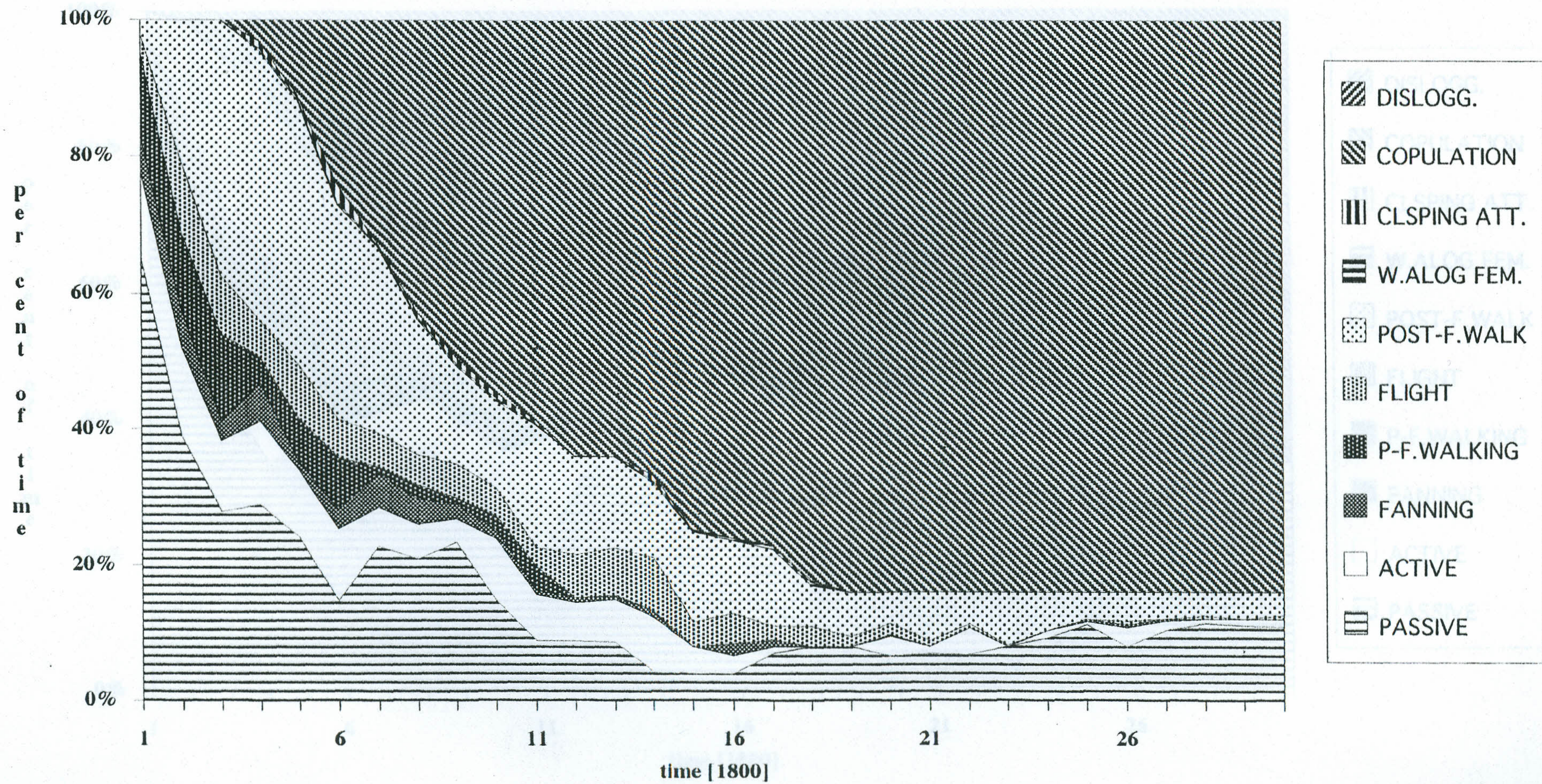

Fig. 4 Time budget for 3m-3f laboratory insects.

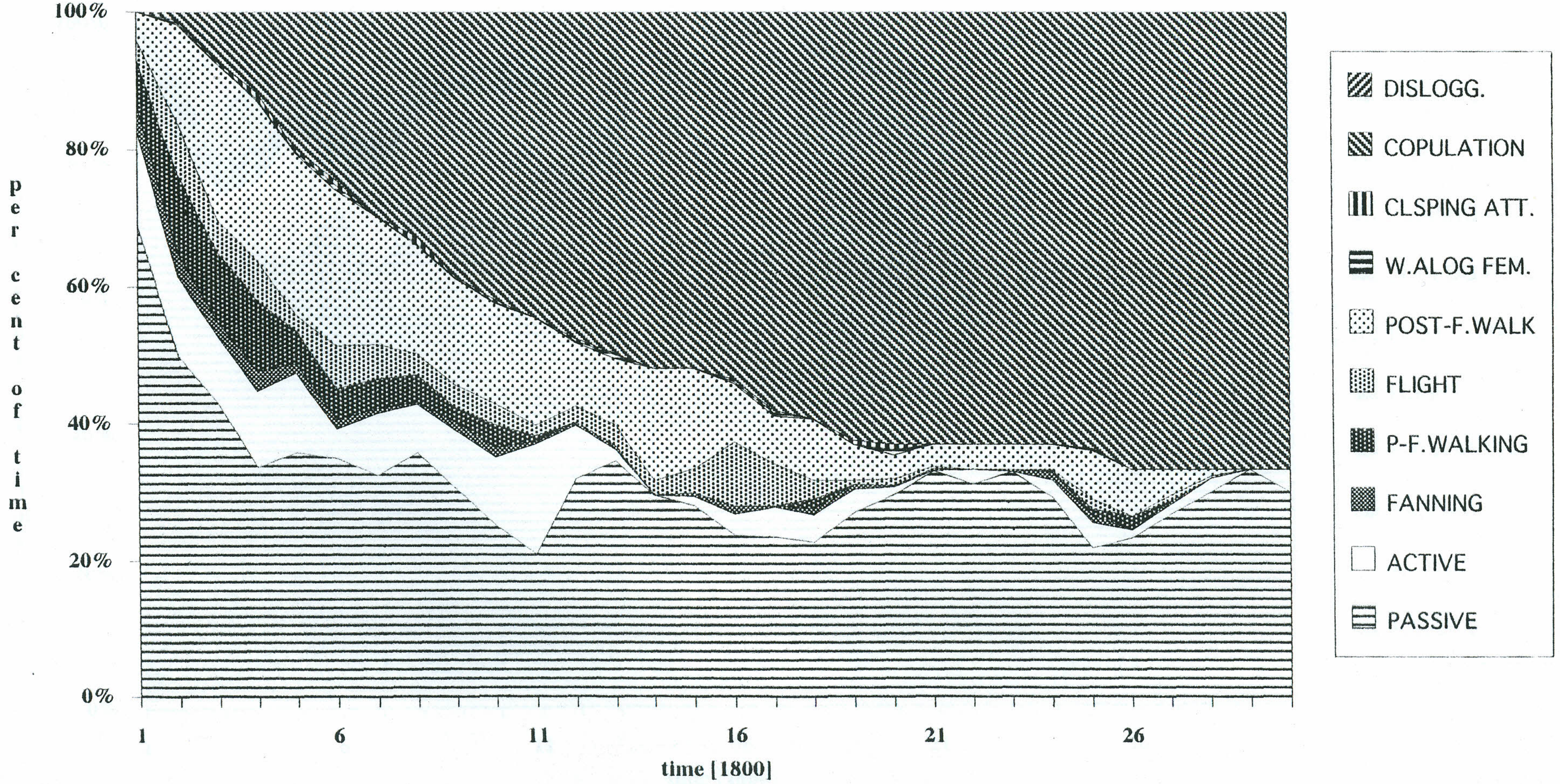

Fig. 5 Time budget for 0m-0f field insects

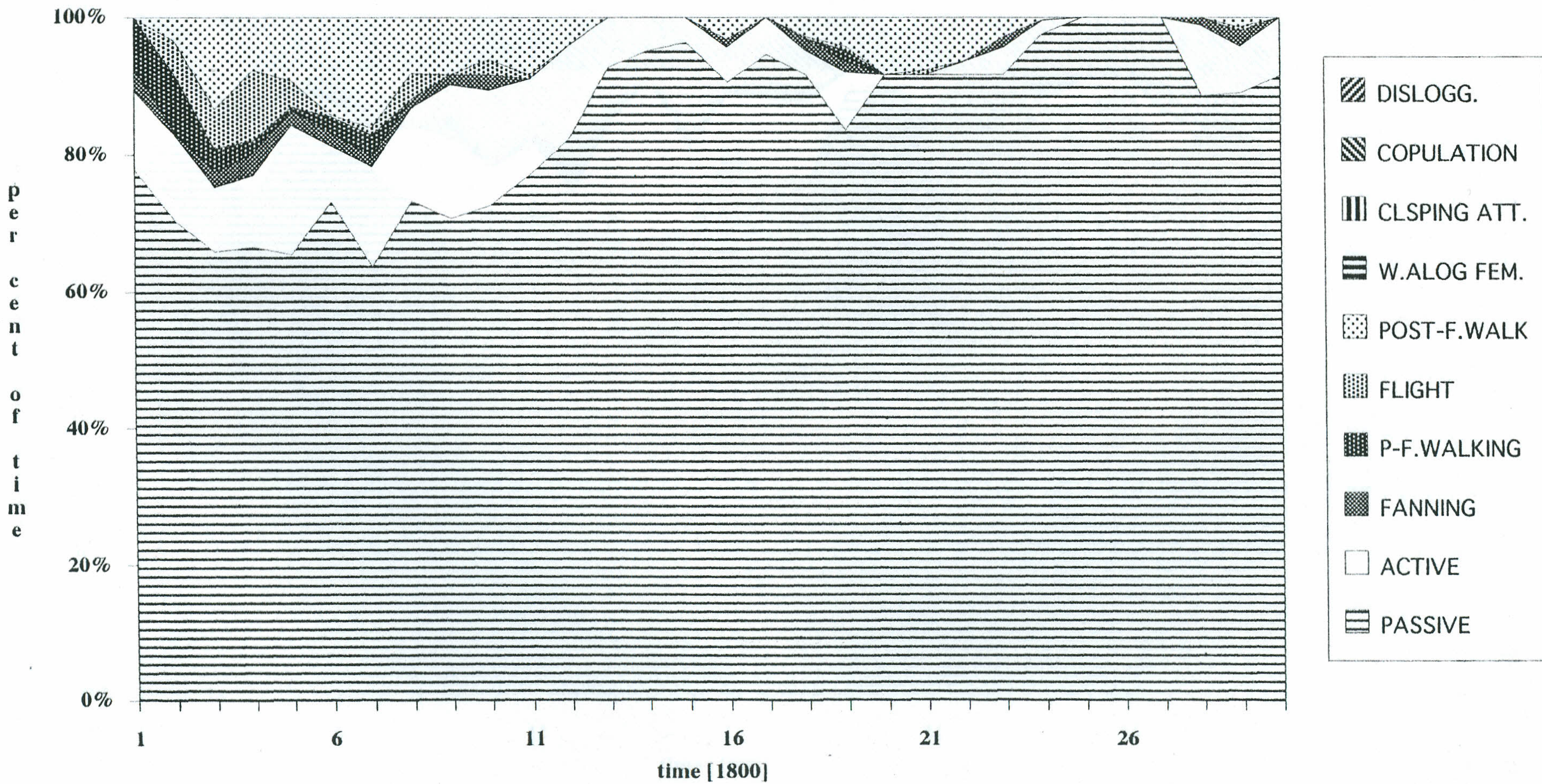

Fig. 6 Time budget for 0m-3f field insects.

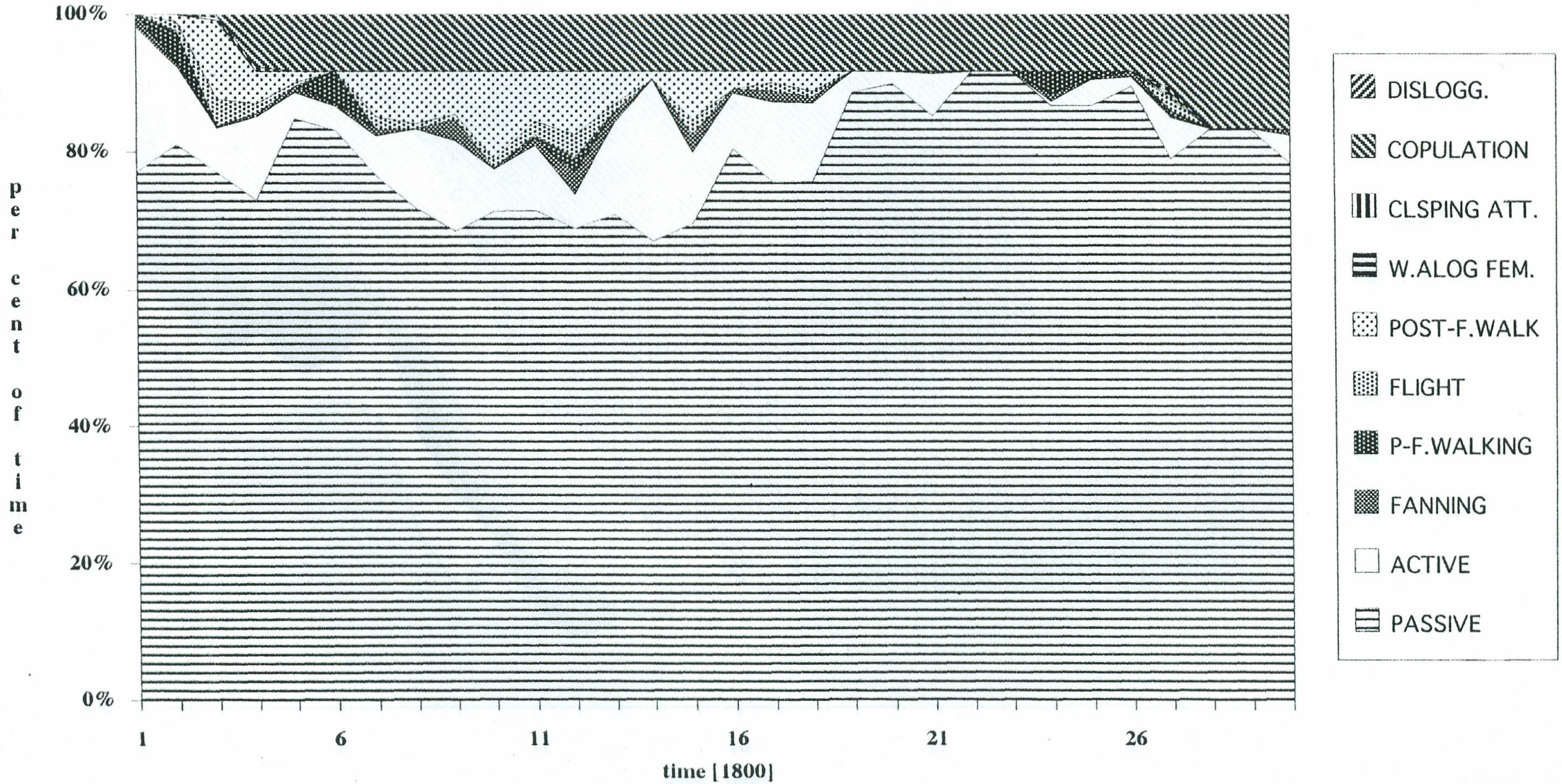

Fig. 7 Time budget for 3m-0f field insects.

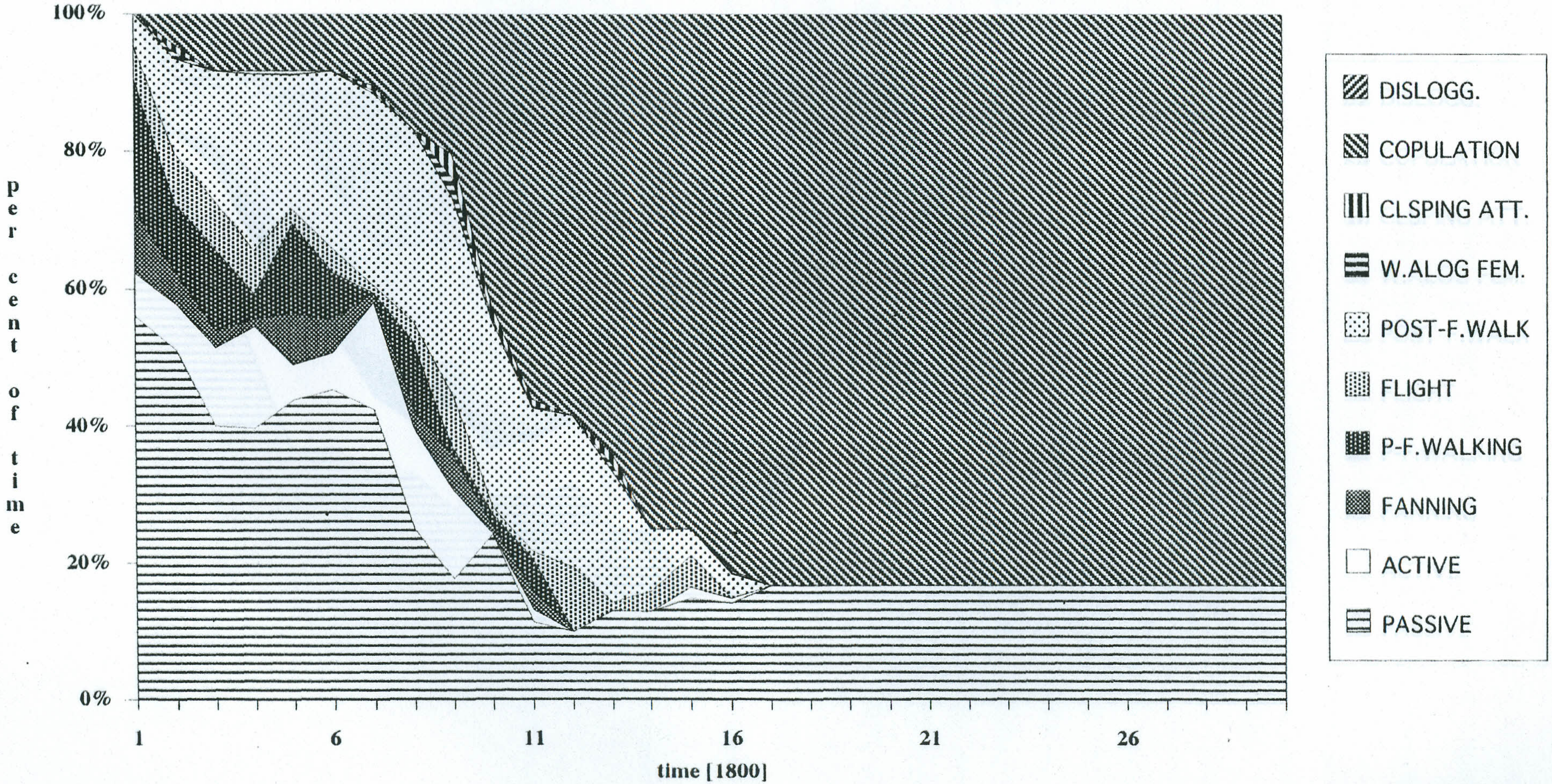

Fig. 8 Time budget for 3m-3f field insects.

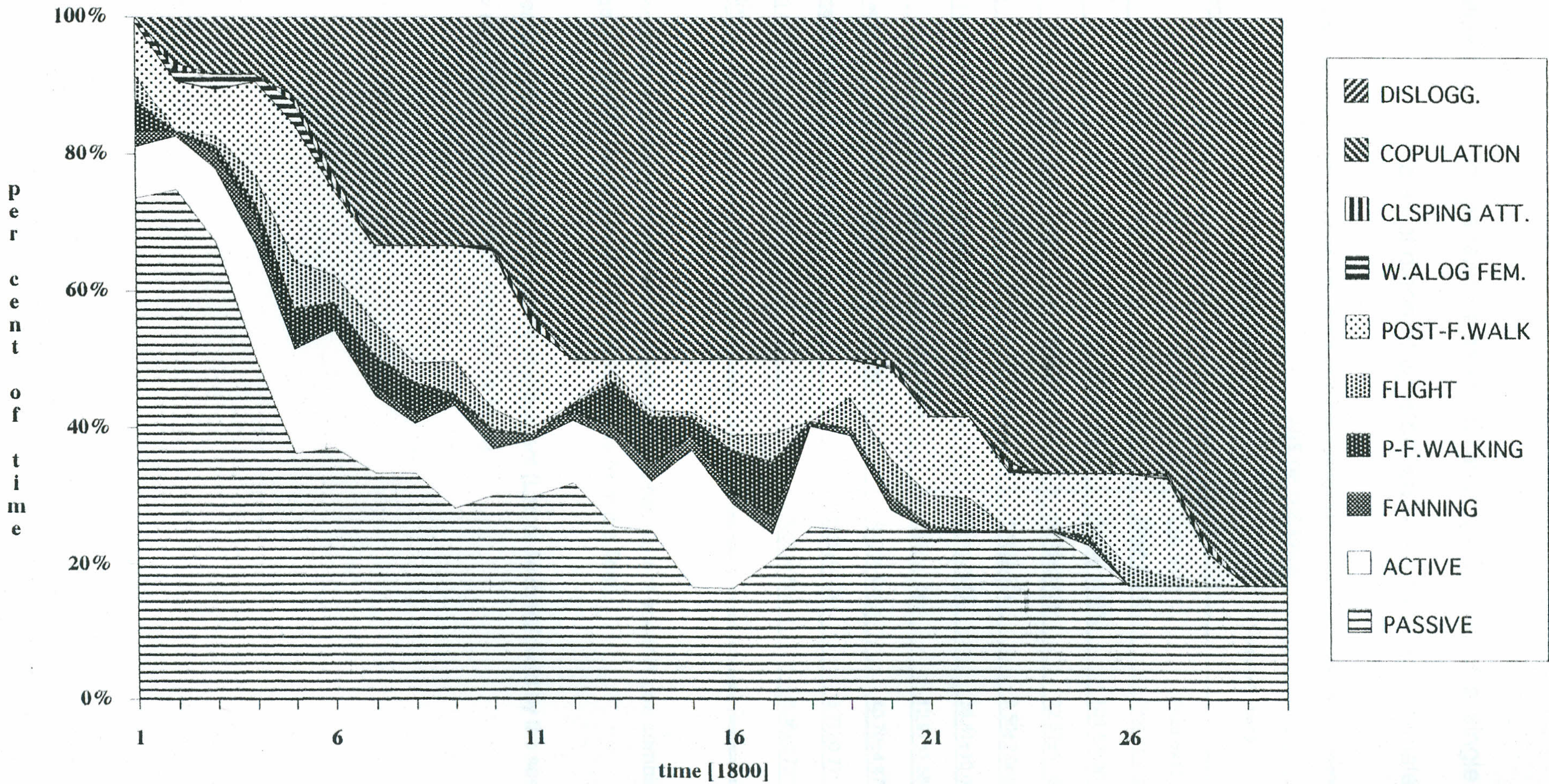

Table 3. Comparison of mean duration (seconds) of a single act of males of different ages paired with young adult females.

MALE BEHAVIOUR	AGE OF THE MALE			
	0-day old males		3-day-old males	
	Lab. n=26 Mean ± S.E	Field n=12 Mean ± S.E	Lab. n=25 Mean ± S.E	Field n=12 Mean ± S.E
Passive	421.55±49.08a	267.05±64.49a	93.25±16.97b	106.83±30.25a
Active	29.64±2.95b	20.96±2.46a	20.49±2.13a	22.57±5.76a
Fanning	6.37±0.88a	4.93±0.35a	8.10±0.72a	9.50±2.06a
Pre-flight walk	45.13±16.14a	16.00±6.97a	25.61±3.6a	36.81±10.02a
Flight	8.71±0.95a	8.79±1.46a	13.90±1.06a	12.97±1.58a
Post.F. walk	22.29±3.66a	23.26±3.38a	46.78±4.41b	40.70±4.87b
W. alongside female	4.25±0.67a	-*	2.83±0.37a	3.71±0.71*
Clapsing attempt	7.29±1.43a	-*	6.05±0.50a	6.36±0.72*
Copulation	-	-	-	-

* Could not be compared since these behavioural activities did not occur in one combination of age category (0-day old male x 0-day old female from the field).

Means in the same row from the same environment (Lab or field) followed by the same letter do not differ significantly (95% significance level).

Table 4. Comparison of mean duration (seconds) of a single act of males of different ages paired with old females.

MALE BEHAVIOUR	AGE OF THE MALE			
	0-day old males		3-day old males	
	Lab. n=26 Mean ± S.E	Field n=12 Mean ± S.E	Lab. n=27 Mean ± S.E	Field n=12 Mean ± S.E
Passive	229.93±35.95a	305.35±67.46a	200.41±42.76a	229.18±510.20a
Active	27.36±2.52a	23.2±3.10a	21.41±2.47a	34.4±5.19a
Fanning	5.98±0.42a	5.06±0.48a	6.01±0.43a	7.09±0.68a
Pre-Flight walk	23.67±4.38a	20.67±6.03a	25.51±2.76a	27.56±5.32a
Flight	8.49±0.61a	5.83±0.51a	10.87±1.01a	11.50±1.02b
Post-Flight walk	23.84±2.53a	20.00±3.36a	37.25±4.12b	43.04±4.90b
W. alongside female	4.36±1.05a	3.00±0.00a	3.36±0.60a	5.73±1.52a
Clapsing attempt	4.86±0.96a	6.00±2.00a	6.05±0.67a	6.50±0.31a
Copulation	-	-	-	-

Means in the same row from the same environment (Lab. or field) followed by the same letter do not differ significantly (95% significance level).

3:2:5:3 Mean number of complete events (frequency of occurrence of the activity)

Mature males from the laboratory when paired with young females had a higher frequency of flying, post-flight walk, walking alongside the female and clasping attempts than immature adult males (Table 5). No statistical difference was detected in the frequency of occurrence of all the behavioural activities between mature and immature males from the field (Table 5). Similarly, when paired with old females mature males from the laboratory flew and attempted to clasp the females at a higher frequency than did immature adult males (Table 6). Mature males from the field walked alongside the female 7 times more than did immature adult males from the same environment (Table 6). Interestingly no statistical difference was found between the behaviour of the males of the same age category with respect to the environment from which they came. Similarly, no statistical differnce was detected when either immature or mature males were paired with young or old females.

Table 5. Comparison of mean number of complete events accomplished by males of different ages paired with young adult females.

MALE BEHAVIOUR	AGE OF THE MALE			
	0-day old males		3-day old males	
	Lab. n=26 Mean ± S.E	Field n=12 Mean ± S.E	Lab. n=25 Mean ± S.E	Field n=12 Mean ± S.E
Passive	1.81±0.22a	1.67±0.38a	1.44±0.5a	1.92±1.03a
Active	4.42±0.41a	6.35±1.51a	3.96±0.78a	2.5±0.56a
Fanning	2.08±0.3a	3.5±1.26a	3.12±0.54a	2.67±0.69a
Pre-Flight walk	0.88±0.2a	3.5±0.42a	1.52±0.29a	1.33±0.33a
Flight	0.81±0.29a	2.33±1.01a	4.40±1.05b	2.92±0.6a
Post-Flight walk	1.08±0.35a	3.5±1.57a	5.16±1.01b	4.42±1.12a
W. alongside female	0.31±0.15a	-*	0.92±0.11b	1.17±0.3a*
Clapsing attempt	0.27±0.13a	-*	0.84±0.07b	0.92±0.15a*
Copulation	-	-*	-	-

* These values could not be compared since the behavioural activities did not occur in one combination of age category (0-day old males x 0-day old females from the field).

Means in the same row from the same environment (Lab or field) followed by the same letter do not differ significantly (95% significance level).

Table 6. Comparison of mean number of complete events accomplished by males of different ages paired with adult females.

MALE BEHAVIOUR	AGE OF THE MALE			
	0-day old males		3-day old males	
	Lab. n=27 Mean ± S.E	Field n=12 Mean ± S.E	Lab. n=27 Mean ± S.E	Field n=12 Mean ± S.E
Passive	1.63±32a	1.92±0.57a	1.37±0.34a	0.92±0.43a
Active	4.67±0.67a	5.00±1.35a	4.15±0.7a	3.83±1.04a
Fanning	2.44±0.44a	2.67±1.08a	2.67±0.37a	2.73±0.55a
Pre-Flight walk	1.00±0.27a	0.5±0.26a	1.59±0.33a	1.33±0.22a
Flight	1.52±0.41a	2.5±1.38a	4.37±0.93b	3.67±1.05a
Post-Flight walk	2.15±0.63a	2.67±1.48a	4.96±1.03a	4.25±1.09a
W. alongside female	0.41±0.15a	0-17±0.11a	0.81±0.13a	1.25±0.33b
Clapsing attempt	0.26±0.09a	1.17±0.11b	0.7±0.1b	0.83±0.11a
Copulation	-	-	-	-

Means in the same row from the same environment (lab or field) followed by the same letter do not differ significantly (95% signifiance level).

3:2:5:4 Mean total time spent for each activity

Mature males from the laboratory spent a longer time in flight, in post-flight walk and in copulation (8, 10 and 11 times respectively longer) than immature adult males when paired with young females (Table 7). However when paired with old females these males spent an average of 3 times longer in the same activities (Table 8). When paired with old females, mature males from the laboratory and the field spent 2 and 3 times less respectively passive. These males attempted to clasp the females for a longer time (3 and 5 times respectively for the laboratory and field males) than immature adult males (Table 8). No statistical difference was found in the total time spent for all activities between the laboratory and field insects. No statistical difference was detected when either immature or mature males were paired with young or old females.

Table 7. Comparison of the mean total time (seconds) spent for each activity by males of different ages paired with young adult females.

MALE BEHAVIOUR	AGE OF THE MALE			
	0-day old males		3-day old males	
	Lab. n=26 Mean ± S.E	Field n=12 Mean ± S.E	Lab. n=25 Mean ± S.E	Field n=12 Mean ± S.E
Passive	1472.88±63.86a	1522.33±90.48a	226.20±70.62a	417.25±154.39a
Active	143.23±3.71a	140.58±35.85a	85.64±22.66a	58.42±19.40a
Fanning	13.23±3.71a	17.25±6.85a	25.28±7.30a	25.33±13.51a
Pre-Flight walk	39.92±21.24a	17.33±8.72a	38.92±9.14a	49.08±20.92a
Flight	7.04±2.49a	20.50±10.98a	61.16±20.66b	37.83±9.49a
Post-Flight walk	24.00±8.08a	81.42±39.527a	242.0±56.2b	179.75±49.32a
W. alongside fem.	1.31±0.66a	-*	2.6±0.54a	4.33±1.97*
Clapsing attempt	1.96±1.03a	-*	5.08±0.61a	5.83±1.16*
Copulation	94.65±46.3a	-*	1073.12±106.46b	1022.17±149.87*

* These values could not be compared since the behavioural activities did not occur in one combination of age category (0-day old males x 0-day old females from the field).

Means in the same row from the same environment (Lab or field) followed by the same letter do not differ significantly (95% significance level).

Table 8. Comparison of mean total time (seconds) spent for each activity by males of different ages paired with old females.

MALE BEHAVIOUR	AGE OF THE MALE			
	0-day old males		3-day old males	
	Lab. n=27 Mean ± S.E	Field n=12 Mean ± S.E	Lab. n=27 Mean ± S.E	Field n=12 Mean ± S.E
Passive	1295.19±113.48b	1426.83±154.35b	572.67±119.49a	545.83±170.26a
Active	135.44±28.47a	128.5±42.41a	94.44±19.33a	134.50±40.16a
Fanning	14.63±3.4a	13.5±4.88a	16.04±3.15a	19.50±4.53a
Pre-Flight walk	23.67±8.07a	10.42±5.59a	40.63±7.89a	36.75±10.40a
Flight	12.89±3.71a	14.58±7.61a	47.52±11.61b	42.17±11.76a
Post-Flight walk	51.41±108.07a	53.33±32.74a	184.89±39.20b	182.92±62.33a
W. alongside fem.	1.78±0.91a	0.5±0.34a	2.74±0.68a	7.17±4.40b
Clapsing attempt	1.26±0.48a	1.00±6.72a	4.26±6.79b	5.42±0.77b
Copulation	262.67±105.24a	151.08±134.38a	837.81±130.38b	825.75±190.62b

Means in the same row from the same environment (Lab or field) followed by the same letter do not differ significantly (95% significance level).

3:2:6 Discussion

The results showed clearly that male age had a positive effect on the success of mating. Hirano and Muramoto (1976) reported that the percentages of females calling and pairs mating in the sweet potato leaf folder, *Brachmia macroscopa* Meyrick, were low on day 1, but heightened with the age, attaining the peaks on day 3 for calling and on day 4 for mating. Bartel and Shorey (1969) reported that peak response to the sex pheromone in *Epiphyas postvittana* Walker was not attained until the second night after moth emergence.

In *C. partellus*, observations from this study indicated that the sexual activity of males was low for newly emerged moths. In the same aged pairs, the low level of mating success in 0-day old pairs was effected by the male's activity. The level of percentage time spent in copulation was high for 3-day old moths irrespective of whether they are paired with newly emerged females or 3-day old ones suggesting that female's age was not limiting the success of mating.

In a related species, *C. suppressalis,* the mating success of the same aged pairs was low with 1-day old moths and the mating activity of females was high up to the age of four-days but decreased rapidly thereafter (Kanno and Sato, 1978). On the other hand the sexual activity of males was low with newly emerged moths, but it was maximum with 3 or 4 days old.

These results were in line with those of Unnithan and Paye (1991) who reported that when *C. partellus* moths were of equal age the percentage of mating on the day of eclosion was low but increased to 80-85% 1-2 days later.

In *Pseudaletia unipuncta* (Haw.) age related sensitivity to the two major components of the female sex pheromone was observed (Seabrook et al., 1979). These authors reported that the sensitivity of the male antennae to the two components was lowest on the day of emergence increasing to a peak on day 3 and then decreasing on day 5 and remained at that level till day 9 after which it decreased steadily until day 13.

It was probable that this difference in responsiveness to the sex pheromone with age is due to the changes in the sensitivity of the central and /or peripheral nervous system implicated in pheromone communication (Seabrook et al.1979). It thus implied that the olfactory neurons in the adult moth's antennae could not be physiologically stable but varied with age as the moth matured (Seabrook et al. 1979). These changes may have been associated with sexual maturation.

The results showed clearly that patterns of behavioural activities varied with age of the male with 3-day old males exhibiting a higher level of locomotory activities than 0-day old ones. This suggested some survival advantage for the males. It implied that on emergence in the field, 0-day old males did not engage in a lot of energy consuming activities such as flight, walking and pre-copulatory activities. Instead they were passive for most of the time probably sitting near the eclosion area waiting to achieve full sensitivity to the pheromone from calling females before becoming sexually mature. Such an option would be of tremedous advantage to the male because it reduced the risk of predation until such a time when engaging in such activities would be of benefit to the males by enabling them to acquire mates. On the other hand, 3-day old males spent more time in locomotory activities probably searching for females since they were sexually mature to mate.

The observation that there were no significant differences between the behaviour of the laboratory and field insects suggested that diet did not significantly influence behaviour. Since the laboratory colony was constantly renewed with field collected insects, not many generations were allowed to breed in the laboratory. This ensured that artificial selecton in the laboratory colony did not occur due to the simplified environment. If this was not the case, a greater difference in the behaviour of the laboratory and the field insects would have been expected.

CHAPTER FOUR

4.0 The effect of proximity of the release points of the synthetic sex pheromone components of the female to the behaviour of *C. partellus* male.

4:1 Introduction

For any effective trapping of insects the lure used should be able to offer continuous attraction over a fairly large distance ranging from several meters to a few centimeters from the bait. To achieve this the signal emitted from the trap should bear sufficient resemblance to the natural one and must be perceived by the receptive insect all the way to the source without significant interruption. In situations where a multicomponent blend is to be dispensed, the way in which the signal is perceived needs to be carefully considered. Components known to react chemically to give rise to products that are antagonistic to the pheromone or that considerably reduce the duration of pheromone present a special problem. The female sex pheromone of *C. partellus* is composed of two major components Z-11-hexadecenal and Z-11-hexadecen-1-ol. These were reported to react together in dilute hexane solution at -20°C and separate dispensing of the two components was recommended (Nesbitt et al., 1979). However, not enough attention has been given to the possible effects of the degree of proximity of the release points of the pheromone components on trap efficiency. In this study the effect of the release points of the two components on the behaviour of the male *C. partellus* was investigated.

4:2 Materials and methods

4:2:1 Insects

Pupae were separated by sex and held in different cages to prevent mating after moth emergence . For convenience , the photoperiod was shifted by 6 hours . The pupae were allowed to adjust to the shifted photoperiod for a few days . The moths were supplied with 5% sucrose solution dispensed from vials plugged with cotton wool .

4:2:2 Preparation of the filter paper dispensers

The dispenser was constructed from two filter papers (Whatman NO. 40) and a piece of aluminium foil. One square filter paper 2.5 cm^2 was loaded with 100 microliters n-hexane solution containing 100 micrograms of the aldehyde and the other paper with 100 microliters n-hexane containing 10 micrograms of the alcohol. For close release, filter papers loaded with the two components were separated only by a piece of aluminium foil and held together with a pin. For release from spatially distinct points the pieces of filter paper were spaced by 3 cm and supported on a block of cork material. The dispensers were loaded with synthetic pheromone around 1700 - 1800 hours and were dispensed in the observation chamber at 8.00 - 11.00 hours a. m .

4:2:3 Ethological observations

The experiments were conducted in a chamber 60 x 60 x 100 cm made of clear glass and aluminium and a wire mesh on the two opposite sides. An electric fan with about 0.2-0.8 m/s wind speed was used to generate air movement across the chamber. The observations were conducted in the laboratory under photoperiod L:D = 12 : 12 , 8-11 hours into the scotophase with the help of a red light. To assess the possible effect of the photophase shift, the results were further confirmed by several observations of insects kept under natural illumination, which were also observed during 8-11 hours into scotophase (2.00-5.00 hours a.m.).

Three treatments were used, a one-day-old virgin female in a cylindrical wire mesh cage (3 cm diameter and 8 cm long); the filter paper dispenser with the components close together, and the filter paper dispenser with the components separated by 3 cm. Each type of pheromone source was placed upwind of the chamber and tested independently. For each experiment, a single virgin one-day-old male was released at the downwind end of the chamber and its behaviour towards the source of the pheromone observed for one hour. For each observation a new individual was used. The following parameters of male behaviour towards the pheromone source were quantified:

a. time spent resting before upwind flight;

b. time taken walking while wing fanning;

c. rate of antennal beats per minute;

d. total time spent resting;

e. total time spent flying (random flight);

f. general vigour (graded arbitrarily from 0 to 10);

g. nearest distance reached relative to the source;

h. time taken to locate the source;

i. time spent flying upwind up to 5 cm from the source (oriented flight); and,

j. time taken to explore within 5 cm of the source.

Three observations were conducted in a single session and one observation for each pheromone source every day. The order of the pheromone sources used during the successive sessions (days) was systematically rotated. Observation of the male behaviour towards each pheromone source was repeated 20 times.

4:2:4 Data analysis

Data analysis was performed using the analysis of variance to determine whether there were significant differences between the treatments. Mean comparison between the treatments for each behaviour category was performed using Tukey's test (Spjotvoll and Stoline, 1973). Due to the high variability of the data log (x + 0.5) was used to transform the data (Sokal and Rolf, 1981).

4:3 Results

Results on the observation of the male behaviour towards the three different pheromone sources show that there were only relatively small differences in the male behaviour in response to virgin females as compared to the paper dispensers with the pheromone components dispensed close to each other (Table 9). Males approaching the virgin females were slightly more vigorous (7.8 compared to 6.1), spent 3.3 times more walking while wing fanning, moved their antennae at a higher rate and walked while wing fanning around the pheromone source 2½ times more than those approaching the dispenser with components close to each other. These males curved their abdomen towards the female. It was noticed that the males moved round the dispenser papers rapidly wing fanning and bending their abdomen to come into contact with the papers. In both cases, however, all males were able to locate the pheromone source although 4 out of 20 males did not directly land on the source in the case of the dispenser with pheromone components dispensed close to each other (came closer than 5 cm).

On the contrary, separation of the release points of the pheromone components resulted in a notable confusion of males and on average the nearest distance to the source reached was 26.6 cm. The males were much less vigorous (2.5 compared to 7.8 for virgin females) and spent less time (135.2 sec. compared to 538.3 sec for virgin females) flying. They rested 1½ times longer and fanned wings while walking 12 and 5 times, respectively, less than the males approaching virgin females as well as the dispenser with components close to each other. Remarkably, only three out of twenty males came closer than 5 cm to the source, but even then they spent considerably less time moving around the source. These males spent 40 and 100 times respectively less time exploring the source than in the cases where dispensers with components close to each other and virgin females were used.

Table 9. Behaviour of *Chilo partellus* males towards virgin female versus the female pheromone components dispensed at different levels of proximity (laboratory observation)[a]

MALE BEHAVIOUR	TYPE OF THE PHEROMONE SOURCE		
	A	B	C
	Virgin female	Paper dispenser	
		components close*	components separated**
Time spent resting before upwind flight	5.6 a	35.1 a	55.4 a
Time taken walking while wing fanning	750.5 a	332.1 b	64.6 c
Rate of antennal beats per minutes	148.1 a	120.4 b	50.8 c
Total time spent resting	2018.8 b	2256.6 b	3103.3 a
Total time spent flying (random flight)	538.3 a	319.2 a	135.2 b
General vigour (graded arbitrally from 0 to 10)	7.8 a	6.1 b	2.5 c
Nearest distance reached relative to the source	0.0 b	0.6 b *	26.6 a
Time taken to locate the source	185.1 a	313.5 a	588.3 a **
Time spent flying upwind up to 5cm from the source (oriented flight)	14.7 a	15.7 a	11.3 a **
Time taken moving 5cm or closer around the source	948.8 a	373.0 b	9.3 c **

* All males came closer than 5 cm to the source and only 4 males did not land directly on the source

** Only 3 males out of 20 got closer than 5 cm to the source and the numbers represent means for those 3 males only

a Within rows, difference between means followed by the same letter are not significant ($P>0.05$; Tukey's test on log - transformed data)

4:4 Discussion

The results showed that the dispenser with the components close to each other was comparable in attractiveness to the calling virgin females. This was demonstrated by the fact that all the males located the source or came closer than 5 cm as in the case of the virgin females. The total time spent resting and flying by the males approaching the virgin females did not significantly differ from that in the case of the dispensers with the components close to each other. However, males approaching calling females moved round the source fanning wings for a significantly longer time than did those approaching the dispensers with components close to each other. This suggested that the dispenser did not wholly simulate the signal emitted by the calling females. Interestingly, it was noticed that the female elevated her abdomen and pumped the ovipositor at a higher rate at the time of male's arrival. This suggested that visual cues at short range may have been an important factor in eliciting greater vigour and prolonged exploring of the source in the males approaching the calling females.

The results showed that even a small separation between the release points of the female *C. partellus* pheromone components substantially decreases trap efficiency. The observation of the male flight behaviour suggested that the decrease was associated with confused behaviour of the male approaching the trap. The three out of twenty males that came closer than 5 cm to the source when the components were separated by 3 cm may have located the source by coincidence. This is so because they spent a significantly longer time to locate the source and a significantly shorter time moving round the source once located as compared to those males that approached calling virgin females or the dispensers with components held close to each other.

It is possible that the pheromone components if dispensed from a point-like source do not get separated within the air-stream carrying them and therefore the integrity of the signal is maintained over a substantial distance (Baker and Haynes, 1989; Liu and Haynes, 1992). This was demonstrated by experiments with pheromone inhibitors where pheromone traps remained effective even when located in an atmosphere permeated with corresponding inhibitors (McLaughlin et al., 1972; Carde et al., 1975; Daterman et al., 1975; Kaae et al., 1974; McLaughlin et al., 1974; Mitchell, 1976). When the inhibitor was dispensed together with the corresponding pheromone from a point-like source, no orientation flights and landing at the source occurred (Witzgall and Priesner 1991). In contrast, placing the inhibitor 5cm apart did not suppress orientation flight to the attractant source. A decrease in trap efficiency from separate release of the pheromone components relative to joint release of the blend has also been reported for the cabbage looper moth (Linn and Gaston, 1981).

CHAPTER FIVE

5:0 Laboratory testing for any inhibitory effect of polyvinyl chloride (PVC) on the behaviour of the male *Chilo partellus* to the synthetic blend of the female sex pheromone

5:1 Introduction

The suppression of orientation by structurally related chemicals is a well known phenomenon in Lepidoptera. Such chemicals commonly known as "attraction inhibitors" or "pheromone antagonists" have been widely demonstrated by field trapping experiments, but only a few attempts have been made to analyze their mode of action. The term "inhibitor " has been used to refer to those chemicals that when liberated with a normally attractive single compound or mixture of compounds, somehow prevents males from becoming trapped in the sticky coating of the baited traps (Tumlinson et al., 1974; Parrilia and Guerrero, 1993). These studies attempted to establish whether PVC, a candidate carrier material for dispensing of the pheromone components, had any inhibitory effects on the behaviour of the male of *C. partellus* to the synthetic blend of the female sex pheromone.

5:2 Materials and methods

5:2:1 Construction of the dispensers

Four different types of dispensers were used in this study and are described as below:

a. The filter paper dispenser with the pheromone components close to each other (A).

This was constructed from two filter papers (Whatman No.40) and a piece of aluminium foil. One square filter paper 2.5 cm^2 was loaded with 100 microliters n-hexane solution containing 100 micrograms of the aldehyde and the other paper with 100 microliters n-hexane containing 10 micro grams of the alcohol.The filter papers loaded with the two components were separated by a piece of aluminium foil to prevent any contact between them and held together with a pin. This was used as the control.

b. Filter paper dispenser assembled with clean unloaded polyvinyl chloride (B).

The filter paper dispenser was constructed as described in (a) above. Small pieces of aluminium foil were placed at the centre of the outer side of each filter paper dispenser. Then two clean polyvinyl chloride pieces measuring 0.5 cm in length and 0.8 cm in diameter were pinned to the filter papers through the aluminium foil, one on each side of the filter paper.

c. The PVC dispenser (C).

This dispenser was made from two polyvinyl chloride pieces one loaded with 0.01% alcohol and the other with 0.1% aldehyde each measuring 0.5cm long and 0.8cm diameter. They were separated by small pieces of aluminium foil to prevent any contact between them.

d. The dispenser with aldehyde on PVC and alcohol on filter paper (D).

This dispenser was constructed from a square filter paper 2.5 cm^2 loaded with 100 microliters n-hexane containing 10 micrograms of the alcohol. The filter paper was then assembled with a PVC piece of the size described in (b) above loaded with 0.1% aldehyde and held together with a pin. Small pieces of aluminium foil were used to separate the filter paper from the PVC to prevent any contact between the two. The PVC dispenser loaded with the alcohol was allowed to "age" for a period of 8-24 days while that loaded with the aldehyde was allowed to age for a period of 15-26 days before use. The dispensers were aged to allow stabilization of the release rate of the pheromone components. The filter papers were loaded with the pheromone between 1700-1800 hours. All the dispensers were assembled between 1700-1800 hours and dispensed in the observation chamber between

07.30 and 11.30 hours every day. Each type of dispenser was supported on a block of cork material and placed at the upwind end of the observation chamber and tested independently. A 1-day-old virgin male was released at the downwind end of the chamber and it's behaviour towards the pheromone source observed for one hour. Four observations were conducted every day in a single session, one observation for each pheromone source. The order of the dispensers used during the successive sessions was systematically rotated. A new individual was used for each observation. The observation of male's behaviour towards each type of dispenser was repeated 10 times. The following parameters of male's behaviour towards the pheromone source were quantified:

a. Time spent resting at the downwind side of the chamber before upwind flight;

b. Time taken to fly upwind about 50 cm or more;

c. Total time spent in flight;

d. The nearest distance reached relative to the source;

e. Time taken moving 5cm or less round the source;

f. Time taken to locate the source;

g. Time taken walking while wing fanning;

h. Total time spent resting;

i. Vigour of activities graded arbitrarily on a scale of 10;

j Rate of antennal beats per minute;

k. Time taken walking without wing fanning.

5:3 Data analysis

Analysis of variance was done on the results using subroutine from the package SAS (SAS Institute, 1987). Mean comparison between the treatments for each behaviour category was performed by calculating the Least Significance Difference (LSD) test at 5% level. Due to the high variability of the data ,the square root of the logs $\sqrt{\log(x+1)+0.5}$ was used to transform the data so as to minimize the correlation between the mean and variances of each behaviour category (Sokal and Rohlf, 1981).

5:4 Results

Table 10 shows the behaviour of male *C. partellus* towards four different types of dispensers loaded with the synthetic pheromonal components of the female. Males approaching the filter paper dispenser spent a significantly shorter period resting before upwind flight than did those approaching the dispensers with the alcohol on filter paper and the aldehyde on PVC.

Table 10. Behaviour of *C. partellus* male towards the PVC dispensers versus the filter paper dispenser.

MALE BEHAVIOUR	DISPENSER TYPE			
	A Mean ± S.E.	B Mean ± S.E.	C Mean ± S.E.	D Mean ± S.E.
Time spent resting before upwind flight	0.00±0.00b	6.00±6.00b	120.00±120.00ab	9.30±4.97a
Time spent flying upwind about 50 cm or more	5.00±0.30a	4.90±0.23a	5.20±0.55a	5.70±0.58a
Total time spent flying	469.10±124.80a	323.00±81.01ab	169.90±55.44b	127.20±28.85b
Nearest distance reached to the source	3.00±3.00b	4.00±4.00b	16.70±4.70a	4.20±2.74b
Time taken moving 5 cm or closer around the source	695.00±170.71a	282.22±46.89a	114.33±37.33b	116.43±20.40b
Time taken to locate the source	370.33±84.82b	504.89±108.40ab	1431.67±606.63a*	498.63±144.96ab
Time taken walking while wing fanning	391.50±88.46a	281.22±38.14a	79.38±16.97b	111.78±28.00b
Total time spent resting	2713.80±161.48b	3051.20±112.83a	3449.70±78.46a	3358.80±44.00a
General vigour graded from 0-10	6.70±0.54a	5.30±0.54a	3.00±0.56b	3.40±0.50b
Rate of antennal beats per minute	122.50±11.19a	95.50±9.96a	52.50±8.67c	65.00±7.45bc
Time taken walking without wing fanning	28.00±18.00a	30.50±10.03a	29.29±12.72a	35.67±29.69a

Means followed by the same letter in the same row are not significantly different at 5% level. Mean comparison performed by use of LSD on transformed data [$\sqrt{\log(x+1)+0.5}$]

* Only 3 males out of 10 got closer than 5 cm to the source and the numbers represent means for those 3 males only.

A: Filter paper dispenser
B: Filter paper dispenser assembled with clean PVC
C: The PVC dispenser
D: Dispenser with aldehyde on PVC and alcohol on filter paper

This period did not significantly differ from that taken by males approaching the filter paper dispenser with clean PVC. The particular males took 3 times longer in flight than did those approaching the PVC dispenser although this did not differ significantly from the period taken by males approaching the filter paper dispensers assembled with clean PVC. However, it differed significantly from that taken by males approaching the filter paper dispenser and the dispenser with the alcohol on filter paper and the aldehyde on PVC. On average, the nearest distance to the source that the males approaching the PVC dispenser reached was 16.7cm which was significantly longer than that reached by the males when they approached the other three dispensers. Also, these males took a significantly longer time to locate the source than did those approaching the filter paper dispenser. They moved their antennae at a lower rate (2.3 times lower) and spent 6 times less time moving 5cm or closer around the source than did those that approached the filter paper dispenser. The males fanned wings while walking 5 times less than did those that approached the filter paper dispenser. However, there was no significant difference in the time taken walking while fanning the wings between males approaching the filter paper dispenser and those approaching the filter paper dispenser with clean PVC. All the males approaching the four different types of dispensers did not differ in the length of time they took walking without fanning wings and flying upwind.

5.5 Discussion

The results showed that the dispenser with clean PVC was comparable to the filter paper dispenser in its performance. This suggested that PVC did not inhibit the male response towards the synthetic pheromone. On the other hand, the dispenser with the two components loaded on PVC had a relatively poor performance compared to the control. Remarkably only 3 males were able to locate the source in the case of this dispenser. It might be that the PCV released the alcohol at a considerably lower rate than the filter paper thus causing the insect's nervous system to fail to integrate the sensory information from this dispenser into a biologically meaningful signal. In such a situation, the insect would not be expected to locate the source and therefore would not be trapped.

It was also possible that the ratio of surface area to volume of the two PVC dispensers combined was relatively smaller than that of the two filter paper dispensers. This may have modified the proportion of surface area of volatilization of the pheromone components. PVC therefore in this situation was a fairly suitable material for dispensing the pheromone since it did not appear to alter the response of males to the pheromone .

In some species that have bi-component pheromonal systems the individual components could have an inhibitory effect on male stimulation by the sex pheromone. This was reported for the smaller tea tortrix *Adoxophyes fasciata* where the individual sex pheromonal components cis-9 and cis-11-tetradecen-1-ol acetate inhibited the subsequent stimulatory response of male moths to the sex pheromone (Hirai et al.,1974). The researchers (Hirai et al., 1974) concluded that such an inhibitory effect of the individual pheromone components on sexual behaviour of the males could play an important role in the isolation of the smaller tea tortrix from any sympatric species that used either cis-9 or cis-11-tetradecen-1-ol acetate as the sex pheromone. A similar phenomenon was reported in *A. orana (F. von R.)* where the main component cis-9-tetradecenyl acetate without the second component cis-11-tetradecenyl acetate did not attract males at all (Minks and Voerman, 1973).

CHAPTER SIX

6.0 SUMMARY, GENERAL DISCUSSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

1. Studies on the influence of age on the attractancy and the responsiveness of females and males were conducted under laboratory conditions. One-day- and three-day-old males were more attracted to one-day-old females than to three-day-old ones. No significant differences in response due to male's age were found when one- and three-day-old males were used.

It was found that 0- and one- day old females did not differ in their attractiveness to the three age categories of males tested. 0-day old males had a significantly lower responsiveness to the three age categories of females tested than either one-or three-day-old males. These observations have practical implications to the researchers when designing and developing a pheromone dispenser for monitoring *C. partellus* populations. The dispenser developed would be expected to sufficiently resemble the signals emitted by 0- and 1-day-old females in the composition and release characteristics of the pheromone. Since 3-day-old males were the most responsive of all the ages tested, the researchers testing the response of male *C. partellus* to the dispensers of the synthetic sex pheromone of the female may find it particularly advantageous to use this age category than the younger ones. In future research should be conducted using moths of all ages to find out whether similar results could be obtained.

2. Studies on the influence of age on the mating success showed that 0-day old males spent the largest proportion of the time while passive and a very small proportion of the time was spent in copulation. Three-day-old males spent a significantly smaller proportion of the time while passive but a larger proportion of the time in copulation.

The low success of mating when 0-day-old males were used suggested that male age has an influence on the mating success. Further research should be conducted to determine whether the observed trend was continued even in very old moths (8-9 days of age). It is also suggested that comparison of Electroantennographic responses of males of various age categories should be conducted and these should then be compared with the behavioural responses of intact males of the corresponding ages. This would shed light on whether there is any relationship between sensitivity of the antennae and the behavioural response of the male moth. No major differences were observed between the behaviour of laboratory and field collected insects and this suggested that the diet did not have a profound effect on the behaviour of the insects.

3. Studies to investigate the behaviour of the male *C. partellus* towards virgin females versus the female synthetic pheromone components dispensed at two different levels of proximity were conducted. Only relatively small differences in the male behaviour in response to virgin females as compared to the paper dispensers with pheromone components dispensed close to each other were observed. Separation of the release points of the pheromone components by 3cm resulted in a significant change in male behaviour and a decrease in the bait performance. Going by these results, it appeared that where components of a pheromone or other semiochemical blend needed to be dispensed separately, special attention should be given to proximity effects resulting from the spacing of component dispensers. This may be important where the components act together synergistically and would be expected to be of less consequence where they act in an additive manner (Lux et al., 1994). It would also be anticipated that the effect may be minimized through appropriate design of the trap. However, the development of a dispensing device that allowed separate but close release of the components and that can simulate release of the blend from a calling female would appear to be the best solution. Further research should be conducted to test the response of males of various age categories to the filter paper dispenser to establish whether the behaviour of these age categories of males was comparable. The knowledge from such work would help to predict which age category of males would be most attracted to the bait of the trap.

4. Tests for any inhibitory effect of polyvinyl chloride (PVC) on the behaviour of the male *C. partellus* to the synthetic blend of the female sex pheromone were conducted. It was found that PVC did not inhibit the response of the males to the synthetic female sex pheromone. The PVC dispenser was found to have a poorer performance than did the filter paper dispenser and this was thought to be due to some differences in the release characteristics of the alcohol by PVC. From these results it seemed that researchers intending to design and develop a pheromone dispenser for *C. partellus* pheromone components could find it particularly advantageous to use PVC as a carrier material for dispensing the synthetic sex pheromone since it did not appear to alter the response of the males to the pheromone.

REFERENCES

Adeyemi, S. A. O. (1969). The survival of stem borer population in maize stubbles. *Bull. Ent. Soc. Nigeria* 2: 15-22.

Alcock, J. E.; M. Banows,; G. Gordhl; J. I. Hubbard; L. L. Kirkendall; D. Pyle; T. L. Ponder, and F .G. Zalom, (1978). The ecology and evolution of male reproductive behaviour in the bees and wasps. *Zoological Jour. of the Linnean Society of London* 64: 293-326.

Alexander, R. D. and G. Borgia, (1979). On the origin and basis of the male-female phenomenon. In Sexual selection and reproductive competation in insects, ed. M.S. Blum and N.A. Blum, New York: Academic Press.

Ampofo, J. K. O.; K.N. Saxena; J.G. Kibuka and E.O. Nyangiri, (1986). Evaluation of some maize cultivars for resistance to the stem borer *Chilo partellus* Swinhoe Lepidoptera: Pyralidae in Western Kenya. *Maydica* 31: 379-389.

Arn, H. (1990). Pheromones Ridyway R. L., Silverstein, R. M. and Inscoe, M. N. (eds.). Behaviour modifying chemicals for insect management. Applications of pheromones and other attractants. Mercel Dekker Inc.; New York and Basel, pp. 717-22.

Baker, T. C. and L.P.S. Kuenen, (1982). Pheromone source location by flying moths: a supplementary non-anemotactic mechanism. *Science* 216: 424-7. [4,5]

Baker, T.C. and R.T. Cardé, (1979b). Analysis of pheromone mediated behaviours in male *Grapholitha molesta*, the oriental fruit moth (Lepidoptera:Totricidae). *Environ. Ent.* 8:956-8.

Bakers, T. C. and K.F. Haynes, (1989). Field and laboratory electroatennographic measurements of pheromone plume structure correlated with oriental fruit moth behaviour. *Physiol. Ent.* 14: 1-12.

Bakers, T. C. (1985). Chemical control of behaviour. Comprehensive insect physiology, biochemistry and pharmacology (ed. by G. A. Kerkut and L. S. Gilbert), pp. 621-672 Pergamon Press, Oxford.

Barrer, P. M. (1976). The influence of delayed mating on the reproduction of *Ephestia cautella* Walker Lepidoptera: Phycitidae. *Jour. Stored Product Res.* 12: 165-9.

Bartel, R.J. and H.H. Shorey, (1969) A quantitative bioassy for the sex pheromone of *Epiphyas postivattana* (Lep.) and factors limiting male responsiveness. *Jour. Insect Physiol.* 15:33-40.

Bartell, R. J. (1977). Behavioural responses of lepidopteran to pheromones: In Chemical control of insect behaviour (eds. Shorey, H. H. and McKelvey, Jr. J. J.), pp. 201-213.

Bartell, R. J. and H.H. Shorey, (1969). Pheromone concentrations required to elicit successive steps in the mating sequence of males of the light brown apple moth, *Epiphyas postvittana* (Lepidoptera) and factors limiting male responsiveness. *Jour. Insect Physiol.* 15: 3-40.

Beever, P. S.; H. David, and O.T. Jones, (1990). Female sex pheromones of *Chilo* spp. (Lepidoptera: Pyralidae) and their developmemt in pest control applications. *Insect Sci. Applic.* 11 : 787-794.

Bell, W. J. and T.R. Tobin, (1982). Chemo-orientation. *Bio. Rev.* 57: 219-60. [2,4,5,15,20]

Bell, W. J.; C. Parsons, and E.A. Martinko, (1972). Cockroach aggregation pheromones: Analysis of aggregation tendency and species specificity (Orthoptera: Blattidae). *Jour. Kans. Ent. Soc.* 45: 414-421.

Benerjee, C.A. (1969). Sex attractants in sod webworms. *Jour. Econ. Entomol.* 62:705-708

Berisford, C. W. and U.E. Brady, (1972). Attraction of Nantucket pine tip moth males to the female sex pheromone . *Jour. Econ. Ent.* 65: 430-433.

Birch, M. C. (1974). Aphrodisiac pheromones in insects. In "Pheromones" (M. C. Birch, ed.), pp. 115-134. Am. Elsevier, New York.

Blight, M. M.; J.M. Kickett; M.C. Smith, and I.J. Wadhams, (1984). An aggregation pheromone of *Sitona lineatus*: Identification and initial field studies. *Naturwinssenschaften*, 71: 480-481.

Borden, J. H. (1967). Factors influencing the response of *Ips confusus* (Coleoptera:Scolytidae) to male attractant. *Can. Ent.* 99: 1164-1193.

Brown, L. N. (1972). Mating behaviour and life habits of the sweet-bay silk moth *Callosamia carolina*. *Science* 176: 73-75.

Brownbridge, M.(1991). Natural *Bacillus thuringiensis* isolates for the management of lepidopteran cereal pests. *Insect Sci. Applic.* 12:57-61.

Buchi, R.; J. Baldinger; S. Blaser and R. Brumetti, (1981). Versuche Zur Bekampfung des maiszun slers, *Ostrinia nubilalis* Hbn., mit der Verwirrungstechnik. *Mitt. Shweiz. Ent. Ges.* 54: 87-98.

Bughio, A. R.; S.S. Akbar, and A. Qureshi, (1977). Rearing and biology of maize borer, *Chilo partellus* Swinhoe (Lepidoptera:Pyralidae). *Pakistan Jour. of Zoology.* 9 (2): 145-156.

Butler, C. G. (1970). Chemical communication in insects: Behavioural and ecologic aspects. *Adv. Chemoreception* 1: 35-78.

C. A. B. (1977a). *Chilo partellus* Swinhoe Distribution maps of pests NO. 184 (revised). Commonwealth Agricultural Bureaux, Commonwealth Institute of Entomology, London.

Campion, P. J. and B.F. Nesbitt, (1983). The utilization of sex pheromones for the control of stem borers. *Insect Sci. Applic.* 4: (1/2), 191-197.

Campion, D. G. (1984). Survey of pheromone uses in pest control. In techiniques in pheromone research (Edited by Hummel H. E. and Miller T. A.), pp. 405-449 Springer-Verlag, New York.

Campion, D. G. (1989). Semiochemicals for the control of insect pests. British Crop Protection Council Monograph No. 43. Progress and Prospects in Insect Control. British Crop Protection Council, Farnharm, U.K., pp. 119-27.

Cardé, R.T; C.C. Doane; J. Granett and W.I. Roelofs, (1975). Disruption of pheromone communication in the gypsy moth: Some behavioural effects of disparlure and an attractant modifier. *Environ. Ent.* 4:944-946.

Cardé, R.T.; J. Konchansky; J.F. Stimmel; A.G. Wheeler Jr. and W.F. Roelofs, (1975). Sex pheromone of the European corn borer (*Ostirnia nubilalis)*: Cis-and trans- responding males in Pennsylvania. *Environ. Ent.* 4:413-414.

Cardé, R.T. (1981). In *the gypsy moth: research toward intergrated pest management* (eds. C. C. Doane and M. L. Mcmanus) pp. 1584-87. *US Dept. Agric. Tech. Bull.* 1584, Washington, D. C. [8,20]

Cardé, R. T. (1990). Principles of mating disruption. In: Ridgway, R.h. Silverstein, R.M. and Inscoe. M.N. (eds), Behaviour - Modifying Chemicals for Insect Management. Applications of Pheromones and other Attactants. Marcel Dekker Inc., New York and Basel, pp. 47-71.

Casagrade, E. (1993). The commercial implementation of mating disruption for the control of the rice stem borer, *Chilo suppressalis*, on rice in Spain. IOBC wprs Bull: *Insect pheromones vol.* 16 (10): 82-89.

Castrovillo, P. J. and R.T. Cardé, (1979). Environmental regulation of female calling and male pheromone response periodicities in the codling moth (*Laspeyresia pomonella*). *Jour. Insect Physiol.* 25:659-667.

Colwell, A.E.; H.H. Shorey; L.K. Gaston, and S.E. Van Vorhis Key, (1978). Short-range precopulatory behaviour of males of *Pectinophora gossypiella* (Lepidoptera:Gelechiidae). *Behavioural Biol.* 22:323-335.

Cordillot, F. and P. Duelli, (1989). Adaptive dispersal in the European corn borer *Ostrinia nubilalis* Hbn. (Lep. :Pyralidae) in North western Switzerland. *Acta phytopathologica et. Entomologica. Hungarica* 24: 65-71.

Dabrowski, Z. T. and E. L. Kidiavai, (1983). Resistance of some sorghum lines to the spotted stem borer *Chilo partellus* under Western Kenya conditions. *Insect Sci. Applic.* 4: 119-126.

Daterman, G. E. (1972). Laboratory bioassay for sex pheromone of the European pine shoot moth, *Rhyaciona bvolianar. Ann. Ent. Soc. Am.* 65: 119-123.

Daterman, G.E.; G.D. Davis, Jr. and R.G. Smith, (1975). Comparison of sex pheromone versus an inhibitor for disruption of pheromone communication in *Rhyacionia buoliana*. *Environ. Ent.* 4:944-946.

Davis, F.M. and C.A. Henderson, (1967). Attractiveness of virgin female moths of the southwestern cornborer. *Jour. Econ. Ent.* 60:279-280.

Durant, J. A.; D.J. Manley and R. T. Cardé, (1986). Monitoring of the European corn borer (Lep.: Pyralidae) in South Carolina using pheromone traps. *Jour. Econ. Ent.* 79: 1539-1543.

Elkinton, J. S. and R.T. Cardé, (1984). Odour dispersion. In *Chemical ecology of insects* (eds. W. J. Bell and R. J. Carde') pp. 73-91. Chapman and Hall, London and New York. [3,4,8,20]

Ellis, P. E. and G. Steele, (1982). The effects of delayed mating on the fecundity of females of *Spodoptera littoralis* (Boisduval) Lepidoptera:Noctuidae. *Bull. Ent. Res* 72: 295-302.

Farkas, S. R. and H.H. Shoery, (1972). Chemical trail-following by flying insects: A mechanism for orienting to a distant odour source. *Sci.* 178: 67-68.

Farkas, S. R. and H.H. Shorey, (1973). Odour following and anemotaxis. *Science* 180: 1302.

Farkas, S. R., and H.H. Shorey, (1974). Mechanisms of orientation to a distant pheromone source. In `Pheromones' (M. C. Birch ed.), pp. 81-95. AM. Elsevier, New York.

Farkas, S. R.; H.H. Shorey; and L. K. Gaston, (1974). Sex pheromones of lepidoptera. Influence of pheromone concentration and visual cues on aerial odour-trail following by males of *Pectinophora gossypiella* . Ann. *Ent. Soc. Am.* 67: 633-638.

Fatzinger, C. W. (1973). Circadian rhythmicity of sex pheromone release by *Dionyctria abietella* (Lepidoptera: Pyralidae) and the effect of diel cycle on its precopulatory behaviour. *Ann. Ent. Soc. Am.* 66: 1147-1153.

Gothif, S. and H.H. Shorey, (1975). Sex pheromones of Lepidoptera: Examination of the role of male scent brushes in courtship behaviour of *Trichoplusia ni. Environ. Ent.* 5: 115-119.

Hardee, D. D.; W.H. Cross, and E.B. Mitchel, (1969). Male boll weevils are more attractive than cotton plants to bollweevils. *Jour. Econ. Ent.* 62: 165-169.

Hedgekar, B. M. and C.D. Dondale, (1969). A contact sex pheromone and some response parameters in lycosid spiders. *Can. Jour. Zool.* 47: 1-4.

Hendry, L. B.; L. Roman, and R.O. Mumma, (1973). Evidence of a sex pheromone in the oak leaf roller, *Archips semiferanus* (Lepidoptera:Tortricidae): Laboratory and field bioassays. *Environ. Ent. Zool.* 7: 116-132.

Hidaka, T. (1972). Biology of *Hyphantria cunea* Druvy Lepidoptera:Arctiidae in Japan. XIV. Mating behaviour. *Appl. Ent. Zool.* 7: 116-132.

Hill, D.S. (1983). Agricultural insect pests of the tropics and their control. University press Cambridge pp. 57.

Hirai, Y.; T. Tamaki and T. Yushima, (1974). Inhibitory effects of individual components of the sex pheromone of a Tortricid moth on the sexual stimulation of males. *Nature* 247:231-232.

Hirai, Y. (1977). Observations on the function of male scent brushes and mating behaviour in *Leucania seperata* W.and *Mamestra brassicae* L. (Lepidoptera:Noctuidae). *Appl. Ent. Zool.* 14 (3):303-309

Hirano, C. and H. Muramoto, (1976). Effect of age on mating activity of the sweet potato leaf roller *Bachmia macroscopa* (Lep.Gele.) *Appl. Ent. Zool.* 11:154-59.

Hutt, R.B. and L.D. White, (1977). Mating response to visual stimulus in the male codling moth. *Environ. Ent.* 6:567-8.

IAPSC (1985). *Chilo partellus* Swinhoe. Distribution maps of major crop pests and diseases in Africa, No. 199, Inter-African Phytosanitary Council, Younde.

Ignoffo, C. M., R.S. Berger; H.M. Graham, and D.F. Martin, (1963). Sex attractant of cabbage looper, *Trichoplusia ni* (Hbn). *Science* 141: 902-903.

Ingram, W. R. (1958). The Lepidopterous stalk borers associated with Graminae in Uganda. *Bull. Ent. Res.* 49: 367-383.

Islam, B.N. and M.Z. Alam, (1979). Mating behaviour of jute caterpillar *Diacrisia obliqua* Walker (Lepidoptera: Arctiidae) I. Precopulatory behaviour patterns in adults. *Appl. Ent. Zool.* 14(3):303-309.

Jackson, R. D. and W.J. Lewis, (1981). Summary of significance and employment strategies for semiochemicals in: Nordlund, D. A.; Jones, R. L. and Lewis, W. J. (eds), Semiochemicals their role in Pest control. John Wiley & Sons Chichester, pp. 283-96.

Jepson, W. F. (1954). *A critical review of the world literature on the Lepidopterous stalk borers of tropical graminacios crops.* Common W. Inst. Ent., London, 127 pp.

Kaae, R.S.; H.H. Shorey; L.K. Gaston and H.H. Hummel, (1974). Sex pheromones in Lepidoptera: Disruption of pheromone communication in *Trichoplusia ni* and *Pectinophora gossypiella* by permeation of the air with nonpheromone chemicals. *Environ. Ent.* 3:87-89.

Kaissling, K.E.(1971). Insect olfaction. *In* Handboook of sensory physiology. Chemical senses (L.M. Beidler ed.), Springer-verlag, Berlin and New York pp. 351.

Kaissling, K. E. and E. Priesner, (1970). The olfactory threshold of the silkmoth. *Naturwissenschaften* 57: 23-28.

Kanaujia, K. R.; R.N. Chaudhary and V.K. Sharma, (1981). Influence of time of day on the emergence of *Chilo partellus* (Swinhoe). *Indian Jour. Ecology.* 8 (1): 116-118.

Kanno, H. and Sato, A. (1975). Effects of maternal age on the biological characteristics of the offspring of the rice stem borer, *Chilo suppressalis* Walker (Lepidoptera:Pyralidae). *Appl. Ent. Zool.* 10 (3): 157-161.

Kanno, H. and A. Sato, (1978). Mating behaviour of the rice stem borer moth, *Chilo suppressalis* Walker (Lepidoptera:Pyralidae) I. Effects of moth age on mating activity. *Appl. Ent. Zool.* 13(3):215-221.

Kennedy, J. S. and D. Marsh, (1974). Pheromone-regulated anemotaxis in flying moths. *Sci.* 184: 999-1001.

Kennedy, J. S. (1978). The concepts of olfactory `arrestment' and `attraction'. *Physiol. Ent.* 3: 91-8.[2,4,8,15,20]

Kennedy, J. S. (1982). Mechanism of moth sex attraction: a modified view based on wind tunnel experiments with flying male *Adoxophyes*. *Les colloques de l`inra* 7: 189-92. [4]

Kennedy, J. S.; A. R. Ludhlow; A. R. and C.J. Sanders, (1980). Guidance of flying male moths by wind-borne sex pheromone. *Physiol. Ent.* 6: 395-412. [2,45,12,20,21]

Kennedy, J. S. (1983). Zigzagging and casting as programmed responses to wind-borne odour: a review. *Physiol. Ent.* 8: 109-20. [2,4,5,6,]

Klassen, W.; R.L. Ridgeway, and M. Inscoe (1982). Chemical attractants in integrated pest management. In: Insect suppression with controlled release pheromone systems. (Edited by Kyodonieus A.F. and Beroza M.)., vol 1, pp. 13-130. CRC Press, Florida, USA.

Kuenen, L. P. S. and T.C. Baker, (1983). A non-anemotactic mechanism used in pheromone source location by flying moths. *Physiol. Ent.* 8: 277-89. [2,4,5,9,20]

Kurmar, H. and K.N. Saxena, (1985). Oviposition by *Chilo partellus* Swinhoe in relation to it's mating, diurnal cycle and certain non-plant surfaces. *Appl. Ent. and Zool.* 20 (2):218 - 221.

Lack, D. (1943). The life of the Robin. London.

Leather, S. R.; A.D. Watt, and D.A. Barbour, (1985). The effect of host plant and delayed mating on the fecundity and life span of the pine shoot beauty moth, *Panolis flammea* (Denis and Schiffermuller) Lepidoptera: Noctuidae :their influence on population dynamics and relevance to pest management. *Bull. Ent. Res.* 75: 641-651.

Leuschner, K. (1990). A review of laboratory and field screening procedures for *Chilo partellus*. *Insect Sci. Applic.* 11: (4/5), 627-638.

Levinson, H. Z. and A.R. Levinson (1973). The dual function of the assembling scent of the female khapra beetle *Trogoderma granarium*. *Naturwinssenschaften*, 60: 352-353.

Levinson, H. Z. and A.R. Levinson, (1979). Trapping of storage insects by sex and food attractants as a tool of integrated control. In chemical Ecology: Odour communication in animals F. J. Ritter (Ed.) Elserier, Amsrerdam, pp. 327-341.

Lingren, P. D.; W.B. Warner, and T.J. Henneberry, (1988). Influence of delayed mating on egg production, egg viability, mating and longevity of female pink bollworm Lepidoptera: Gelechiidae. *Environ. Ent.* 17 (1): 86-89.

Linn, C.E., Jr. and L.K. Gaston, (1981). Behavioural function of the components and the blend of the sex pheromone of the cabbage looper, *Trichoplusia ni*. *Environ. Ent.* 10:751-755.

Liu, Y.B. and K.F. Haynes, (1992). Filamentous nature of pheromone plumes protects intergrity of signal from background chemical noise in cabbage looper moth, *Trichoplusia ni*. *Jour. Chem. Ecol.* 18(3): 299-307.

Low, B. S. (1978). Environmental uncertainties and the parental strategies of marsupials and placentals. *Amer. Naturalist* 112: 197-213.

Lux, S.A. (1989). Stochastic model of the kharpra beetle (*Trogoderma granarium* Everts) reproductive behaviour. International Ethological Conference XXI, 9-17. August, Utrecht, The Netherlands.

Lux, S.A. (1990). Prospects for application of quantitative analysis of insect behaviour to pest control. 5th International Working Conference on Stored-Product Protection, 9-14 September, Bordeaux, France.

Lux, S.A.; A. Hassanali; W. Lwande and F.N. Njogu, (1994). Proximity of release points of pheromone components as a factor confusing males of the spotted stem borer, *Chilo partellus*, approaching the trap. *Jour. Chem. Ecol.* 20(8):2065-2075.

Marsh, D.; J.S. Kennedy, and A.R. Ludlow, (1978). An analysis of anemotactic zigzagging flight in male moths stimulated by pheromone. *Physiol. Ent.* 3:221-40.

McLaughlin, J.R.; L.K. Shorey; H.E. Hummel and F.O. Stewart, (1972). Sex pheromones of Lepidoptera. XXXIII. Evaluation of disruptive effect of tetradecyl acetate on sex pheromone communication of *Pectinophora gossypiella*. *Jour. Ent.* 65:1592 - 1593.

McLaughlin, J.R; E.R. Mitchell; D.L. Chambers and J.H. Tumlnson, (1974). Perception of Z-7-dodecen-l-ol and modification of the sex pheromone response of male loopers. *Environ. Ent.* 3:677-680.

Mcneil, J.N.; J.J. Turgeon, and W.I. Roelofs, (1983). Responsiveness of *Pseudaletia unipuncta* males to the female sex pheromone. *Physiol. Ent.* 8:339-444.

Minja, E. (1990). Management of *Chilo* species infesting cereals in eastern Africa. *Insect Sci. Applic.* 11:489-499.

Minks, A.K. and S. Voerman, (1973). Sex pheromones of the summer fruit tortrix moth, *Adoxophyes orana*: Trapping performance in the field. *Ent. Exp. Applic.* 16:541-549.

Mitchell, E.R. (1976). Inhibition of pheromone perception by male cabbage loopers and beet armyworms: Proximity vs. atmospheric permeation. *Environ. Ent.* 5:770-772.

Mohyuddin, A.I. and M.R. Attique, (1978). An assessment of loss caused by *Chilo partellus* Swinhoe to maize in Pakistan. PANS 24, 111-113.

Murlis, J. and C.D. Jones, (1981). Fine scale structure of odour plumes in relation to insect orientation to distant pheromone and other attractant sources. *Physiol. Ent.* 6: 71-86.

Nesbitt, B.; P.S. Beevor; D.R. Hall; R. Lester; J.C. Davies and K.V. Seshu Reddy (1979). Components of the sex pheromone of the female spotted stalk-borer, *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae): Identification and preliminary field trials. *Jour. Chem. Ecol.* 5:153-163.

Neupane, F. P. (1990). Status and control of *Chilo* spp. on cereal crops in Southern Asia. *Insect Sci. Applic.* 11 : 501-534.

Norris, M. J. (1933). Contributions towards the study of insect fertility. II. Experiments on the factors influencing fertility in *Ephestia kuhniella* (Z.) Lepidoptera: Pycitidae. *Proc. Zool. Soc. Lond.* 1933, 903-934.

Ochieng, F. O.; Onyango F. O. and M.D.O. Bungu, (1985). Improvement techniques for mass-culture of *Chilo partellus* Swinhoe. *Insect Sci. Applic.* 6:(3):425-428.

Odindo, M.O.(1991). Management of cereal stem borers especially *Chilo partellus*, using Microsporidia. *Insect Sci. Applic.* 12:51-55.

Omollo, E. O. (1983). Screening of local and exotic maize lines for stem borer resistance with special reference to *Chilo partellus* . *Insect Sci. Applic.* 4: 105-108.

Omollo, E.O. and K.V. Seshu Reddy, (1985b). Effect of different sorghum-based cropping systems on insect pests in Kenya. In Proc. of the International Sorghum Entomology Workshop, 15-21 July 1984, Texas A&M University, College Station, Tx USA, ICRISAT, Pantacheru, India. pp. 395-401.

Ongwaro, K. (1983). Intensity levels of stem borers in maize and sorghum and the effect on yield under different intercropping patterns. *Insect Sci. Applic.* 4: 33-37.

Ostaff, D.P.; R.F. Shephered, and J.H. Borden, (1974). Sex attraction and courtship behaviour in *Landina fiscellaria* lugubrosa (Lepidoptera:Geometridae). *Can. Ent.* 106:493-501.

Outram, I (1971). Aspects of mating in the spruce budworm, *Choristonuera fumiferana* (Lepidoptera: Tortricidae). *Can Ent.* 103:1121-1128.

Parrilla, A. and A. Guerrero, (1993). Inhibition of the sex pheromone perception in the processionary moth *Thaumetopoea pityocampa. IOBC WPRS Bull.* 16 (10):36-40.

Pats, P. and S. Wiktelius, (1989). Tethered flight of *Chilo partellus* Swinhoe (Lepidoptera:Pyralidae). *Bull. Ent. Res.* 79: 104-114.

Pats, P. (1990). Activity of *Chilo partellus* (Lepidoptera:Pyalidae): eclosion, mating and oviposition time. *Bull. Entomol. Res.* 81: 93-96.

Pats, P. (1992). Reproductive biology of the cereal stem borer, *Chilo partellus.* Dissertation, Uppsala, Sweden pp. 8-51.

Perez, R. and W.H. Long, (1964). Sex attractant and mating behaviour in the sugar cane borer. *Jour. Econ. Ent.* 57:688-690

Proshold, F. I.; C. P. Kapkenko and C.K. Graham, (1982). Egg production and oviposition in the tobacco budworm: effect of age at mating. *Ann. Ent. Soc. Am.* 75: 51-55.

SAS Institute Inc. (1987). SAS/STAT™ Guide for personal computers, version 6 Edition. Cary, NC: pp. 1028.

Schneider, D. (1970). Olfactory receptors for the sexual attractant (bombykol) of the silk moth in "The neurosciences: Second study program" (F. O. Schmitted.), pp. 511-518. Rockfeller Univ. Press, New York.

Seabrook, W.D.; K. Hirai; H.H. Shorey, and L.K. Gaston, (1979). Maturation and senescence of an insect chemosensory response. *Jour. Chem. Ecol.* 5:587-598.

Seshu Reddy K.V., (1983). Studies on the stem-borer complex of sorghum in Kenya. *Insect Sci. Applic.* 6:3-10.

Seshu Reddy, K. V. (1985a). Relative susceptibility and resistance of some sorghum lines to stem borers in Western Kenya. *Insect Sci. Applic.* 6: 401-404.

Seshu Reddy, K. V. (1985c). Integrated approach to the control of sorghum stem borers. In proc. Int. Sorghum Entomol. Workshop, 15-21 July 1984, Texas A & M. Univ. College Station, Texas USA; International Crops Reseasch Institute for the Semi Arid Tropics (ICRISAT) Patancheru, AP 502324, India: pp. 205-215.

Seshu Reddy, K. V. and P.T. Walker, (1990). A review of the yield losses in graminaceous crops caused by *Chilo* spp. *Insect Sci. Applic.* 11: (4/5) 481-488.

Shorey, H. H. (1964). Sex pheromones of noctuid moths II. Mating behaviour of *Trichoplusia ni* (Lepidoptera:Noctuidae) with special reference to the role of the sex pheromone. *Ann. Ent. Soc. Am.* 57: 371-377.

Shorey, H. H. (1973). Behavioural responses to insect pheromones. *Ann. Rev. Ent.* 18: 349-380.

Shorey, H. H. (1974). Environmental and physiological control of insect sex pheromone behaviour. In "Pheromones" (M. C. Birch, ed.), pp. 62-80. Am. Elsevier, New York.

Shorey, H. H. (1976). Mechanisms of movement and orientation to pheromone source in: Animal communication by pheromones Academic Press, inc. pp. 19-33.

Shorey, H.H.; S.U. McFarland and L.K. Gaston, (1968a). Sex pheromones of noctuid moths XIII. Changes in pheromone quantity, as related to reproductive age and mating history in females in seven species of Noctuidae (Lepidoptera). *Ann. Ent. Soc. Am.* 61:372-376.

Shorey, H.H.; K.L. Monin, and L.K. Gaston, (1968b). Sex pheromones of noctuid moths. XV. Timing of development of pheromone responsiveness and other indicators of reproductive age in males of eight species. *Ann. Ent. Soc. Am.* 61:857-861.

Shorey, H.H. and L.K. Gaston, (1970). Sex pheromones of noctuid moths XX. Short-range visual orientation by pheromone-stimulated males of *Trichoplusia ni*. *Ann. Ent. Soc. Am.* 63: 829-832.

Singh, B. U. and B.S. Rana, (1989). Varietal resistance in sorghum to spotted stem borer, *Chilo partellus* Swinhoe. *Insect Sci. Applic.* 10: 30-37.

Sithole, S. Z. (1990). Status and control of the stem borer, *Chilo partellus* Swinhoe (Lepidoptera: Pyralidae) in Southern Africa. *Insect Sci. Applic.* 11 :481-488.

Sithole, S. Z. (1989b). Sorghum stem borers in Southern Africa In Int. Workshop on Sorghum stem borers, 17-20 Nov. 1987; ICRISAT centre, India Patanchenu, A.P.502 324, India; ICRISAT. pp 41-47.

Sokal, R.R. and F.J. Rohlf, (1981). Transformations: in Biometry pp. 419-427.

Spjotvoll, E. and M.R. Stoline, (1973). An extension of the T-method of multiple comparison to include the case with unequal sample sizes. *J. Amer. Stat. Assoc.* 68:975-978.

Steinbrecht, R. A. (1970). Zur morphometric der antenne des seidespinners, *Bombyx mori* L.: Zahl and Verteilung der viechsensillen (Insecta:Lepidoptera). *Z. Morphol. Tiewe* 68: 93-126.

Struble, D.L. and L.A. Jacobson, (1970). A sex pheromone in the red-backed cutworm. *Jour. Econ. Ent.* 63:841

Tanaka, F.; S. Yabuki; S. Tatsuki; H. Tsumuki; H. Kanno; M. Hatori; K. Usui; M. Kurinara; K. Uchiumi and J. Fukami, (1987). Control effect of communication disruption with synthetic pheromones in paddy fields in the rice stem borer, *Chilo suppressalis* Walker (Lepidoptera: Pyralidae). *Jpn. Jour. Appl. Zool.* 31 (2): 125-133.

Tatzuki, S. (1990). Status of applicatiopn of sex pheromone of the rice stem borer moth, *Chilo suppressalis* in Japan. *Insect Sci. Applic.* 11: 4/5: 807-812.

Thornhill, R. and J. Alcock, (1983). Sexual selection and the prevalence of polygyny. In The evolution of insect mating systems pp. 85-89.

Tinbergen, N. (1935). Uber die orientierung des Bienenwolfes II. Die Bienenjagd. *Zs Vergl. Physiol.* 21: 699-716.

Tinbergen, N. (1936c). Eenvoudige proeven over de zintuigfunties van larvae en imago van de geelgerande watertor. *De levende Natuur*, 41: 225-36.

Tinbergen, N. (1942). An objective study of the innate behaviour of animals. *Biblioth, biotheor.* 1: 39-98.

Tinbergen, N. (1969). Behaviour as a reaction to external stimuli in: The study of instinct. Oxford University Press pp. 15-56.

Trematerra, P. and F. Battaini, (1987). Control of *Ephestia kuehniella* (Zeller) by mass trapping. *Jour. Appl. Ent.* 104: 336-340.

Trivers, R. L. (1972). Parental investment and sexual selection. In Sexual selection and the descent of man, 1871-1971, (ed. B. Campbell). Chicago: Aldine.

Tumlinson, J.H.; C.G. Yonce; R.E. Doolitttle; and R.R. Heath, (1974). Sex pheromones and reproductive isolation of the lesser peachtree borer and the peachtree borer. *Sci.* 185:614-616.

Unnithan, G. C. (1988). Certain factors determining mating, fecundity and egg fertility in the sorghum stem borer, *Chilo partellus*. Proceedings XVIII International Congress of Entomology, Vancouver, B. C., Canada, July 3-9, 379.

Unnithan, G. C., and K. N. Saxena, (1990). Factors determing pheromonal trapping of the borer *Chilo partellus* Swinhoe (Lepdoptera:Pyralidae). *Jour. Appl. Ent.* 110: 183-193.

Unnithan, G. C. and S.O. Paye, (1991). Mating, longevity, fecundity and egg fertility of *Chilo partellus* (Lepidoptera: Pyralidae): Effects of delayed or successive mating and their relevance to pheromonal control methods. *Environ. Ent.* 20 (1): 150-155.

van Hamburg, H. (1979). The grain-sorghum stalk borer *Chilo partellus* Swinhoe (Lepidoptera:Pyralidae): Seasonal changes in adult populations in grain sorghum in Transvaal. *Jour. Ent. Soc. sth. Afr.* 43 (1) 71-76..

Von Frisch K. (1927. Aus dem leben der Bienen. Berlin.

Waldow, U. (1970). Elektrophysiologische untersuchungen an Feuchte-, Trockern-, und Temperaturre Zeptoren auf der Antennae der Wanderhuschrecke. *Z. Vg. Physiol.* 69:249 - 283.

Walker, W. F. (1980). Sperm utilization strategies in non-social insects. *American Naturalist* 113: 201-208.

Warui, C. M. and J.N. Kuria, (1983). Population incidence and the control of maize stalk borer *Chilo partellus* and *C. orichalcociliellus* Strand and *Sesamia calamistis* Hmps, in Coast Province, Kenya. *Insect Sci. Applic.* 4 (1/ 2), 11-18.

Wheatly, P.E. (1961). The insect pests of agriculture in the coast province of Kenya. V. maize and sorghum. *E. Afr. For. Agri. Jour.* 27:105-107.

Witzgall, P. and E. Priesner, (1991). Wind-tunnel study on attraction inhibitor in male *Coleophora laricella* Hbn. (Lepidoptera:Coleophoridae). *Jour. Chem. Ecol.* 17:1355-1362.