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COMPARATIVE STUDIES ON THE ADULT DISPERSAL BEHAVIOUR OF *BUSSEOLA FUSCA* (FULLER) (LEPIDOPTERA: NOCTUIDAE) AND *CHILO PARTELLUS* SWINHOE (LEPIDOPTERA: PYRALIDAE).

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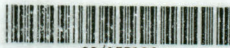
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ABSTRACT

DEDICATION

This thesis is dedicated to my parents Benjamin Njeru Mbugi and Niceta Ngungi Njeru for bringing me up and taking me to school. I have come a long way due to their love and support. They are truly my inspiration and I love them.

Ulea and *Diastyle* are two species of leaf-miners which have been reported to cause effects on maize fecundity, longevity, pupal weight and flight. This study investigated mated female moths of the two stem borer species. Field and laboratory studies showed that *B. pica* reared on a normal diet laid marked eggs on the Calco Red dyed diet could still lay marked eggs. The *Diastyle* species was more appropriate for further marking experiments because it laid red eggs which can easily be detected on maize plants during field conditions. *Bassareola fusca* and *C. partellus* reared on different leaf-miner diets showed different growth and development on whorled sorghum, wild sorghum and wild sorghum species (*Sorghum versicolor* and *S. crinale*). The best host plant performance was on napier grass (*Pennisetum purpurascens*). The poor performance observed on *P. purpurascens* may be attributed to physical factors or to poor nutrient contents. The two wild sorghum species were therefore set as important alternate hosts or trap crops. In addition, host plant preference experiments where insects reared on a plant host ("rearing host") were tested for oviposition alternately with each of the other two ("test hosts") revealed that for both species, moths which were reared on a given host preferred to lay more eggs on that host. For example, *B. pica* reared on sorghum was given and tested for oviposition alternately with wild sorghum and napier grass. It preferred to lay more eggs on sorghum. Similarly, *Diastyle* reared on maize and tested for oviposition alternately with whorled sorghum and wild sorghum (*S. versicolor*) preferred to lay more eggs on maize. These findings reveal that there can be a variation in an insect's oviposition preference to a host as a result of its previous larval food experience. This level of oviposition preference in favour of the plant species used when the insect was reared is a phenomenon related to an "host shift" (Henderson, 1933). However, this principle was not evident in trials of

ABSTRACT

Two oil soluble dyes, Calco Red N-1700 and Sudan Blau-670 were added to the artificial diet of *Chilo partellus* and *Busseola fusca*. The two dyes effectively marked the larvae, adults, eggs and first stage F1 larvae. The dye treatments did not have any effects on mean fecundity, longevity, pupal weights and flight duration of mated female moths of the two stem borer species. Further experiments showed that, *B. fusca* reared on a normal diet for 18 days and transferred to the Calco Red dyed diet could still lay marked eggs. The dye was found to be more appropriate for further marking experiments because marked moths laid red eggs which can easily be detected on maize plants during dispersal studies. *Busseola fusca* and *C. partellus* reared on different host plants showed better growth and development on cultivated sorghum, maize and the wild sorghum species (*Sorghum versicolor* and *S. arundinaceum*) while the poorest performance was on napier grass (*Pennisetum purpureum*). The poor performance observed on *P. purpureum* may be attributed to presence of antibiotic factors or to poor nutrient contents. The two wild sorghum species may therefore act as important alternate hosts or trap crops. Two-choice oviposition preference experiments where insects reared on a given host ("rearing host") were tested for oviposition alternately with each of the other hosts ("test hosts") revealed that for both species, moths which were reared on a given host preferred to lay more eggs on that host. For example, *B. fusca* reared on cultivated sorghum and tested for oviposition alternately with either maize or napier grass preferred to lay more eggs on sorghum. Similarly *C. partellus* reared on maize and tested for oviposition alternately with cultivated sorghum and wild sorghum (*S. versicolor*) preferred to lay more eggs on maize. These findings reveal that there can be a variation in an insect's oviposition response to a plant as a result of its previous larval food experience. This altered oviposition preference in favour of the plant species upon which the larvae were reared on is a phenomenon referred to as Hopkins' host selection principle (Hopkins, 1917). However, this principle was not evident in multiple-

choice oviposition preference experiments indicating that its validity as a general principle operating in adult oviposition preferences of *B. fusca* and *C. partellus* moths still remains to be proved. Results of the experiment investigating changes in insect density from a central release point using oviposition by internally marked female moths as a measure of insect density showed that, for *C. partellus* there was a profound falling off in the mean number of eggs and egg batches with increasing distance. Hence, the maize plants which were near the release point received the highest number of eggs and egg batches than those that were far away. This phenomenon referred to as "edge effect" could have been brought about by a situation whereby a large proportion of *C. partellus* female moths preferred to disperse horizontally as opposed to a vertical dispersal which could have taken them high up and possibly even outside the sampling area. As for *B. fusca*, the mean egg batches and egg numbers showed no significant differences and were more or less uniformly distributed throughout the dispersal distance, hence "edge effect" was not evident. Results also showed that at each concentric circle, more eggs of *C. partellus* were recovered than those of *B. fusca*. The higher recovery rate for *C. partellus* eggs is usually associated with very low dispersal rates whereas on the other hand, the lower recovery rate for *B. fusca* eggs is associated with high dispersal rates. Results of the experiment involving sampling to recover eggs and larvae from the wild populations of *B. fusca* and *C. partellus* showed that, the maize plants at the edge of the experimental plot (bordering the wild host plants) received the highest number of *C. partellus* eggs and egg batches, hence "edge effect" was evident. In contrast, the mean number of eggs, egg batches and larvae of *B. fusca* showed a more or less uniform distribution and therefore "edge effect" was not evident. Therefore *B. fusca* and *C. partellus* behave quite differently and the former distributes its eggs more or less uniformly whereas the latter lays more eggs on the nearest host plants. An important implication of "edge effect" is that *C. partellus* can be controlled by use of trap crops or by applying insecticides only on the margins of the field where

infestation is severe. Most eggs of *C. partellus* will be laid on the trap crop, which can be destroyed or cut as fodder. However, trap crops unless very attractive may have very little value for the protection of crops against the invasion of crops by *B. fusca* because the latter is capable of dispersing its eggs in a more or less uniform manner and even more widely.

1.1.1 Economic importance of maize and sorghum

Maize (*Zea mays* L.) is the most important cereal crop in the world after wheat and rice (Parveglione, 1972). It is a major crop in tropical Africa, Asia and America where it is grown for various purposes which include food for animals and as a source of raw materials for many industrial products. Secondly, sorghum (*Sorghum bicolor* (L.) Moench) is the most widely grown cereal crop in Africa, Central and South America (Reys, 1989), and it is grown throughout tropical Asia and South East Asia (Chandurwar, 1989; Makasara and Chawanapong, 1985). The sorghum crop in eastern Africa is important and the cultivated area is equivalent to 13% of the world area outputs. It is the most widely cultivated crop in the arid areas of West Africa (Adey, 1976) and is consumed by humans, used as feed for poultry and livestock in large quantities (Adey, 1976; Reys, 1989). In India, it is also partially grown for animal protection (Pagi and de Wail, 1975; Perera *et al.*, 1987).

CHAPTER ONE

1 GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

1.1.1 Economic importance of maize and sorghum

Maize (*Zea mays*, L.) is the most important cereal crop in the world after wheat and rice (Purseglove, 1972). It is a major crop in tropical Africa, Asia and America where it is grown for various purposes which include food, feed for animals and as a source of raw materials for many industrial products. Similarly, sorghum (*Sorghum bicolor* [L.] Moench) is the most widely grown cereal crop in Africa, Central and South America (Reys, 1989), and it is grown throughout tropical Asia and South East Asia (Chundurwar, 1989; Maksongsee and Chawanapong, 1985). The sorghum crop in eastern Africa is important and the cultivated area is equivalent to 13% of the world area outputs. It is the most widely cultivated crop in the savanna areas of West Africa (Ajayi, 1989) and is consumed by humans, used as feed for poultry and livestock in form of grain, forage, and fodder (Ajayi, 1989; Reys, 1989). In Brazil, it is commercially grown for alcohol production (Paul and de Walt, 1985; Perevia *et al.*, 1987).

1.1.2 Factors limiting the production of maize and sorghum

Notable factors limiting the production of maize and sorghum include poor soils, inadequate rainfall, weeds, diseases and insect pests (Allan, 1972; Purseglove, 1972). Of major importance is the damage caused by phytophagous insects among which lepidopterous stem borers play a significant role in the reduction of yields (Nye, 1960; Hill, 1975; Youdeowei, 1989; Seshu Reddy and Walker, 1990).

1.1.3 Insect pests of maize and sorghum

Among several insects that attack maize and sorghum, lepidopterous stem borers are ubiquitous and an economically important group. These insects infest maize and sorghum crops throughout their growth, from seedling stage to maturity. Irrespective of country, or type of crop culture, a field of maize or sorghum is usually infested by one or more stem borer species. Seventeen species of stem borers have been found to attack maize and sorghum in various parts of Africa (Seshu Reddy, 1983; Kfir, 1990; Bosque-Perez and Mareck, 1990; Khan *et al.*, 1991). The most important species of stem borers in Africa belong to two families namely Noctuidae which is represented by *Busseola fusca* Fuller and *Sesamia calamistis* Hampson and Pyralidae which is represented by *Chilo partellus* Swinhoe, *C. orichalcociliellus* Strand, and *Eldana saccharina* walker (Seshu Reddy, 1983; Warui *et al.*, 1986). *B. fusca* and *C. partellus* are by far the most destructive, with the former being prevalent

in higher altitudes and the latter in lower altitudes (Nye, 1960; Bowlen, 1973; Tassema, 1982; Seshu Reddy, 1983).

1.1.4 Yield losses and control of stem borers

Estimates of yield losses due to stem borer attack vary greatly from one region to another and one season to another, but they are in the range of 20-40% of the potential yield depending on the pest population density and the phenological stage of the crops at infestation (Anon., 1988; Youdeowei, 1989; Seshu Reddy and Walker, 1990). To avert these losses different control strategies such as chemical, host plant resistance, biological and cultural methods have been used (Harris, 1962; Adesiyun and Ajayi, 1980; Walker, 1981; Mlambo, 1983; Barrow, 1985, 1989; Sithole, 1987; Gebre-Amlak, 1988; Nwanze and Mueller, 1989; Kfir, 1990). A number of natural enemies of stem borers have been reported, but in Africa the overall rate of parasitism is low and only increases when borer damage is well advanced (Harris, 1962). Several cultural measures have been used in controlling cereal stem borers: early planting, disposal of plant residue by burning, or burial by deep ploughing during off-season, removal and destruction of volunteer and alternative host plants, and crop rotation. Subsistence farmers have long practised intercropping. The use of resistant varieties is economical and environmentally safe. However, its use is very limited since little research work has been done on varietal resistance in Africa (Sithole, 1989).

1.1.5 Role played by wild host plants in stem borer outbreaks

The discovery of a suitable host by many herbivorous insects is an essential phase in their life cycle. Complex visual, olfactory and gustatory stimuli methods are employed by the insects in the search of their hosts. Wild grasses are presumably the aboriginal host plants for cereal stem borers and several species are attacked (Myers, 1932; Gupta and Avasthy, 1954; Ingram, 1958; Carl, 1962; Harris, 1962, 1990). Stem borer larvae feed in communities of wild and cultivated gramineous plants that have stems sufficiently large enough to accommodate their feeding tunnels. The tunneling larvae are thus protected from contact insecticides and some natural enemies (Harris, 1990).

In Africa where the bulk of maize is grown on small plots surrounded by land on which wild gramineous plants grow (Bowden, 1976), it is not surprising that stem borers infest cultivated crops in high populations. Therefore, to understand the population dynamics of stem borers in cultivated crops, detailed knowledge of the ecological relationships between stem borers and the native grasses is essential (Bowden, 1954). Unfortunately, very little research work has focused on the role of wild gramineous plants in stem borer ecology (Mohamed, 1997).

According to Pats and Wikteliuss (1992), newly planted maize or sorghum is colonized by *B. fusca* and *C. partellus* moths emerging from old stubble or from the wild host plants and thus the level of infestation is dependent on the

density of moths in the source population. Observations in Bilar, India by Nagarkatti and Nair (1973) revealed that wild grasses influenced borer population and the extent of damage in sugarcane. They found that whenever *Sorghum fusca* and *S. halepense* were found and *Pennisetum typhoideum* was grown in areas around sugarcane fields, the incidence of borers increased in sugarcane. Presumably, the increase was due to migration of moths from the wild hosts. Similarly, studies in Kenya by Overholt *et al.* (1994) have shown that some wild grasses such as wild sorghum species (*Sorghum versicolor* and *S. arundinaceum*), guinea grass and napier grass, remain vegetative through out the year and are attacked by the borers even during the non cropping season. These wild hosts allow continuous reproduction of the borers and are therefore a source of infestation. On the other hand, wild hosts adjacent to cultivated crops also provide an extremely important refuge for natural enemies as well as a source of nectar, pollen, and host/alternate prey (Altieri *et al.*, 1977; Altieri and Whitcomb, 1979).

Busseola fusca and *C. partellus* belong to a group of lepidopterans that have evolved in close association with wild grasses (Harris and Nwanze, 1992). However, the original host plant with which *B. fusca* and *C. partellus* evolved is not known, but the following indigenous African grasses have been recorded as hosts:- *Sorghum versicolor* (Steud), *S. arundinaceum* (Desv.), *Pennisetum purpureum* Schum., *Panicum maximum* L., *Hyparrhenia rufa* Nees (Stapf),

Rottboelia cochinchinensis (Lour) W.D. Clayton and *Echinochloa pyramidalis* (Lam.) Hitchc. And Chase (Randriamananoro, 1996; Mohamed, 1997; Khan *et al.*, 1997).

From the foregoing literature review it is apparent that for most cultivated crops, the number of exogenous insects invading at the beginning of the growing season, either from adjacent areas or from far distances is a vital factor determining the final pest abundance in a given situation. Therefore, understanding of such movements is needed to help estimate the scope of future population suppression programmes.

1.1.6 Insect dispersal and migrations

Dispersal may be defined as any movement from an aggregation or a population and may refer to the movement of newly hatched larvae away from their egg mass (Henson, 1959) or the migration of the adult from their population territory (Southwood, 1962, 1971; Johnson, 1969). Taylor and Taylor (1976) refer to all such processes as migration, restricting immigration and emigration to movement in and out of the population's habitat. The study of dispersal is basic to our understanding of species ecology not only for its own sake, but because it underpins our knowledge of population dynamics, distribution, optimal foraging, mate location, host choice, and population structure and differentiation, and has practical consequences for the management of many insect pest species (Comins, 1977; Curtis and Rawlings, 1980).

In particular, dispersal of insects can lead to pest outbreaks in many crops (Joyce, 1976). Strategies for the timing of dispersal of insects by flight vary in relation to the timing of mating behaviour (Johnson, 1969). For example, males and females can fly unmated to a new habitat and mate there or they can mate near the site of emergence or enroute so that the mated female carries her progeny to the new habitat. Insect control for example by mating disruption or mass trapping with pheromones could fail due to immigration of mated females from outside the treated area. Thus, for such control measure to be effective one must know when and where reproductive activities take place.

1.2 Literature review

1.2.1 Distribution, ecology and biology of *Busseola fusca*

The African maize stalk borer *B. fusca* is a pest that is endemic to Africa and is distributed throughout the maize and sorghum growing areas (Mally, 1920; Jepson, 1954; Hill, 1975). It is a pest of great economic importance attacking maize, sorghum, millet, sugarcane and various cultivated and wild grasses (Harris and Nwanze, 1992). Distribution maps have been published by the Inter-African Phytosanitary Council, IAPSC (1985) and the CAB International Institute of Entomology, CIE (1988). *B. fusca* has been reported in most countries in Africa south of the Sahara starting from Guinea in the west to Somalia in the east, and southward to South Africa. The pest is particularly notorious in the cool highland areas of East Africa where the bulk of maize is

grown (Nye 1960; Seshu Reddy, 1983). Studies in Kenya and Ethiopia have shown that the occurrence of the pest was rare at altitudes below 1200m (Tassema, 1982) and was dominant at higher and cooler altitudes (1140-2500m) (Seshu Reddy, 1983). These are also incidentally some of the areas (1200-2000 m) known for high productivity of maize in Kenya (Allan, 1972). However in Southern Africa *B. fusca* occurs at lower altitudes and this shows the capability of the pest to adapt itself to low lying and warmer areas (Sithole, 1989).

Maize is susceptible to *B. fusca* attack when plants are three to five weeks old (between 26-45 cm tall) (Khaemba, 1985; Barrow, 1989) with damage being caused by the larval stage (de Pury, 1968; Schmutterer, 1969; Bowlen, 1973). Larvae cause extensive foliar damage leading to production of many holes ("windows") on the leaves of infested plants. They also bore into the stem destroying it and finally lead to the death of the shoot, a condition referred to as the "dead heart" effect (de Pury, 1968; Schmutterer, 1969; Bowlen, 1973). When infestation coincides with tasselling and silking stages, the moths usually lay eggs on the sheaths of older leaves or on the ear husk leaves. The emerging larvae damage tassels resulting in reduced pollination and also damage the developing seeds in cobs (Jepson, 1954; Swaine, 1957). Adult moths emerge from the pupae in the stems and stubble during the evening and are active at night, resting on plants and plant debris during the day. Usually on the night of emergence, the female moths release a pheromone to attract the males. The

pre-oviposition period is about 24h and the female prefers to lay eggs in batches beneath the leaf sheaths of the youngest fully unfolded leaf. The number of eggs laid by the female moth under controlled conditions range from 360-723 (Usua, 1968b; Unnithan, 1987). The eggs which are globular and measure 1.0 mm in diameter are whitish when newly laid but turn black just before hatching (Tams and Bowden, 1953; Hill, 1975; Schmutterer, 1969). Oviposition takes place during 3-4 consecutive nights after emergence and the eggs are laid in batches of 30-100 under the inner surfaces of the leaf sheaths. The incubation period is 6-11 days depending on the temperature and relative humidity. The newly hatched larvae remain at the site of oviposition for 1-2 days and then migrate up to the stem and down into plant funnel. They later bore into the stems and feed for 3-5 weeks before pupating.

The larval period may take up to 50 days depending on temperature, humidity and age of the plant at the infestation period. The average pupal period is 10-14 days and pupae are obiect in form and brown measuring about 25 mm in length. Adult moths have a wing span of about 30-40 mm and live for about a week. Sexes of the moths are recognized by shape of the antennae, the female having filiform antennae while those of male being pectinate. Under favourable conditions, the life cycle is continuous and there may be two or three generations per year depending on the prevailing environmental conditions and the availability of suitable host plants. However, under adverse conditions (e.g, very dry or cold weather), larvae enter into diapause and development is halted

until favourable conditions prevail (Nye, 1960; Mohyuddin and Greathead, 1970; Unnithan and Seshu Reddy, 1989). The diapausing larvae as such are a potential source of inoculum, which perpetuate infestation from season to season.

1.2.2 Distribution, ecology and biology of *Chilo partellus*

The spotted cereal stem borer *C. partellus* is a serious pest of maize and sorghum in many parts of the tropics (Neupane, 1990; Sithole, 1990). It is a pest that is widely distributed and is thought to be indigenous to Asia (Bleszynski, 1970). The pest was first recorded in Africa in 1932 (Tams, 1932), but it was not reported again until some 20 years later in Tanzania (Duerdon, 1953). Since that time, the geographic distribution of *C. partellus* has continued to expand with reports from Kenya, Uganda, Rwanda, South Africa, Ethiopia, Sudan, Somalia, Botswana, Malawi, Mozambique, Swaziland, Zimbabwe, Zaire (Nye, 1960; Ingram, 1983; Harris, 1990). In West Africa *C. partellus* has been reported from Togo and Cameroon (IAPSC, 1985). The veracity of the West African report is questionable because surveys in the region failed to recover *C. partellus* (Bosque-Perez and Mareck, 1990; Schulthes *et al.*, 1991; Shanower *et al.*, 1991; Gounou *et al.*, 1993). However, if *C. partellus* is not already in the West Africa, it is likely to invade the region eventually. In Madagascar, *C. partellus* was first recorded in 1972, and by 1975 it was considered to be the most damaging stem borer in maize, surpassing the indigenous *C. orichalcociliellus* (Delobel, 1975). Similarly,

surveys in Kenya coast by Overholt *et al.* (1994) indicate that the exotic *C. partellus* may be gradually displacing the indigenous *C. orichalcociliellus*.

The genus *Chilo* is taxonomically complex but was reviewed by Bleszynski (1970). *C. partellus* is the most economically important stem borer pest of maize and sorghum in East and Southern Africa at elevation below 1800m (Seshu Reddy, 1983, Harris, 1989; Neupane, 1990; Sithole, 1990). It is found in young maize and sorghum but prefers mature sorghum. Maize plants aged 3 to 4 weeks have been reported to be preferred for oviposition by *C. partellus* (Dabrowski and Nyangiri, 1984; Ampofo, 1985). An outbreak of the pest during early crop development can have a devastating effect on the yield. Larvae damage crops by boring and causing “dead hearts”. The pre-oviposition period is 24h and nearly all the eggs are laid in the first two days after emergence. Chadha and Roome (1980) recorded egg batch sizes ranging from 10-200 eggs. The maximum number of eggs laid by a caged female was 417 in six groups (Ingram, 1958). The eggs are translucent when laid, but turn white on the first day and then become grey when they are about to hatch. The egg is flat, scale like and ovoid. Groups of eggs are laid anywhere on the host plant, though most frequently on the lower surface of mature leaves near the midrib (Ingram, 1958; Ampofo, 1985).

Laboratory observations by Ingram (1958) showed that the egg hatches in 8 days, larval stage lasts between 28 and 33 days, pre-pupal is 24h and the adult

emerges 8-10 days later, giving a total life cycle of about 7 weeks. Under favourable conditions, the life cycle is continuous and there may be several generations in a year but during adverse conditions, larvae enter into diapause and development is halted until favourable conditions prevail. The diapausing larvae can be found in stubbles left in the field and as the next rainy season starts, the diapause is broken and pupation takes place giving rise to the first generation adults (ICRISAT, 1983).

According to Pats (1991), the majority of *C. partellus* males emerge within the first hours of scotophase while females emerge five hours later. The asynchrony of eclosion times ensures that mating occurs during the last hours of scotophase on the night of eclosion. Oviposition occurs during the first six hours of scotophase the following night but the majority of the eggs are deposited during the first two hours.

1.2.3 Growth and development of stem borers on various host plants.

Growth and development of an insect on its host plant is usually one of the means used to determine the suitability of the plant and the mechanisms of resistance of plant to the insect. Kumar *et al.* (1993) recorded a faster development of *C. partellus* on susceptible maize cultivar as compared to resistant ones and reported that the larvae feeding on resistant plants would

require a longer period of time to complete a generation than on susceptible plants.

van Rensburg and van den Berg (1991) studied the growth and development of *B. fusca* and reported that *Pennisetum purpureum* did not contribute to larval survival but it may serve to maintain low levels of borer population in the absence of more suitable hosts. They also stated that the suitability of a given crop as a host plant seems to be a combination of its attractiveness to the moths and its ability to support larval development.

Gebre-Amlak (1988) reported that there were no significant differences in the larval periods of *B. fusca* among the wild and main host plants except between maize and the wild sorghum, *Sorghum verticilliflorum* (thin stems). He also stated that fresh pupal weights did not show any significant difference between host plant species. However, he concluded that *P. purpureum* and *S. verticilliflorum* (thick stems) were found to be major host plants for *B. fusca*. Randriamananoro (1996) working on *B. fusca* reported that larval development on whole plants was faster on susceptible maize cultivar inbred A, susceptible sorghum cultivar IS 18363, *S. arundinaceum* and *S. versicolor* than on *P. purpureum*, resistant maize MP 704, resistant sorghum cultivar IS 1044, *P. trachyphyllum*, *E. pyramidalis* and *H. rufa*. Larval weight gain was highest on *S. arundinaceum* followed by IS 18363, *S. versicolor* and Inbred A while growth index was highest on *S. arundinaceum* and lowest on *H. rufa*. The

higher the growth index, the more suitable the plant was for insect's growth and development.

Mohamed (1997) working on *C. partellus* reported that larval period was significantly short on Inbred A and *S. versicolor* than on *Panicum maximum*, *P. purpureum*, *E. pyramidalis* and *H. rufa* and concluded that larval survival, growth and development varied according to the level of resistance in the plants. Similarly, Kumar *et al.* (1993) reported that resistant maize cultivar MP 704, V-37 and Poza Rica 7832 retarded development of *C. partellus* larvae due to resistance through antibiosis. Davis and Williams (1986) reported that resistant maize hybrids caused significant adverse effects on survival, growth and development of the southwestern corn borer, *Diatraea grandiosella* Dyar. Similarly, Davis *et al.* (1989) reported that the feeding and survival rates of *D. grandiosella* Dyar larvae and European corn borer, *Ostrinia nubilalis* (Hubner), on the resistant maize hybrids were significantly less than on susceptible hybrids.

1.2.4 Physiological basis of feeding in insects

Since the pioneering studies of Grevillius (1905) and Verschaffelt (1910) to explain the chemical basis of insect-host plant interactions, several species of insects have been investigated to determine the proximate, experiential, genetic and ultimate causes of host finding (Courtney and Kibota, 1989). Unfortunately, many of these studies started with a priori expectation that the

host finding by insects could be described just in terms of the chemicals involved. Additionally, implicit in their working hypotheses was that a few key stimuli associated with plants elicited rather simple and automatic behaviours that resulted in host finding (Fraenkel, 1959; Dethier, 1971, 1976). This resulted in the perpetuation of terms denoting behavioural effects and focused attention on chemical stimuli alone rather than the behaviours that are the result of the integration of multiple inputs (Kennedy, 1978). More recently, however, it is generally accepted that complex neural and metabolic processes, along with autogenetic, experiential, and phylogenetic influences, are integrated in the recognition and acceptance of host plants by insects (Dethier, 1982; Miller and Strickler, 1984; Ramaswamy, 1988; Courtney and Kibota, 1989). In fact, after reviewing the literature, Courtney and Kibota (1989) tabulated 12 reasons why host chemistry alone may be unimportant in determining host choices in phytophagous insects.

Many recent studies on the physiological basis information processing and its relevance to host finding and acceptance by larvae increased our understanding of the chemical basis of larvae insect-plant interactions (Blaney *et al.*, 1986; Schoonhoven *et al.*, 1992). Behavioural, ultrastructural and electrophysiological research has greatly increased our knowledge of the possible functions of the various sensory receptors in host finding. From these studies one can conclude that certain sensory modalities may take precedence over others depending on the context in which the insect is present, but

typically, the various sensory modalities appear to act in concert, resulting in discrimination of feeding (Ramaswamy, 1988). Unfortunately, because of the emphasis given to chemical determinants of insect-plant interactions, and being more tractable, much more is known about chemosensory codes and central processes than of other sensory modalities (Ramaswamy, 1994).

Reese and Beck (1976) working on the effects of allelochemicals on the black cut worm, *Agrotis ipsilon* Hufnagel reported that certain allelochemicals could exert chronic effects on the growth, ingestion of food, utilization of food and pupation. Growth and pupation were inhibited by *P*-benzoquinone (reduced form of hydroquinone which is commonly found in plants) through reduced ingestion. Duroquinone, a synthetic chemical inhibited survival, growth and pupation through reduced ingestion and efficiency of conversion of assimilated food, which further reduced the overall efficiency of conversion of ingested food. The biologically active concentrations were well within the range at which many allelochemicals occurred in plants. Ng *et al.* (1990) reported that *Diatraea grandiosella* Dyar and *Spodoptera frugiperda* (J.E. Smith) reared on resistant plants had higher mortality and slower development than those reared on susceptible plants. Chapman (1982) showed that lepidopterous larvae reared on sub optimal and optimal plant hosts exhibited differences in growth. Similarly larval nutrition and temperature during development were shown to affect egg production and calling by *Pseudaletia unipunctata* (Haw.) (Mc Neil and Turgeon, 1982).

1.2.5 Physiological basis of oviposition in insects

Reviews by Ramaswamy (1988) and Renwick and Chew (1994) discuss the involvement of various sensory modalities in the evolution of oviposition behaviour in insects. Presumably, the various receptors provide sensory codes that are decoded and integrated by the central nervous system (CNS) resulting in the appropriate responses (Dethier, 1982). In moths as in other species of insects, the compound eyes perceive spatial patterns and form true images (Prokoby and Owens, 1983). Ocelli (simple eyes), which are found in most moths, are poor image formers, and they probably only detect light and dark expanses, such as the horizon line, fluctuating light intensities, or polarized light. Most moths are nocturnal, and little information is available on the use of vision in the location of oviposition site by these insects (Ramaswamy, 1994). Yamamoto *et al.* (1969) suggested that *Manduca sexta* females use vision to approach a plant or an inanimate object, such as an artificial leaf, at distances from 4 to 15 cm. Their interpretation of such behaviour is that these moths use non-specific visual cues to search and approach a plant and that landing itself is dependent on the presence of appropriate odours. Similarly, *Etiella zinkenella* (Hattori, 1986, 1988) and *Heliothis virescens* (Ramaswamy, 1990) hover in front of a potential host plant before landing. Further investigations by van Leerdam *et al.* (1984) and Navasero and Ramaswamy (1991) have shown that night-flying moths may utilize structural visual cues for acceptance or rejection of potential hosts. In a large field cage, given a choice of plants with different growth habits, *H. virescens* females exhibited a rank order of oviposition with

erect species, such as tobacco, velvet leaf, cotton, pigeon peas and ground cherry being preferred over the procumbent species, such as geranium, lupine, and crimson clover. In contrast, females exposed to terminals (only vegetative parts of approximately similar surface areas included) of the species inside a 1 cubic metre wire cage exhibited a rank order of preference that was totally different. In the laboratory cage, in the absence of any structural cues, the procumbent species also became highly acceptable to females. Acceptability of erect types may partially be due to the larger size of erect plants (height and spread), which increases the likelihood of finding and contact by the insect and suggests the involvement of vision in host discrimination based on use of structural profiles. In small arenas, such as laboratory cages, in the absence of structural cues, other sensory modalities (e.g. chemical and mechanical) may override visual stimuli.

The choice of oviposition site is partly dependent on the trichomatous characteristics of the substrate (Ramaswamy, 1988) and many species of moths exhibit high preference for the abaxial (lower, ventral) surfaces of susceptible plants over adaxial (upper, dorsal) surfaces. One of the hypothesized reasons for increased oviposition on the abaxial surfaces is the better protection afforded eggs (Ramaswamy, 1988), especially because of the presence of higher densities of trichomes (Jackson *et al.*, 1983; Navasero and Ramaswamy, 1991). Detection of physical structures, such as trichomes, is mediated by mechanoreceptors on the ovipositor and/ or on the tarsi. In studies involving

ablation of receptors on the ovipositor and/ or de-afferentation of sensory nerves from the ovipositor of *Bombyx mori*, Yamaoka and Hirao (1971, 1973) and Yamaoka *et al.* (1971) showed that phasic-type mechanoreceptors provide sensory information regarding surface structure and allow for the proper positioning of eggs on the substrate.

In many species oviposition correlates positively with increasing trichome density (Benedict *et al.*, 1983; Ramaswamy *et al.*, 1987). Such a preference for hirsute surfaces for oviposition has been inferred to increase the survival of immatures (Ramaswamy, 1988). Hairy leaves have lower surface wind velocities (Woolley, 1964), thicker boundary layer (Devlin, 1975), cooler temperatures due to lower leaf absorption of midday solar energy (Ehleringer, 1984), and warmer temperatures at night due to lowered heat loss through long wave radiation (Edwards and Wratten, 1980). These characteristics, it has been suggested, influence significantly not only oviposition but also egg and larval development and survival (Ramaswamy, 1988). In contrast, ovipositing females of some moth species prefer smooth surfaces. Among the factors governing the ovipositional responses of the stem borer *C. partellus* on the various maize cultivars, trichomes on the leaf surface are known to inhibit egg laying by the moths. Ampofo (1985) has shown that the lower leaf surfaces of maize plants are relatively smooth and that *C. partellus* females oviposit preferentially on the lower leaf surfaces. Kumar and Saxena (1985a, b) on the other hand demonstrated experimentally that removal of trichomes from the leaf

surface would render the maize leaf prone to oviposition by *C. partellus*. Kumar (1988) showed that ovipositional responses of *C. partellus* to susceptible maize cultivar inbred A was greater than those of the resistant maize cultivar Nyamula. These responses are elicited by certain characters of the plant that are perceivable prior to the moth's arrival on the plants (distance-perceivable) as well as those perceived after the arrival on the plants (contact-perceivable). The detection of smooth or hairy surfaces is by the mechanoreceptive sensilla on the tarsi and ovipositor and, possibly, even the antennae and proboscis, which have numerous sensilla with mechanosensitive neurons (Chapman, 1982).

Both volatile and non volatile plant chemicals stimulate feeding and oviposition in many species of moths (Ramaswamy, 1988). Non-volatile substances are perceived typically by contact chemoreceptors located on the various appendages, including antennae, proboscis, tarsi and ovipositor (Baker and Ramaswamy, 1990). The ability to perceive host surface chemicals could be vested in any or all sensilla in these appendages. In contrast, volatile gaseous molecules are perceived by olfactory sensilla located primarily on the antennae. Contact chemoreception is by far the major and the most common sensory modality involved in host acceptance for feeding or oviposition, regardless of larval specificity i.e. monophagous, oligophagous or polyphagous. Moths accept or reject a potential oviposition substrate based on the presence or absence of "sign" chemicals, presence and concentration of general chemicals

(such as sugars, amino acids, vitamins etc) and deterrent chemicals and moisture (Stadler, 1984; Ramaswamy, 1988). According to Bell (1990), only with the confluence of relevant external information regarding the resources, appropriate biological characteristics of the insect, including locomotory patterns and sensory perception capabilities, and the insects internal milieu, including deprivation and its needs, will the insect be successful in finding a host. The latter component (i.e.), physiological state, initiates the moth's search for hosts and affects its searching behaviour, especially in the choice it makes. Thus, a moth will not search for food or oviposition substrates when it is satiated or if it is in its normally inactive periods. According to Singer (1982), some species of butterflies will accept previously unacceptable hosts for oviposition when they have been deprived oviposition resources. Circadian rhythms, age, and mating or nutritional status are known to affect host-finding responses in insects (Chapman, 1982; Bowen, 1991). For example females of *Heliothis virescens* exhibit a periodicity in oviposition, feeding, and calling during the scotophase and will not oviposit or call during the photophase (Ramaswamy, 1990).

On the other hand, oviposition of cereal stem borers on non host plants has been studied. van Rensburg and van den Berg (1991) tested the oviposition preference of *B. fusca* on different host plants and reported that more eggs were laid on fodder crops than on either maize or sorghum; and stem cuttings were accepted by moths for oviposition as well as the whole plants. Among-

Nyarko *et al.* (1994) reported that in maize-sorghum-cowpea, sorghum-cowpea and maize-cassava intercropping systems, about a third of the total eggs laid by *C. partellus* were couled on non-host crop cowpea and cassava.

1.2.6 Relationship between mating and oviposition in insects

Several studies with moths have suggested that mated females are significantly more responsive to host-plant cues than virgin females. For example, Landolt (1989) reported that in a wind tunnel, a significantly greater percentage of mated *Trichoplusia ni* females flew upwind and contacted a potential host than did virgin females. Similarly, changes in visual responses with mating status have been reported in some lepidopterans. For example, young virgin *Pieris* spp females show a preference for blue, purple and yellow, the colours of the flowers they feed on. However, when mature and mated, the females prefer green and green-blue, corresponding to the colours of the leaves on which they oviposit (Chapman, 1982). Such findings suggest that mating may result in physiological changes that affect peripheral receptor responses. Whether these changes are as a result of the transfer of factor(s) by males during copulation or as a result of physiological changes within the female due to copulation is not known. Mating results in several physiological changes in the females whereby a switch over from virgin-female to mated-female behaviour occurs. These include suppression of pheromone production and receptivity (Gillot and Friedel, 1977; Raina, 1989; Ramaswamy *et al.*, 1992) and increases to oviposition stimuli (Chapman, 1982; Landolt, 1989). Males of several species

of drosophilid flies transfer proteins secreted by accessory glands to females during copulation; the sex peptide causes mated females to lose sexual receptivity and also stimulates oviposition (Ramaswamy, 1994). During copulation in orthopterid insects, the male transfers accessory gland secretions that contain prostaglandins or the enzyme and precursor for prostaglandin synthesis; prostaglandins in turn, trigger the switch over from virgin-female to mated-female behaviours, including oviposition behaviour (Stanley-Samuelson and Loher, 1986). Further, Suwagara (1986) has determined that the oviposition-stimulatory prostaglandin transferred by the male is detected by nerves in the genital chamber and triggers oviposition behaviour in females. Males of several species of moths are known to transfer juvenile hormone, ecdysteroids, proteins, peptides, lipids, and inorganics, in addition to sperm, during copulation. These factors trigger pheromonostasis, enhance egg production, protect developing embryos from desiccation (Ramaswamy *et al.*, 1994), and may also trigger the switch over from virgin-female to mated female behaviours.

1.2.7 Genetic variation in host selection by insects

Variation in an insect's response to a plant as a result of its previous experience is a widespread and perhaps universal phenomenon among phytophagous insects (Bernays and Chapman, 1994). This phenomenon commonly referred to as induction of preference has been extensively studied among larvae of lepidoptera where over 24 species have been shown to develop an altered

preference in favour of the plant they have already experienced (de Boer and Harrison, 1984; Jaenike, 1988; Papaj and Prokoby, 1988).

A lot of documented literature has emphasized variation in feeding and oviposition behaviour that result from ecological interactions, developmental or physiological state, and various types of experience. However, there is also limited evidence that intraspecific variation in host plant choices can also be due to heritable differences. With the advent of electrophoretic techniques, geneticists have found out that there is no single ("wild-type") insect but instead there exists considerable variations and heterozygosity. This led way to the more recent studies of genetic variation and microevolution, including that of host use by phytophagous insects (Bernays and Chapman, 1994).

Increasingly, it is being found out that within a population, there are groups of individuals that utilize different hosts, and it is assumed that these are genetic variants within the species. At a study site in Nevada, Singer *et al.* (1988) found that some females of the checker spot butterfly *Euphydras editha* preferred to oviposit on *Collinsia sp.* (Scrophylariaceae) while others chose to oviposit on *Plantago sp.* (Plantaginaceae). Heritability of this postalighting preference was demonstrated. In a second study, the same species showed three different patterns of ovipositon preference within the same population. One group of insects preferred *Collinsi sp.*, a second group *Plantago sp.*, while the third chose both equally. In a third study, there were two types of *E.*

editha, “specialists” that consistently chose only some individuals of the host plant *Pedicularis semibarbata*; and “generalists” that accepted all the known host plants. Rearing studies indicated that the differences in oviposition behaviour were heritable.

The insect neurophysiological and/or plant features underlying the changes in preference reported above are unknown, although it is assumed that the differences are related to the presence or absence of certain secondary metabolites. Therefore the variation in preference exhibited by insects either for feeding or oviposition may be a reflection of the changing selection pressure due to a continually changing host population (Bernays and Chapman, 1994).

1.2.8 Hopkins' host selection principle

While contributing to a conference discussion, Hopkins (1917) proposed that the chemical experience of the larva of an endopterygote insect could be transferred through the pupae to affect the response to the chemical by the adult. This became known as Hopkins' host selection principle or larval memory theory. It postulates that a memory of the larval food predisposes the adult female of phytophagous insects to oviposit on the same species as that upon which they themselves had fed as larvae (Hopkins, 1917; Craighead, 1921; Howanitz and Chang, 1963b). Ramaswamy (1988) refers to it as preimaginal conditioning and defines it as the tendency of adult insect individuals to feed or reproduce on the food-plant type they consumed as

larvae. To test the validity of this principle, the larval progeny of a female insect are reared on different host plants, after which the adult females are tested for oviposition preference (Wiklund, 1974). Although a great number of insect species have been tested, the validity of this theory as a general principle still remains to be proven and there is more evidence against it (Thompson and Parker, 1928; Thorpe, 1930; 1939; Dethier, 1954; de Wilde *et al.*, 1960; Takata, 1961; Palmitter, 1966; Hsiao and Fraenkel, 1968; Wiklund, 1974; Wenhua and Logan, 1994). According to Thorpe (1939), Corbet (1985) and van Emden *et al.* (1996), apparent 'larval learning' displayed by adult insects has been more frequently interpreted as arising from contact with the chemical in or on the organism at the time the adult emerges. Therefore, they hypothesize that chemical traces from the exposure of an insect to a host plant influences the behaviour of the insect in subsequent stages. In the case of moths, as in other insects, the studies conducted have yielded conflicting data on the role of Hopkins' host selection principle. The often cited example for the evidence of Hopkins' host selection principle is a study of Yammamoto *et al.*, (1969) on *Manduca sexta*. Unfortunately this study does not provide any data and the authors simply state that "moths reared during the larval stages on jimson-weed or tobacco and exposed to the same plants as diet-reared moths showed ovipositional preferences for the same plant on which they were reared". Further, they stated that "imprinting" to the odours of plants seems to be the operating influence. In subsequent study, Yammamoto and Jenkins (1972) reared *M. sexta* larvae on a diet, jimson-weed or tobacco and tested the

ensuing moths individually for oviposition on tobacco and jimson-weed. They found that diet-reared moths preferred tobacco, jimson-weed-reared moths preferred jimson-weed, and tobacco-reared moths preferred neither. However, the lack of test protocols and statistics prevents any convincing interpretation of these findings.

Kuznetsov (1952) showed that the moths *Euproctis chrysorrhoea* (L.) and *Stilpontia salicis* (L.) preferred to oviposit on the plants on which they had developed as larvae. However, the experiments were carried out without replicates and no statistical analysis was carried out to show the significance of the differences, hence the results are not convincing. Hovanitz and Chang (1963b) reared *Pieris rapae* for 8 to 12 generations on various plants and found ovipositional preference for larval food plants. Similarly, Hsiao, (1978) reported that larval host conditioning on a less suitable host, led to higher oviposition on the same host by *Leptinotarsa decemlineata*. The above studies suggest that no concrete evidence is available to unequivocally state that Hopkins' host selection principle is operative in adult preferences of moths.

1.2.7 Study of insect movements and marking techniques

The distance moved by organisms from their place of birth to their place of mating and reproduction, can be an important determinant of the scale of genetic variation and geographic differentiation which is observed between and within populations. Within a continuous population, limited dispersal will tend

to create localised areas of inbreeding (Martin and Roger, 1994). The paucity of studies providing direct evidence of both short- and long-distance movements by insects reflects the logistical difficulties that such studies entail (Aikman and Hewitt, 1972; Wiggett and Boag, 1989). Direct observation, biotelemetry, and other techniques employed in the movement studies of larger animals are impractical for insects (Hendrix *et al.*, 1987). Movement of insects has been studied by many researchers; a thorough review was made by Johnson (1969).

The evaluation of changes in insect population density during a management programme is often very expensive and complicated that such assessments are inadequately carried out or entirely neglected (Bottrell, 1979). It is important to have reliable and convenient methods for monitoring populations of *C. partellus* and *B. fusca*, in order to develop suitable control strategies for reducing losses caused by these pests. Monitoring of these pests has been mainly based on sampling the immature stages of the pest by destructive sampling of the crop. This method is laborious and often can only be done after the pest damage has occurred.

Mathez (1972) claimed that *C. partellus* is unable to fly very far from the point of emergence but static tethered experiments by Pats and Wiktelius (1989) showed that it has the capacity to migrate over long distances. The two authors also reported that mated *C. partellus* females flew for a longer time than

unmated ones. In addition to this, females also flew for a longer time than males and this is an observation which has been reported as a common feature among lepidoptera (Johnson, 1969). Mated *C. partellus* females were able to fly and lay eggs alternately for at least three nights in a row and flight did not affect the number of eggs deposited. These findings by Pats and Wiktelius (1989) indicate that female eclosion and mating most likely occur at the same location. Once mated, the females disperse and deposit eggs in fresh habitats the following night.

According to Harris and Nwanze (1992), the flight and migration capacity of *B. fusca* has not been widely studied and the moth is considered to be a weak flier. Mally (1920) indicated that female moths located and moved to crops from an emergence site at least a mile away. Migration over long distances has not been reported, although it would look feasible in some circumstances. Smithers (1959) states that although the exact distance that *B. fusca* flies is unknown, there is no doubt that the females do fly for long distances when necessary, but it seems unlikely that they do so if males and plants suitable for oviposition are available. The study of such movements is merited especially because there are occasions when the incidence of *B. fusca* attack on early crop is higher than can be explained by local circumstances (Harris and Nwanze, 1992).

At present movement by lepidopterous pests can be studied by the mark, release and recapture experiments in which many individuals, marked with a tracer such

as a dye or radioactivity, are released from the same place and some are subsequently recaptured in a surrounding network of traps (Rose *et al.*, 1985; Hagler, 1997). According to Pats (1989) and Hagler (1997), the mark-release-recapture experiments on insects should use a marking method, which is cheap, quick in application and detection, furthermore it must be safe to handle and be harmless both to the marked animal and the environment. Similarly, it would be advantageous if eggs, spermatophores as well as the adults will be marked. The technique of marking insects by mixing dye with laboratory larval diet has been used for numerous insect species. Gast and Landin (1966) successfully marked the boll weevil *Anthonomus grandis* Boh. With Calco Red N-1700. The boll weevil has also been marked by many others; for instance Lloyd *et al.* (1968), using the same dye. This marking technique has been especially successful for the European corn borer, *Ostrinia nubilalis* (Hubner) (Raun, 1967), the tobacco budworm *Heliothis virescens* (F.) (Hendricks and Graham, 1970), the corn earworm *Heliothis zea* (Boddie) (Jones *et al.*, 1975) and *C. partellus* (Swinhoe) (Pats, 1989). None of the above authors reported any deleterious effects of the marker dye. However, Wilkinson *et al.* (1972) reported that this dye caused significant differences in pupal weight, longevity and egg production among three lepidopterous species. Nevertheless, these differences were not considered sufficient to prevent the use of the dye in mark-release experiments.

Other techniques which have been used to mark insects include the use of dominant or co-dominant genetic markers (Bartlett, 1967; Huettel, 1979),

elemental compositions ("chemoprints") (Bowden *et al.*, 1984) and pollen grains (Kapp, 1969; Hendrix *et al.*, 1987; Mikhola, 1971).

1.2.10 Insect movement patterns and egg distribution

There have been many experiments on the mobility of different insect species but only in a few cases has there been any measure of this movement (Dobzhansky and Wright, 1943). Dispersal of insects may be affected by many factors. According to Jones (1977), most insects move about to seek food, shelter or mates, or to avoid predation. Therefore, insects released on bare cultivated fields may disperse for longer distances than insects released in their food crop (Riegert *et al.* 1954; Baldin *et al.*, 1958). Density is also important because high densities of insects bring about an over-crowding dispersal (Riegert *et al.*, 1954). Movement of insects may also be influenced by the wind speed and direction, and also by the day-to-day differences in temperature (Riegert *et al.*, 1954). Whatever their objectives in moving, the success of insects in achieving those objectives affect their survival and reproductive rate. Thus, the population dynamics of any insect species may depend on its movement pattern: one cannot be completely understood without the other.

According to Johnson (1969), among insect species, the sexes do not always migrate together and males and females may present distinct behavioural, physiological and ecological problems in this respect. Whatever the species of migrant insect the females are always included in migrations, those of the newly

emerged generation leaving the site where they were produced. The significance of this is clear; it is the function of all females to lay eggs in suitable places, and migrant females in particular oviposit at relatively long distances from the source. The males may or may not accompany them, for their function is only to fertilize the females; this can be done at the source without the males migrating, en route, or at the journey's end. The type of insect movement commonly investigated relates to diffusion or dissemination of insects, which are all initially at a central point. The assumption of dispersal from one central point is a necessary simplification for the derivation of a model of insect movement; but cannot wholly reflect the real situation of insects dispersing from a finite area (Freeman, 1977). As pointed earlier, there may be several biological reasons for movement, but whatever the cause, the effect is that insects move in such a way that their population density (number/unit area) decreases with distance from the central point (Freeman, 1977). During a study of regression of insect density on distance from the centre of dispersion using twig feeding by *Scolytus multistriatus* (Marsham) as a measure of insect density, Wadley and Wolfenberger (1944) found pronounced falling off in density with increasing distance from the centre. The downward slope of the plotted curve tended to level off as the distance increased. However, in neither infestation could indications of directional influence be found. The best result in fitting were given by the curve of the equation $Y = a + \log X + c/X$, in which X is distance and Y the percentage of twigs attacked. Similar results showing a

pronounced falling off in density with increasing distance from the centre of dispersion have been reported by Rose (1973).

Jones (1977) on the other hand studying the movement pattern and egg distribution in cabbage butterflies found that Australian and Canadian females behave quite differently and as a result distribute their eggs in different ways. The Australian butterflies lay fewer eggs in any given area, i.e. disperse their eggs more widely and generate a less aggregated distribution. On the other hand, Canadian butterflies disperse their eggs less widely resulting in a more aggregated distribution.

1.2.11 Insect flight range

The flight range is the mean distance flown by individuals of species (Johnson, 1969). It is usually estimated from regressions of density on distance. According to the same author, many studies of dispersal involve mark-release-recapture experiments where workers set out to investigate gradients of density in the horizontal plane. In doing this, the worker may have made a hypothesis about dispersal without being aware of having done so, for he/she has tacitly assumed that his/her samples represent the whole of the dispersing population. There are two distinct aspects of dispersal to be considered in mark-release-recapture experiments. Firstly, there is the detectable gradient of concentration of individuals extending horizontally up to a mile or more from the source; and secondly, there is the undetected part of the population that flies up and away

from the source beyond the limit of the sampling area and that may represent the major part of the dispersing population. According to Johnson (1969), most species of flying insects form horizontal gradient of density that may be very important to the economic entomologist. However, such a gradient tells little about the dispersive powers of the population produced at the source, for it does not provide the data appropriate for such problems. Such gradients must then either be integrated in zones around the source (a difficult task) and the results related to the numbers of the insects dispersing from the source, or they must be related also to the vertical gradients. According to Fitt (1989), some insects such as *Heliothis* spp display a characteristic vertical take off flight, which carries them above the flight boundary layer and enables them to undertake migratory movement in upper wind systems.

1.2.12 The edge effect

Edge effect is a commonly observed phenomenon and brings about a situation where the insect lays more eggs on the plants situated at the edge of plots adjacent wild hosts than in the centre (Harcourt, 1961; Kobayashi, 1965). In a situation where dispersal of insects is from a central release point, edge effect brings about a situation where the insect lays more eggs on the plants nearest to the release point.

Although the edges that are created when habitats are fragmented may have some negative effects on some bird species (Wilcove, 1985), their effects on

insects are often positive (Brown, 1991; Cappuccino and Root, 1992; Roland and Kaupp, 1995). Many butterfly species oviposit preferentially on edges (Courtney and Courtney, 1982). Little is known about the advantages that ovipositing on the edge may afford these species. Harcourt (1963) suggested that edge effect occurred because insects were continuously leaving the plot to feed and then returning to lay more eggs. Therefore the plants on the edge accumulate more visits and hence more eggs are laid on them than the other plants. In a forest situation, edge plants growing in the sun may have leaves that are of higher nutritional quality (Collinge and Londa, 1989). Microclimate may also differ between edges and the interior habitats (Saunders *et al.*, 1991). Few studies have compared insect oviposition on edge and on non-edge plants. Kirk (1965) reported that, rice weevils *Sitophilus oryzae* (L) emerging from maize storage bins flew to the edges of maize fields up to a mile distance, but migration ended when plants in a suitable state of development were reached, and the infestation showed steep gradients from the edges of the field inwards. Similarly, Kieckhefer and Medler (1966) working on leafhoppers and Wright and Ashby (1949) working on carrot fly reported that, more insects accumulated along the edges of fields than inwards. Ruppel (1965) stated that the short flights of *Cicadulina pastulae* Ruppel and DeLong were the reason for the greater incidence of maize streak disease around the border or edge of plots. Rose (1973) reported that serious maize streak infection was limited to crops adjacent to infested grasses and gradients in the incidence of the disease from the edge of the field were short.

Cappuccino and Martin (1997) examining the response of birch tubemaker *Acrobasis betulella* Hulst to habitat isolation and edges found out that larvae were found more on the edges than in the interior of birch forests and developed faster on edges. They proposed that living on the edges may help larvae grow faster because these sites are warmer, because host plant quality is higher, or some combination of the two. The importance of high temperatures for egg and larval development has been documented in several studies (Casey, 1993). The developmental advantage of edges has been shown for eggs of the Chrysanthemum lacebug *Corythuca marmorata* in experimental patches of goldenrod (Cappuccino and Root, 1992). Since every day on the host plant is another day vulnerable to predators and parasites (Price *et al.*, 1980), insects that develop faster may suffer less mortality (Loader and Damnan, 1991). Mortality from pathogens may also be lower on the edge plants since ultraviolet radiation deactivates virus particles (Broome *et al.*, 1974). Roland and Kaupp (1995) showed that the transmission of nuclear polyhedrosis virus among the forest tent caterpillar larvae was lower for larvae feeding on the edge plants.

1.2.13 Insect movement modelling

According to Stinner *et al.* (1983), mathematical models of insect species can be descriptive, explanatory or predictive. Freeman (1977) distinguishes between types of models by whether the mathematical model simply describes what has happened (descriptive), explains what has happened in terms of parameters of biological significance (explanatory), or provides a forecast of

what may be expected in the future (predictive). The majority of insect movement models are descriptive, even though evolutionary and management questions about the role of movement may require complex explanatory and predictive models. Regardless, it would seem obvious that the variation in behaviours and spatio-temporal scales among species, as well as different interests of researchers, should lead to a wide variety of models and modelling approaches (Stinner *et al.*, 1983).

Descriptive models of movements consist of a family of regression equations relating frequency of catch or insect density to time or distance from a point source of dispersing organisms (Freeman, 1977; Inoue, 1978; Ito and Miyashita, 1965; Taylor, 1978; 1980). Movement of some insect species have been described as a function of weather variables (Rainey, 1958; 1976; Meyer and Norris, 1973; Rose *et al.*, 1975; Buschman *et al.*, 1981) or distance of separation between individuals (Taylor, 1981). Without modification, descriptive (regression) models of insect movement are unlikely to apply to a wide range of situations because the parameters that a posteriori fit the model to data are influenced by both abiotic and biotic conditions encountered during the movement process. Also, such models are not applicable to situations where insects do not originate from a point source and this is the case for many insect pests because they are polyphagous and dispersed over large geographical areas (Stinner *et al.*, 1983).

Descriptive and explanatory models are valuable aids in gaining a biological/ecological understanding of insect movement. However, for insect pest species, the desired application of movement models is to predict pest influxes (Johnson *et al.*, 1975; Bartifield *et al.* 1980). Clark *et al.* (1978) admit the immense difficulty in developing truly predictive models of habit-movement and pest population dynamics. However, they also point out that movement studies have progressed from an earlier preoccupation with statistical problems of pattern distribution (Mardia, 1972) to the present treatment of movement as an ecological process on the same order as predation or reproduction. In these latter processes, a shift in perspective from treatment as static parameters to component-structured ecological processes has yielded substantial improvements in both theory and experimentation (Gilbert *et al.*, 1976). Hopefully, a similar shift in perspective for the study of movement of insect pests is underway.

1.2.14 Static tethering for monitoring flight duration of insects

Many winged, adult insects of agricultural, veterinary and medical importance are highly mobile. In development of forecasting and control strategies, the need to predict an insect's flight performance over time under various physiological and environmental conditions has lead to the development of a wide range of techniques to monitor flight behaviour (Cooter and Armes, 1993).

Direct visual observation (Tooper, 1987) of moths in the field using night goggles (Lingren *et al.*, 1986), or electronic optical systems such as infrared viewers (Riley *et al.*, 1983; Schaefer and Bent, 1984) and low-light level video cameras (Riley *et al.*, 1990), can provide useful information about the takeoff, feeding, and reproduction behaviours, local activity, and movement over short distances close to the ground. Radar (Greenbank *et al.*, 1980; Riley *et al.*, 1983; Riley, 1989) has been used to monitor take off leading to emigration and long range displacement at high altitude. These methods produce the best results when used to monitor large, dense, and relatively discrete populations where the identity of the targets can be assumed with some degree of confidence. Mark-release-recapture experiments (Rose *et al.*, 1985; Showers *et al.*, 1989) can give information about the range and direction of displacement, circumstantial evidence for flight on particular winds, and the pattern of local dispersal (Armes *et al.*, 1989; King *et al.*, 1990).

However, direct methods of measuring the flight performance, in terms of duration and the distance flown for large, highly mobile insects will usually involve tethering them to some recording device. One of the simplest technique that has traditionally been used to monitor flight performance in insects is the static tethering (Cooter and Armes, 1993). It involves attaching the insect to a fixed support, making the insect fly and then recording the time over which wing beating is observed. Some insects fly spontaneously when tarsal contact with a substrate is broken (Dingle, 1965), whereas others require the additional

continuous stimulation of a stream of air (Ohkubo, 1973). The flight activity data recorded consists of either the longest, or the summed, flying time induced during a set number of stimulation, or the time spent flying during a standard test period. According to various authors (Gatehouse and Hackett, 1980; Dingle, 1985; Cooter and Armes, 1993), a short coming of static tethering is that they do not permit continuous recording of the time and duration of successive flights by an insect. In most reported studies takeoff was not spontaneous but was induced by removal of tarsal contact. Furthermore, termination of flight was recorded only when the insect had ceased to beat its wings while still suspended, and was therefore usually, if not always due to exhaustion. In the field, flight is rarely terminated by exhaustion under normal conditions, so flight duration recorded in these ways can have little meaning in behavioural, as opposed to physiological terms. As a result, absolute estimates of flight endurance based on these methods carry a large degree of uncertainty, and their most prudent use is probably to provide qualitative comparisons of the effects of experimentally manipulated factors on flight (Cooter and Armes, 1993). This has been the approach used in several studies (e.g. Stewart and Gaylor, 1994).

Nevertheless, static tethering techniques have been widely used under laboratory conditions to provide valuable information on the aspects of flight. Pats and Wiktelius (1989) used static tethering technique to investigate the flight duration of *C. partellus* and found out that mated females flew for a

longer time than unmated ones. Females also flew for a longer time than males and flight did not affect the number of eggs deposited by the females. They therefore concluded that the static tethering technique was an accurate device for measuring flight duration. Similar static tethered flight studies carried out by Downham and Cooter (1998) with the leafhoppers *Cicadulina storeyi* China and *C. mbila* Naude', showed that depending on species, the factors of age, gender, gravid status and rearing on virus infested maize had significant effects on flight, whereas host plant species and mated status appeared unimportant. Downham and Cooter (1998) found that *C. mbila* males were more likely to fly, and made longer flights, than conspecific females but there was no effect of gender among *C. storeyi*; gravid status was not important for *C. mbila*, whereas gravid female *C. storeyi* flew more than non gravid.

1.3 Justification

Studies on insect movements are often difficult (Aikman and Hewitt, 1972; Wiggett and Boag, 1989). Direct observation, biotelemetry and other techniques employed in the movement studies of larger animals are impractical for insects due to their small size (Hendrix *et al.*, 1987). One of the methods which has been widely used to study the movement of lepidopterous pests is the mark-release experiments (Southwood, 1971; Rose *et al.*, 1985). In this method, one must come up with a marking technique which should be quick in application, detection and must be safe to handle and harmless to the marked insect and the environment. One marking method which has been used for

numerous insect species is the technique of mixing dye with laboratory diet on which insects are reared and hence is the one which was used in the current study. Although Pats (1989) successfully marked *C. partellus* with Calco Red N-1700 dye and reported that the dye had no effect on larval period and pupal weight, there are various aspects of the insect's biology that needed to be investigated further before the dye could be used for marking it for dispersal studies. These included investigating whether the dye had any effects on longevity, fecundity and flight duration of the insect. As regards *B. fusca*, no work has been reported involving use of the internal dyes for marking it.

Majority of studies on insects have focused on long-range movements. The short-range movements have been neglected though they may be the most important agronomically. If the economical suppression of *B. fusca* and *C. partellus* is to be accomplished, an understanding of the movement (dispersal) and egg deposition patterns is required. Despite the enormous impact of the two pests on cereal crop production in Kenya, little research has centered on these aspects. Such information is of critical importance for the application of integrated pest management in agricultural systems

Along with the study of movements and egg deposition patterns, it would also be important to investigate Hopkins' host selection principle. The latter postulates that larval food is somehow remembered by the adult female and influences her to lay more eggs on the same plant species it was reared on.

Despite the relevancy of Hopkins' host selection principle to aspects of oviposition behaviour in phytophagous insects, few workers have directed their attention to it. The principle is important because for example if it is valid, a modification in feeding preference by the insect larvae could result in their progeny restricting their preference to a few host plants. Little work has also been reported on the degree of the retention of the induced preference and the length of exposure required to induce a new preference.

1.4 Objectives of the study

1. To assess the effectiveness of Calco Red N-1700 and Sudan Blau-670 as internal markers of *B. fusca* and *C. partellus*.
2. To investigate oviposition preference of *B. fusca* and *C. partellus* moths reared on different hosts.
3. To investigate movement and egg deposition patterns of *B. fusca* and *C. partellus* released from a central point within a maize field.
4. To investigate how distance from the wild hosts influences colonisation of a susceptible host by *B. fusca* and *C. partellus*.

CHAPTER TWO

2 EVALUATION OF CALCO RED N-1700 AND SUDAN BLAU-670 DYES AS INTERNAL MARKERS FOR *CHILO PARTELLUS* AND *BUSSEOLA FUSCA***2.1 Introduction**

Recent emphasis on the control of insects has focused on finding a method of marking adults in order to determine patterns of dispersal and competitiveness of laboratory-reared insects compared with natural populations. The various marking techniques of insects have been documented by many authors and a thorough review was done by Southwood (1978).

The most appropriate marking method should be cheap, quick in application and detection. Also, it must be safe to handle and harmless to the marked insect and the environment. One such method which has been used for numerous studies is the technique of mixing Calco oil Red N-1700 dye with artificial diet on which insects are reared (Pats, 1989). Other dyes which have been reported to be appropriate internal markers include oil soluble deep Black BB (Hendricks *et al.*, 1971), oil soluble Blue (Hendricks, 1971), Sudan Blau-670 (Pats, 1989), Sudan Red No. 460 and Sudan Blue No. 670 II (Ostlie *et al.*, 1984).

Longevity of an insect is generally recorded as the period of adult survival and insect fecundity as the number of eggs laid. Insect longevity and fecundity may

be affected by the food consumed during the immature stages. Measuring adult longevity and fecundity is therefore necessary for the evaluation of the suitability of food to an insect.

Studies of migratory behaviour under field conditions are associated with certain problems. For instance, some insects are lost from sight and it is difficult to capture long distance fliers. However, some limited studies under laboratory conditions can provide valuable information on some aspects of flight. Tethered flight techniques have been widely used as a convenient means of assessing the relative flight performance of a variety of insect species (Dingle, 1965; Sharp *et al.*, 1975; Solbreck, 1980; Forse and Solbreck, 1985; Cooter, 1993; Reynolds *et al.*, 1997). The aim of the present study was to evaluate use of Calco oil Red N-1700 and Sudan Blau-670 as suitable internal markers for *B. fusca* and *C. partellus*. Aspects of importance that were considered included investigating larval periods, pupal weights, longevity, fecundity and flight duration of the insects reared as larvae on a normal diet and those reared on dyed diet.

2.2 Materials and methods

2.2.1 Marking technique

Each dye (0.5 g) was dissolved in 5ml maize oil and mixed with 1 litre of artificial diet. For experiments with *B. fusca*, the resulting diet (15ml) was poured into individual glass vials and in each vial a newly hatched larva was introduced. A group of 20 vials made a replication and there were six replications. For *C. partellus*, the resulting diet (200ml) was poured into five 500ml glass jars and 50 newly hatched larvae were placed in each jar. Control experiments were carried out using undyed diet (normal diet). The pupal weights and larval periods (hatched egg to formation of pupa) were compared. Observations were also made on the colour of the larvae, adults, eggs and first stage F1 larvae. In another experiment *B. fusca* larvae were reared in the normal diet for 18 days and thereafter transferred to a diet containing Calco Red dye. Other conditions remained the same.

Student's *t*-test was used to compare the means of two treatments and analysis of variance (ANOVA) was used to compare the means of more than two treatments using statistical analysis system (SAS) programme (SAS, 1987). Student-Newman-Keuls test was used to separate the means.

2.2.2 Adult longevity and female fecundity

Longevity of adults and fecundity of females fed as larvae on a normal diet and a diet containing dye were investigated. After emergence, a pair of moths (male

and female) were introduced into a numbered wire mesh cage and fed on distilled water soaked onto a sterilized cotton wool. Stem cuttings of susceptible sorghum cultivar were provided for oviposition. The stem cuttings were renewed daily until the death of the female moth. Individual adult longevity in days for both male and female moths were recorded. The number of eggs laid by an individual female moth was recorded daily and pooled for statistical analysis.

2.2.3 Tethered flights

The moths were tethered onto a simple flight mill which was raised 18cm above the bench (Plates 1 and 2). The head of an upside-down number 0 insect pin was attached to the dorsal side of the thorax (pronotum) using glue obtained from boiled *Euphorbia* spp latex) and the other end was inserted into the underside of the horizontal stand of the flight mill (Plates 3 and 4). The moths held onto a small piece of paper were then suspended in a horizontal position (Plate 5). By removing the paper, the moths lost tarsal contact and were induced to fly (Plates 6 and 7). The experiments started at 9.00 h each day and were carried out in a laboratory illuminated with red light only. Two categories of moths per species were tested: mated normal and mated Calco Red marked females. In order to get newly mated moths, female pupae were placed in a cage with adult males so that they could mate with emerging females immediately. All moths were flown and the time taken for 10 flight stops was recorded. The moths were stimulated to start flying again immediately after a stop by generally touching the abdomen with a camel hairbrush.

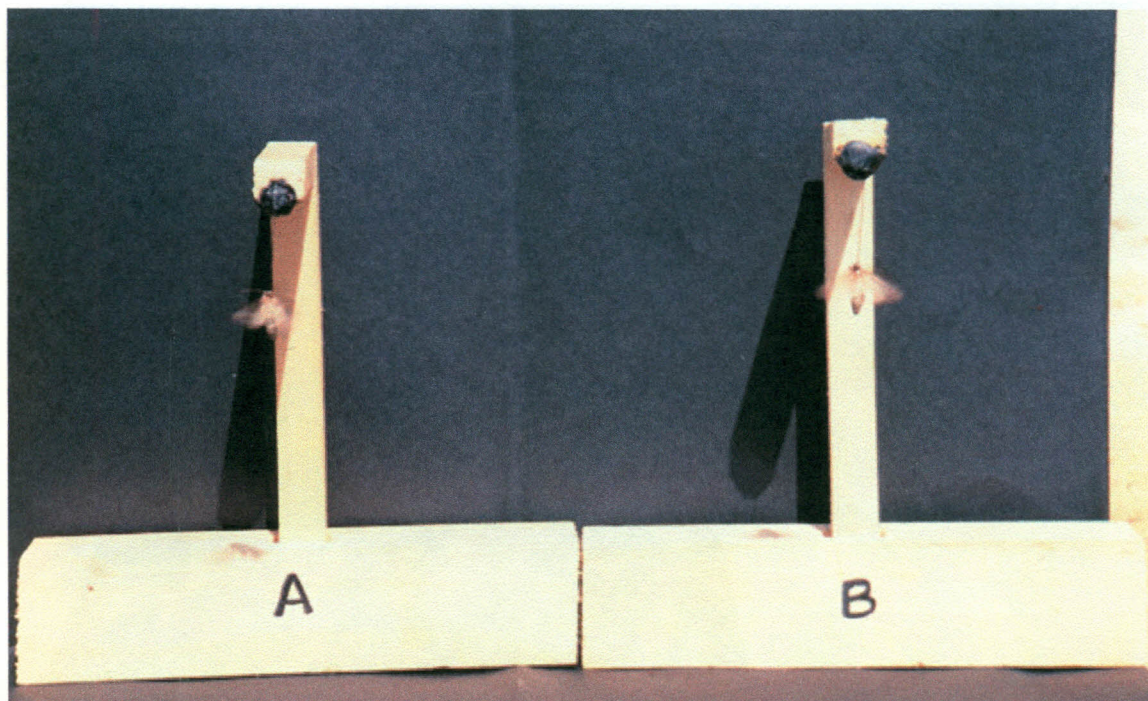


Plate 1. Simple flight mills (A & B) for studying static tethered flights of stem borer moths.

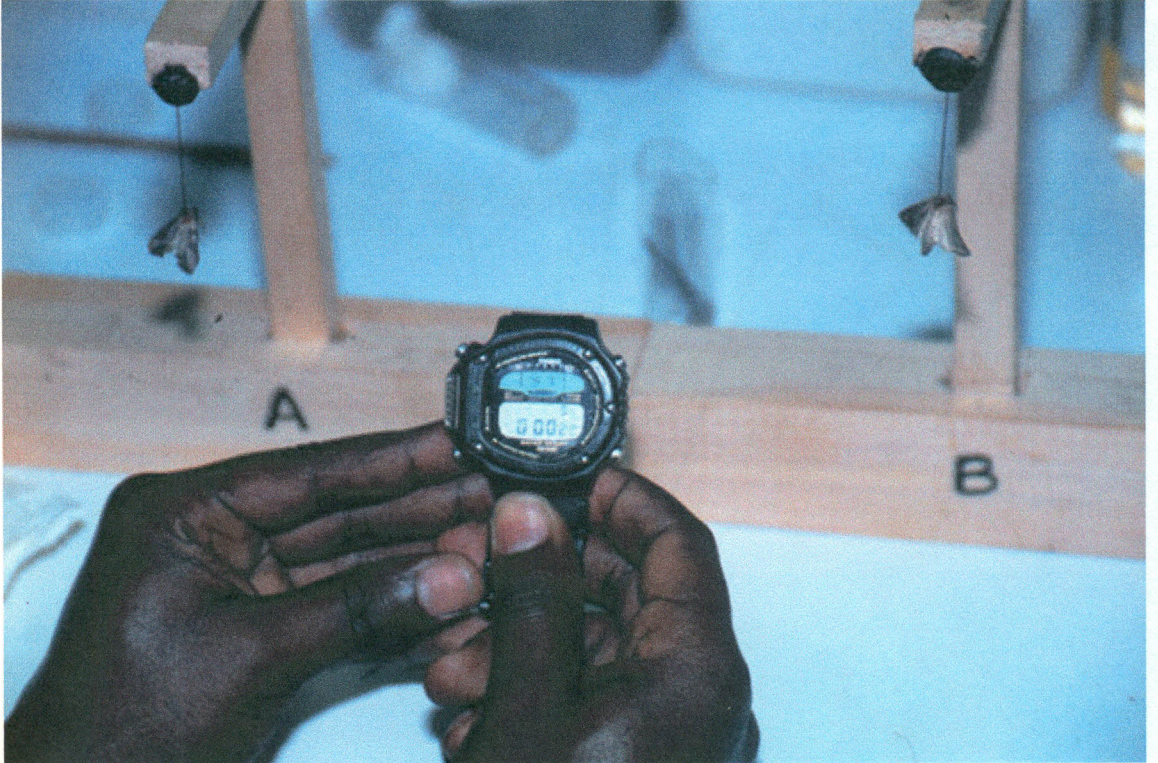


Plate 2. Timing flight duration of stem borer moths during static tethered flight studies.

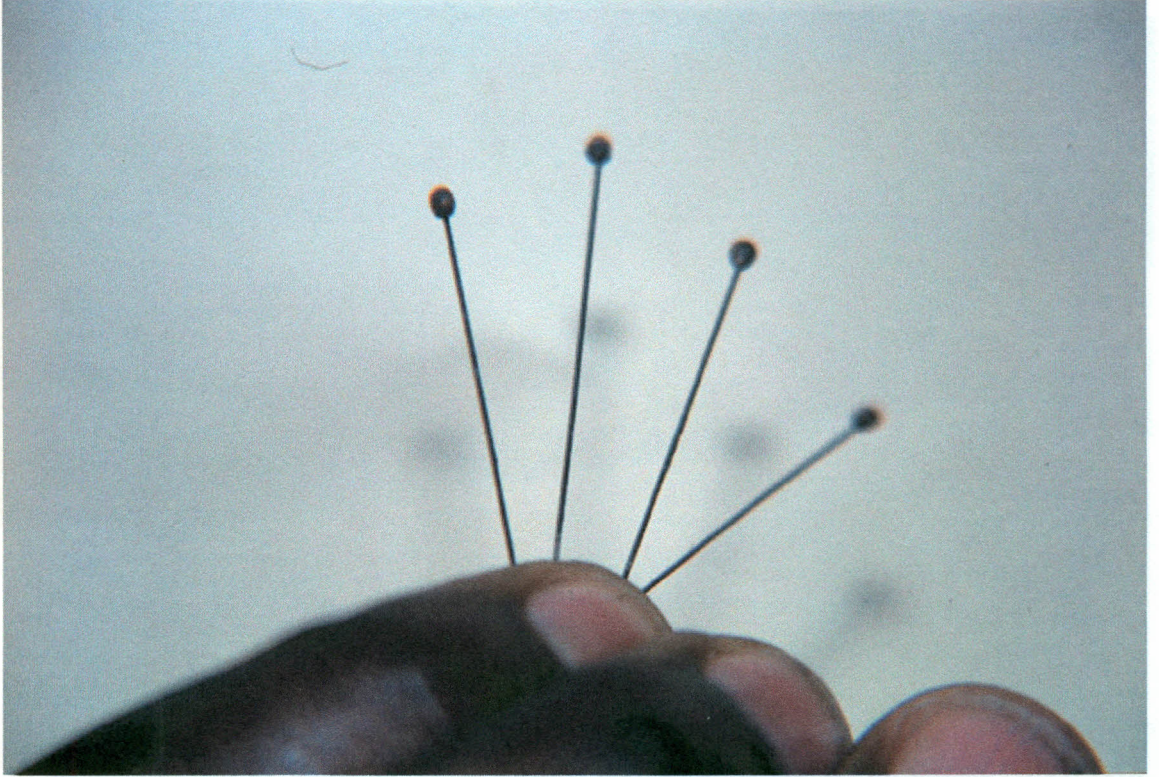


Plate 3. Heads of No. 0 insect pins studded with *Euphorbia* sp. glue for stem borer moths attachment during static tethered flight studies.



Plate 4. Gluing of an insect pin onto the dorsal side of the thorax of *B. fusca*.

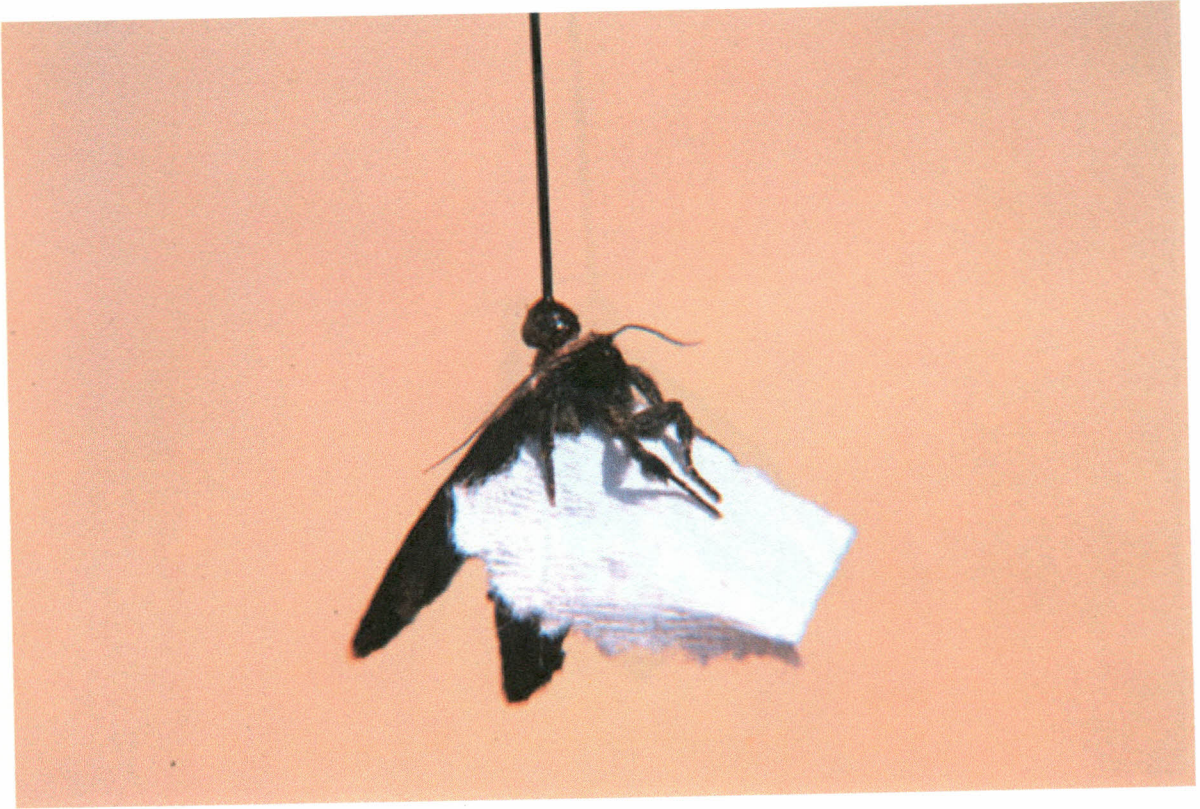


Plate 5. *Busseola fusca* moth holding onto a small piece of paper.

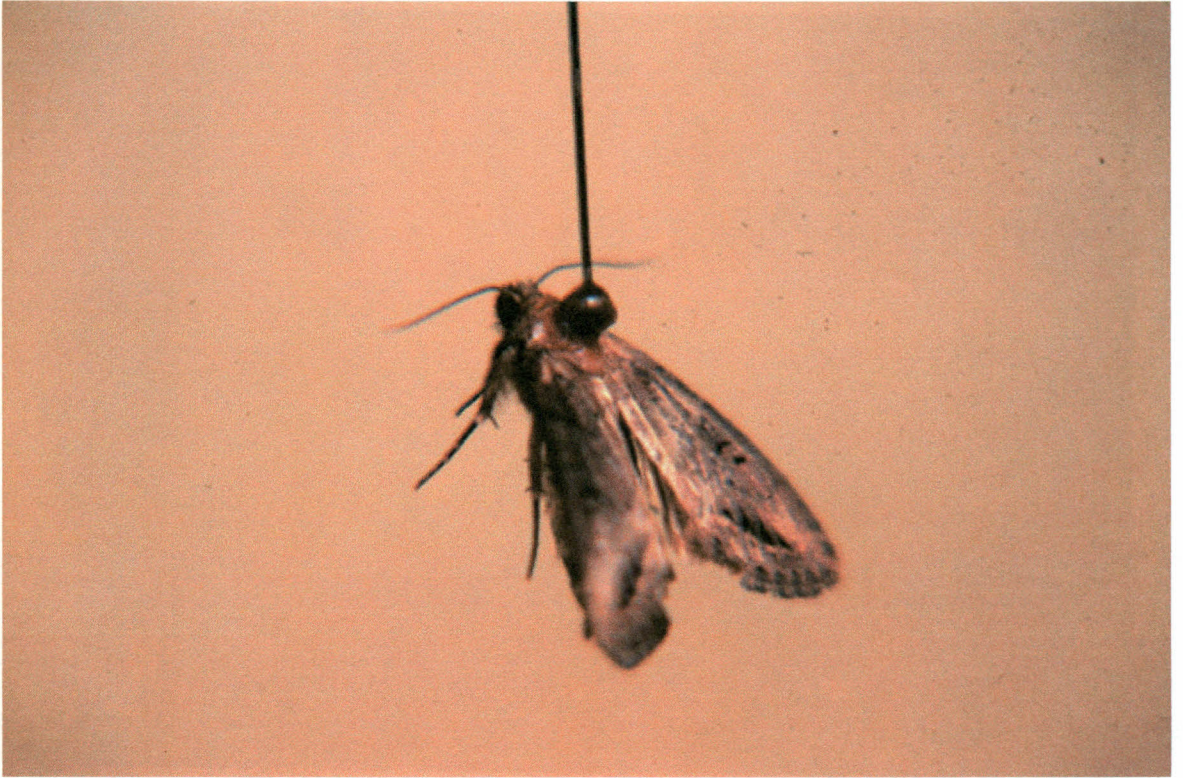


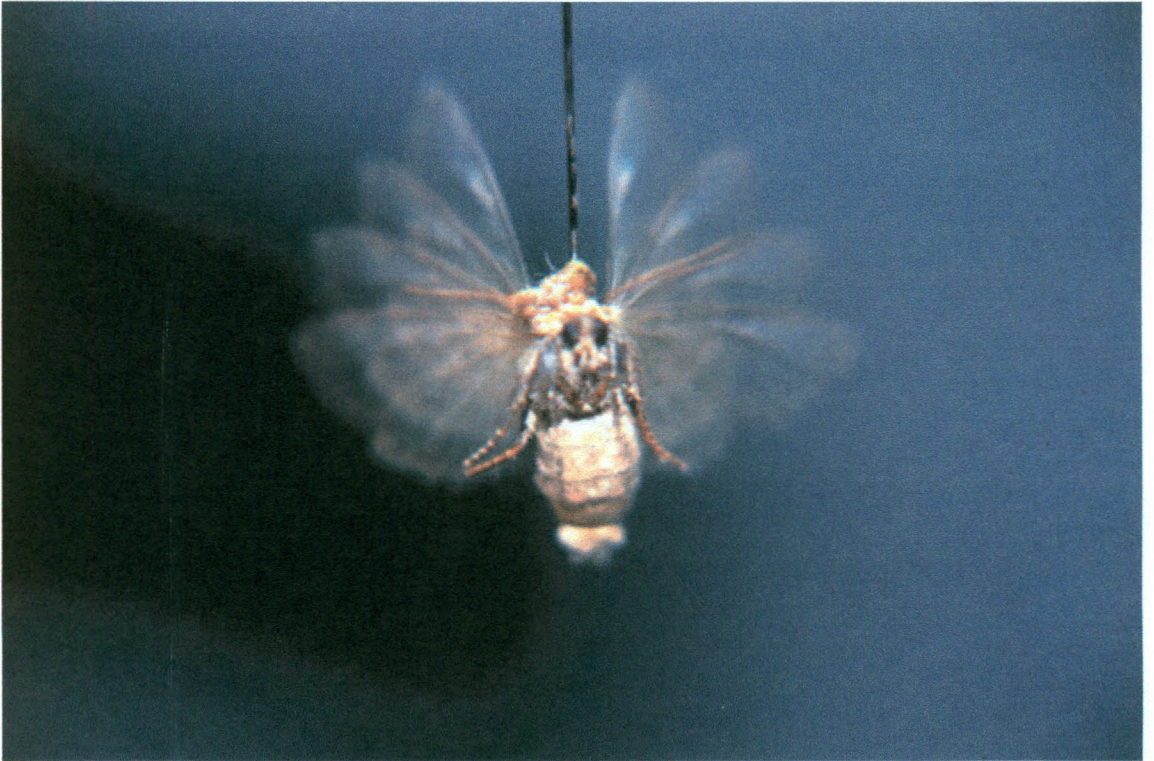
Plate 6. *Busseola fusca* moth tethered onto the flight mill.

1. Results

1.1 The effect of marking eyes on larval and pupal survival of *C. pinivore* and *C. fumifer*

The first part of the experiment was to determine if the survival of larvae

is not significantly different from those of unmarked larvae in a similar setting.



in a diet containing Cobalt Red N-1700 dye, the larvae, pupae and the moths

Plate 7. A flying *Busseola fusca* moth tethered onto the flight mill.

2.3 Results

2.3.1 The effect of marking dyes on larval and pupal development of *C. partellus* and *B. fusca*

The mean pupal weights of *C. partellus* and *B. fusca* reared on a normal diet were not significantly different from those of insects reared on a diet containing Calco Red N-1700 dye. The mean larval periods of *C. partellus* and *B. fusca* reared on a normal diet were significantly shorter than those of insects reared on a diet containing Calco Red N-1700 dye (Tables 1 and 2). Similarly, the mean larval period of *C. partellus* and *B. fusca* reared on a normal diet were significantly shorter than those of the insects reared on a diet containing Sudan Blau-670 dye (Tables 3 and 4). However, the mean pupal weight of *B. fusca* reared on a normal diet was significantly higher than that of insects reared on a diet containing Sudan Blau-670 dye (Table 4).

Both dyes successfully marked the larvae, adults, eggs and first stage F1 larvae. On a diet containing Calco Red N-1700 dye, the larvae, eggs and first stage F1 larvae were all coloured red (plate 8 and 9) whereas on a diet containing Sudan Blau-670 dye, only the larvae and the eggs were coloured blue (plate 8) but the first stage F1 larvae were coloured greyish-blue (blue colour was not very distinct).

Table 1: Mean larval period (\pm SE) and mean pupal weight (\pm SE) for *Chilo partellus* reared on normal artificial diet and a diet containing Calco Red N-1700 dye.

Treatment	Larval period (Days)	Pupal weight (g)
Normal	29.3 \pm 0.002a	0.083 \pm 0.003a
Calco Red	32.5 \pm 0.002b	0.087 \pm 0.002a

Means with the same letter within a column are not significantly different at P = 0.05

Table 2: Mean larval period (\pm SE) and mean pupal weight (\pm SE) for *Busseola fusca* reared on normal artificial diet and a diet containing Calco Red N-1700 dye.

Treatment	Larval period (Days)	Pupal weight (g)
Normal	39.8 \pm 0.528a	0.197 \pm 0.005a
Calco Red	54.7 \pm 0.798b	0.185 \pm 0.004a

Means with the same letter within a column are not significantly different at P = 0.05

Table 3: Mean larval period (\pm SE) and mean pupal weight (\pm SE) for *Chilo partellus* reared on normal artificial diet and a diet containing Sudan Blau-670 dye.

Treatment	Larval period (Days)	Pupal weight (g)
Normal	29.8 \pm 0.205a	0.066 \pm 0.001a
Sudan Blau	32.9 \pm 0.154b	0.067 \pm 0.002a

Means with the same letter within a column are not significantly different at P = 0.05

Table 4: Mean larval period (\pm SE) and mean pupal weight (\pm SE) for *Busseola fusca* reared on a normal artificial diet and a diet containing Sudan Blau-670 dye.

Treatment	Larval period (Days)	Pupal weight (g)
Normal	39.1 \pm 0.637a	0.211 \pm 0.007b
Sudan Blau	59.7 \pm 0.963b	0.164 \pm 0.005a

Means with the same letter within a column are not significantly different at P = 0.05

There were no significant differences between the mean larval periods of *B. fusca* reared on a normal diet and those of the insects reared on a normal diet for 18 days and transferred to a diet containing Calco Red N-1700. Similarly the mean pupal weights of *B. fusca* reared on a normal diet were not significantly different from those of insects reared on a normal diet for 18 days and transferred to a diet containing Calco Red N-1700 (Table 5).

Table 5: Mean larval period (\pm SE) and mean pupal weight (\pm SE) for *Busseola fusca* reared on a normal artificial diet and those reared on a normal artificial diet for 18 days and then transferred to a diet containing Calco Red N-1700 dye.

Treatment	Larval period (Days)	Pupal weight (g)
Normal	40.5 \pm 0.466a	0.212 \pm 0.004a
N/Calco Red	41.2 \pm 0.963a	0.205 \pm 0.003a

Means with the same letter within a column are not significantly different at P = 0.05

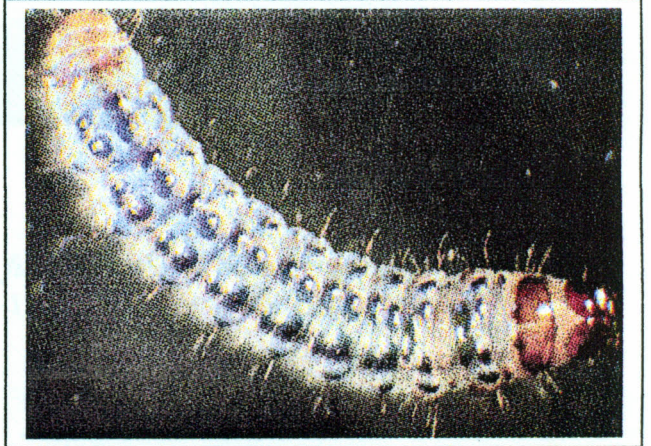
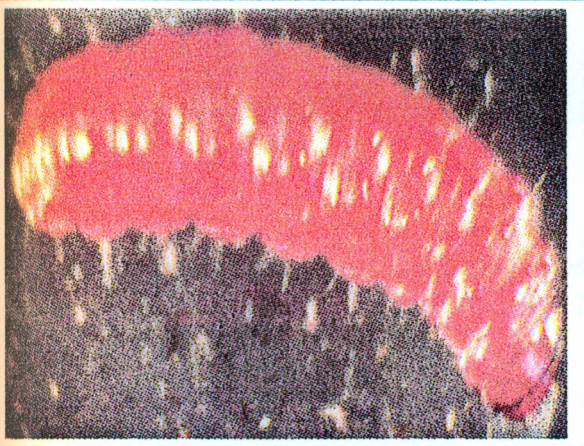


Plate 8. A larva of *Busseola fusca* reared on a normal diet (up middle); a red coloured larva of *Busseola fusca* reared on a diet incorporated with Calco Red N-1700 dye (up left) and a blue coloured larva of *Chillo partellus* reared on a diet incorporated with Sudan blau -670 dye (up right).

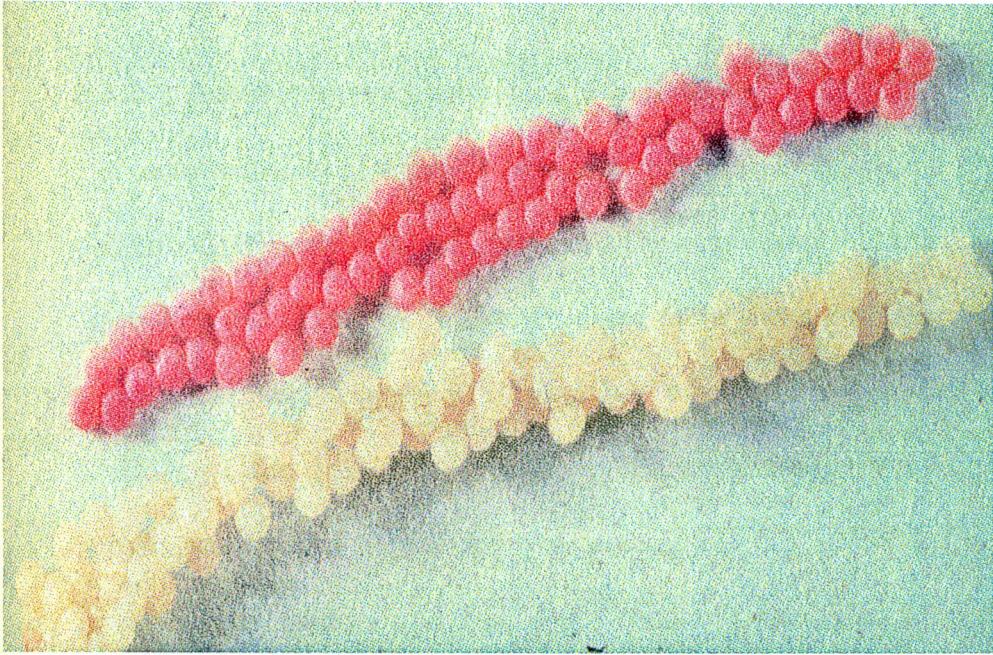


Plate 9. Red-coloured eggs laid by *Busseola fusca* females which were reared on a diet incorporated with Calco Red N-1700 dye (above) and normal eggs (below).

2.3.2 Adult longevity and female fecundity

The mean fecundity of either *C. partellus* or *B. fusca* reared on a normal diet was not significantly different from that of insects reared on a diet containing Calco Red dye (Table 6). However, there were some significant differences between the mean longevity of *C. partellus* reared on a normal diet and a diet containing Calco Red dye (Table 7). The mean longevity of *C. partellus* females reared on a normal diet was not significantly different from that of female insects reared on a dyed diet. Similarly, the mean longevity of *C. partellus* males reared on a normal diet was not significantly different from that of male insects reared on a dyed diet. However for both diets, the mean longevity of *C. partellus* males was significantly higher than that of females. There were no significant differences between the mean longevity of *B. fusca* reared on a normal diet and those reared on a diet containing Calco Red dye (Table 8).

Table 6: Mean fecundity (\pm SE) for *Chilo partellus* and *Busseola fusca* reared on a normal diet and a diet containing Calco Red N-1700 dye.

Insect pest	Diet	\bar{X} No. eggs
Chilo partellus	Normal	576.0 \pm 52.076a
	Dyed	579.0 \pm 39.523a
Busseola fusca	Normal	482.0 \pm 50.706a
	Dyed	477.6 \pm 43.743a

Means having the same letter within each column for each row are not significantly different at $P = 0.05$

Table 7: Mean longevity for *Chilo partellus* reared on a normal diet and a diet containing Calco Red N-1700 dye.

Insect pest	Diet	Sex	\bar{X} No. days \pm S.E
<i>Chilo partellus</i>	Normal	Female	9.128 \pm 0.506a
		Male	12.589 \pm 0.665b
	Dyed	Female	9.292 \pm 0.459a
		Male	12.765 \pm 0.906b

Means having the same letter within each column are not significantly different at P=0.05

Table 8: Mean longevity for *Busseola fusca* reared on a normal diet and a diet containing Calco Red N-1700 dye.

Insect pest	Diet	Sex	\bar{X} No. days \pm S.E
<i>Busseola fusca</i>	Normal	Female	7.647 \pm 0.499a
		Male	8.294 \pm 0.499a
	Dyed	Female	7.824 \pm 0.214a
		Male	8.529 \pm 0.244a

Means having the same letter within each column are not significantly different at P=0.05

2.3.3 Tethered flights

There were no significant differences between the mean flight duration of either *C. partellus* or *B. fusca* female moths reared on a normal diet and those of insects reared on a diet containing Calco Red dye (Table 9).

Table 9: Mean flight duration (time for 10 stops) (\pm S.E) for mated *Chilo partellus* and *Busseola fusca* female moths reared on a normal diet and a diet containing Calco Red N-1700 dye

Insect pest	Diet	\bar{X} Flight duration (min)
Chilo partellus	Dyed	10.7 \pm 0.927a
	Normal	10.8 \pm 0.721a
Busseola fusca	Dyed	6.6 \pm 0.299a
	Normal	6.4 \pm 0.625a

Data transformed using square-root

Means having the same letter within each column for each row are not significantly different at $P=0.05$

2.4 Discussion

Adding two oil soluble dyes, Calco Red N-1700 and Sudan Blau-670 to the larval diet of *C. partellus* and *B. fusca* was shown to be an effective method for marking moths for mark-release experiments. Both dyes successfully marked the larvae, adults, eggs and first stage F1 larvae. Similar results showing suitability of the dyes in marking insects have been reported by Lloyd *et al.*, 1968, Raun 1967); Hendricks and Graham, 1970; Jones *et al.*, 1975; Ostlie *et al.*, 1984 and Pats, 1989.

In the present study, insects reared on a dyed diet had a longer larval period than those reared on the normal diet, but their pupal weights were not different except in *B. fusca* where the insects reared on the normal diet were heavier than those reared on Sudan Blau dyed diet. Pats (1989) reported that Sudan Blau 670 prolonged the development time for both male and female *C. partellus*

whereas Ostlie *et al.* (1984) reported a reduced larval survival as well as a delayed development when Sudan Blue No. 670 II was mixed into the larval diet of *O. nubilalis*. On the other hand, Brewer (1982) found that individuals of *H. virescens* reared on a dyed diet were about twice as heavy as those reared on a normal diet. Wilkinson *et al.* (1972) also observed significant differences in pupal weights, longevity and egg production between Calco Red N-1700 dyed and normal insects. However, these differences were not considered sufficient to prevent the use of the dye for marking insects for mark-release experiments.

In another experiment it was shown that, *B. fusca* reared on a normal diet for 18 days and transferred to a diet containing Calco Red could still lay marked eggs. Similarly, Pats (1989) successfully marked *C. partellus* by transferring 21-day old larvae from the normal diet to the dyed diet. By larval transfer, the time the larva is exposed to the dye is reduced and consequently this also minimizes the possible deleterious effects of the dye.

Of the two dyes that were tested, Calco Red N-1700 was found to be more appropriate for further marking experiments because marked moths laid bright red eggs which can easily be detected on maize plants.

Calco Red dye also had no effect on the fecundity and longevity of both *C. partellus* and *B. fusca*. For both species, the mean fecundity and longevity of

insects reared on a normal diet were not significantly different from those reared on a diet containing Calco Red dye. The overall *B. fusca* female longevity was within a range of 7.6 to 7.8 days whereas the male's ranged from 8.3 to 8.5 days and this conformed to the range which was recorded by Unnithan (1987) and Randriamananoro (1996). Unnithan (1987) also reported that there were no significant differences in the longevity of male and female *B. fusca*. As regards *C. partellus*, female longevity was within a range of 9.1 to 9.3 days whereas the male's ranged from 12.6 to 12.8 days. These results showed that males live longer than females. Fecundity (egg production) is an indicator of antibiosis and hence it is affected by the nature of food. The overall *B. fusca* female fecundity was within the range of 360 to 723 eggs which was reported by Usua (1968 b) and Unnithan (1987) whereas that of *C. partellus* was within the range of 361 to 814 eggs reported by Mohammed (1997). Therefore, since there were no significant differences in fecundity between marked and normal insects, it can be deduced that Calco Red had no antibiotic effects on the insects. In conclusion, these findings show that Calco Red dye could be used effectively for marking the insects during dispersal studies because the dye had no effect on either fecundity or longevity of the insects.

Experiments on flight duration revealed that for both species, the mean flight duration of mated female insects reared on a normal diet was not significantly different from those reared on a diet containing Calco Red dye. However, results showed that *C. partellus* females flew for longer time than *B. fusca*

females implying that *C. partellus* has a stronger dispersal potential than *B. fusca*. According to Cooter and Armes (1993), flight termination during static tethering is due to exhaustion. Therefore, there is a possibility that *B. fusca* females flew for a shorter time because being larger and heavier, they got exhausted faster under static tethered position than the smaller and lighter *C. partellus*. Like fecundity, flight duration is an indicator of antibiosis and hence it is affected by the nature of food. Therefore, since there were no significant differences in flight duration between marked and normal insects, it can be deduced that Calco Red had no antibiotic effects on the insects. An important observation that was noted is that for both insect species there was a great variation in flight duration between the individuals tested. A similar variation, has been found in tethered flight studies on other insect species (Dingle, 1965; Kishaba *et al.*, 1967; Ono and Nakasuji, 1980). In conclusion, these findings further showed that Calco Red dye could be used effectively for marking the insects during dispersal studies because the dye had no effect on their flight duration.

CHAPTER THREE

3 GROWTH, DEVELOPMENT AND OVIPOSITION PREFERENCE OF *BUSSEOLA FUSCA* AND *CHILO PARTELLUS* REARED ON DIFFERENT HOST PLANTS

3.1 Introduction

Acceptability of plants as potential food by insects is affected by structure, colour, growth habit and stages, and pubescence of plants, in addition to chemical characteristics and moisture and nutrient status (Ramaswamy, 1988; Renwick and Chew, 1994). Within a given plant, various parts may vary in their physical and chemical attributes such as trichome types and densities, colour and structure, and the amount of associated allelochemicals and primary chemicals. How these attributes are detected and what processes occur at the level of peripheral nervous system (PNS) and the central nervous system (CNS) are key factors in understanding the functional dynamics of insect interactions with their host plants. Reviews by Ramaswamy (1988) and Renwick and Chew (1994) also discuss the involvement of various sensory modalities in the evolution of feeding and oviposition behaviour of insects. The survival of many phytophagous insects depends on the ability of the adult to select a suitable host plant for oviposition. Oviposition responses are among the different factors determining the suitability or resistance of plants to stem borers (Saxena, 1985). In the field, various stimuli from the environment in the vicinity of the plants are reported to influence the adults orientation and subsequent oviposition on a

plant, irrespective of the plant characteristics (Saxena, 1985a). According to the same author (1990), the number of eggs laid on a plant is one of the factors that determine plant colonization by a particular insect. The higher the number of eggs laid on the host, the greater the insect's ovipositional preference for the plant and consequently, the greater would be its attractiveness. Furthermore, ovipositional response of an insect to a host is attributed to the role of the distance-perceivable (chemicals) and contact-perceivable (physical or mechanical) character of the host. However, Norris and Kogan (1979) stated that ovipositional responses might be the result of visual, hydro or olfactory stimuli. The objective of this study was to investigate whether there are differences in growth, development and oviposition preference by *B. fusca* and *C. partellus* reared on different host plants.

2.2 Two-choice oviposition preferences

3.2 Materials and methods

3.2.1 Growth and development of *B. fusca* and *C. partellus*

Busseola fusca and *C. partellus* pupae/ larvae were collected in August 1996 from sorghum, maize, *S. versicolor* and *S. arundinaceum* plants grown by use of irrigation in an experimental plot at Mbita Point Field Station (MPFS). *Pennisetum purpureum* had also been planted but unfortunately, no insects were recovered from it and the first instar larvae that were used to start a colony on *P. purpureum* were obtained from the mass rearing laboratory in MPFS. The larvae that were collected from the field were reared until pupation

in stem cuttings of their respective host plants. The eggs that were obtained from the emerging moths were used for rearing the first generation of each pest on its respective host plant. Newly hatched larvae were introduced into cuttings of the shoots with the leaf whorls of 2 to 3 weeks old plants. Infested shoots were kept in 100ml glass jars and the larvae were transferred to fresh cuttings of shoots/ stems after every 3 days. Successive larval stages were fed on stem cuttings taken from plants of the more advanced age until pupation. The insects were continuously reared on their respective host plant species for three generations before data collection started. For all sets of experiments, larval periods and pupal weights were compared.

3.2.2 Two-choice oviposition preference

The experiment was conducted with stem cuttings in the laboratory. In this type of experiment, for example insects reared on sorghum ("rearing host") were tested for oviposition alternately with each of the other hosts ("test host") as follows: -sorghum x maize, sorghum x *S. versicolor*, sorghum x *S. arundinaceum*, sorghum x *P. purpureum*. The experiments were repeated with insects reared on maize, *S. versicolor*, *S. arundinaceum* and *P. purpureum*.

One cutting of about 20cm length per host was introduced in a cage measuring 25cm diameter with a height of 15cm in opposite diagonals without touching each other. A petri dish (15cm diam.) was placed at the base of the cage and was lined with 2cm of wet sand to maintain moisture of the cuttings. Two

mated females of either *B. fusca* or *C. partellus* were released in the cage in the evening and allowed to oviposit for two consecutive nights. After the first night, the cuttings were carefully removed and replaced with new ones. The number of eggs laid during the two nights were counted and pooled up for analysis. The experiment was replicated five times.

3.2.3 Multiple choice oviposition preference

Experiments were conducted in the laboratory under the same conditions as ovipositional responses in the two-choice tests. The same methods were used, except that the stem cuttings were from the five different host plants. The stem cuttings (two per each host) were arranged randomly along the circumference of a circle of 1m diameter and covered with a wire mesh cage of 1.20m x 1.0m (diameter x height). Ten (10) mated female moths were introduced in a small wire cage and placed at the center of the cage. The small cage was carefully opened in the evening to release the moths. The number of eggs laid on each host species was recorded on the following day. The test was replicated five times and the number of eggs laid were pooled for statistical analysis.

Student's *t*-test was used to compare the means of two treatments and analysis of variance (ANOVA) was used to compare the means of more than two treatments using statistical analysis system (SAS) programme (SAS, 1987). Student-Newman-Keuls test was used to separate the means.

3.3 Results

3.3.1 Growth and development of *B. fusca* and *C. partellus*

There were some significant differences between the mean larval periods and pupal weights of *B. fusca* reared on the various host plants (Table 10). The longest mean larval period (45.09 ± 0.958) was recorded on *P. purpureum*, followed by *S. arundinaceum* while the shortest (32.68 ± 0.391) was recorded on *S. versicolor*. The mean larval periods on maize and sorghum were not significantly different from that on *S. versicolor*. The mean pupal weight on *P. purpureum* (0.189 ± 0.001) was significantly lower than that on maize, sorghum, *S. versicolor* and *S. arundinaceum* which showed no significant differences.

There were some significant differences between the larval periods and pupal weights of *C. partellus* reared on the various hosts (Table 11). The mean larval period on *P. purpureum* (38.31 ± 2.408) was significantly higher than that on maize, sorghum, *S. versicolor* and *S. arundinaceum* which showed no significant differences. The mean pupal weight on *S. arundinaceum* (0.103 ± 0.104) was significantly higher than on maize, sorghum, *S. versicolor* and *P. purpureum*, which were not significantly different from each other.

Table 10: Mean larval period (\pm SE) and mean pupal weight (\pm SE) of *B. fusca* reared on various hosts.

Rearing host	Larval period (days)	Pupal weight (g)
Maize	33.62 \pm 0.359 a	0.257 \pm 0.007 b
Sorghun	32.88 \pm 0.359 a	0.251 \pm 0.006 b
<i>S. versicolor</i>	32.68 \pm 0.391 a	0.243 \pm 0.006 b
<i>S. arundinaceum</i>	35.86 \pm 0.597 b	0.243 \pm 0.006 b
<i>P. purpureum</i>	45.09 \pm 0.958 c	0.189 \pm 0.005 a

Means having the same letter within a column are not significantly different at $P=0.05$.

Table 11: Mean larval period (\pm SE) and mean pupal weight (\pm SE) of *C. partellus* reared on various hosts

Rearing host	Larval period (days)	Pupal weight (g)
Maize	27.33 \pm 0.457 a	0.071 \pm 0.005 a
Sorghun	29.31 \pm 0.384 a	0.083 \pm 0.084 ab
<i>S. versicolor</i>	28.69 \pm 0.741 a	0.074 \pm 0.077 ab
<i>S. arundinaceum</i>	28.57 \pm 0.459 a	0.103 \pm 0.104 c
<i>P. purpureum</i>	38.31 \pm 2.408 b	0.069 \pm 0.072 a

Means having the same letter within a column are not significantly different at $P=0.05$.

3.3.2 Two-choice oviposition preference

There were some significant differences between the number of eggs laid by *C. partellus* females in a two-choice oviposition preference, i.e *C. partellus* reared on a given host ("rearing host") and tested for oviposition alternately with each

of the other hosts ("test hosts"). The number of eggs laid on the "test hosts" were not significantly different from those laid on the "rearing host" when *C. partellus* was reared on Sorghum, *S. arundinaceum*, *S. versicolor* and *P. purpureum* (Table 12). However, when it was reared on maize, some significant differences were observed in the experiments involving maize x sorghum and maize x *S. versicolor*. In both cases, the number of eggs laid on maize ("rearing host") was significantly higher than those laid on either sorghum or *S. versicolor* ("test host").

There were also some significant differences between the number of eggs laid by female *B. fusca* in a two-choice oviposition preference, i.e. *B. fusca* reared on a given host ("rearing host") and tested for oviposition alternately with each of the other hosts ("test hosts"). The number of eggs laid on the "test hosts" were not significantly different from those laid on the "rearing host" when *B. fusca* was reared on *S. arundinaceum*, *S. versicolor* and *P. purpureum* (Table 13). However, when it was reared on maize and on sorghum, some significant differences were observed in the experiments involving sorghum x maize, sorghum x *P. purpureum* and maize x *P. purpureum*. In the case of insects reared on sorghum, the number of eggs laid on it were significantly higher than those laid on either maize or *P. purpureum*. Similarly, the number of eggs laid on maize by the insects which were reared on this crop were significantly higher than those laid on *P. purpureum*.

Table 12: Two-choice oviposition preference of the 4th generation *C. partellus* females tested on various host plants

“Rearing host” A	“Test host” B	\bar{X} Eggs (no.) A	\bar{X} Eggs (no.) B
Sorghum	Maize	13.52 ± 0.593 ns	12.33 ± 1.166
Sorghum	<i>S. arundinaceum</i>	13.41 ± 2.622 ns	13.55 ± 1.224
Sorghum	<i>S. versicolor</i>	13.89 ± 2.084 ns	11.44 ± 2.604
Sorghum	<i>P. purpureum</i>	16.43 ± 2.082 ns	11.29 ± 1.161
Maize	Sorghum	15.36 ± 1.246 *	13.04 ± 1.409
Maize	<i>S. arundinaceum</i>	13.49 ± 1.061 ns	13.33 ± 0.701
Maize	<i>S. versicolor</i>	13.34 ± 0.501 *	10.56 ± 0.555
Maize	<i>P. purpureum</i>	16.58 ± 1.625 ns	13.20 ± 1.077
<i>S. arundinaceum</i>	Sorghum	12.72 ± 1.495 ns	11.33 ± 1.069
<i>S. arundinaceum</i>	Maize	11.98 ± 0.986 ns	12.29 ± 1.423
<i>S. arundinaceum</i>	<i>S. versicolor</i>	10.57 ± 0.809 ns	10.35 ± 0.577
<i>S. arundinaceum</i>	<i>P. purpureum</i>	13.04 ± 0.585 ns	8.51 ± 2.425
<i>S. versicolor</i>	Sorghum	12.07 ± 1.061 ns	11.75 ± 1.197
<i>S. versicolor</i>	Maize	10.84 ± 0.963 ns	10.33 ± 1.315
<i>S. versicolor</i>	<i>S. arundinaceum</i>	11.45 ± 1.104 ns	8.99 ± 0.875
<i>S. versicolor</i>	<i>P. purpureum</i>	10.50 ± 1.178 ns	10.26 ± 0.879
<i>P. purpureum</i>	Sorghum	10.05 ± 1.437 ns	12.37 ± 1.703
<i>P. purpureum</i>	Maize	10.92 ± 1.404 ns	12.16 ± 0.277
<i>P. purpureum</i>	<i>S. arundinaceum</i>	11.39 ± 0.991 ns	9.56 ± 1.133
<i>P. purpureum</i>	<i>S. versicolor</i>	11.69 ± 1.014 ns	10.79 ± 1.657

Mean value followed by * is significantly different from the corresponding mean value in the same row at P= 0.05, ns= not significant. Data on the number of eggs was modified by square root transformation.

Table 13: Two-choice oviposition preference of the 4th generation *B. fusca* females tested on various host plants

Rearing host A	Test host B	\bar{X} Eggs (no.) A	\bar{X} Eggs (no.) B
Sorghum	Maize	14.44 ± 3.003 *	7.67 ± 2.027
Sorghum	<i>S. arundinaceum</i>	13.38 ± 3.107 ns	13.31 ± 1.530
Sorghum	<i>S. versicolor</i>	13.27 ± 2.173 ns	11.77 ± 3.437
Sorghum	<i>P. purpureum</i>	16.18 ± 2.467 *	5.81 ± 2.527
Maize	Sorghum	14.06 ± 1.754 ns	13.20 ± 2.259
Maize	<i>S. arundinaceum</i>	10.37 ± 2.447 ns	12.39 ± 3.319
Maize	<i>S. versicolor</i>	13.01 ± 1.496 ns	12.51 ± 1.766
Maize	<i>P. purpureum</i>	14.99 ± 3.124 *	7.24 ± 1.353
<i>S. arundinaceum</i>	Sorghum	11.49 ± 1.485 ns	10.79 ± 1.314
<i>S. arundinaceum</i>	Maize	15.45 ± 0.547 ns	12.11 ± 1.815
<i>S. arundinaceum</i>	<i>S. versicolor</i>	13.88 ± 0.963 ns	11.81 ± 0.364
<i>S. arundinaceum</i>	<i>P. purpureum</i>	11.85 ± 0.688 ns	9.27 ± 2.747
<i>S. versicolor</i>	Sorghum	13.85 ± 1.418 ns	13.50 ± 1.466
<i>S. versicolor</i>	Maize	12.96 ± 0.999 ns	12.64 ± 1.184
<i>S. versicolor</i>	<i>S. arundinaceum</i>	16.28 ± 2.167 ns	13.35 ± 0.919
<i>S. versicolor</i>	<i>P. purpureum</i>	13.75 ± 0.637 ns	10.90 ± 2.075
<i>P. purpureum</i>	Sorghum	10.27 ± 1.428 ns	14.32 ± 2.772
<i>P. purpureum</i>	Maize	11.93 ± 2.039 ns	12.83 ± 1.683
<i>P. purpureum</i>	<i>S. arundinaceum</i>	12.78 ± 2.226 ns	13.19 ± 0.095
<i>P. purpureum</i>	<i>S. versicolor</i>	14.19 ± 1.523 ns	13.19 ± 1.148

Mean value followed by * is significantly different from the corresponding mean value in the same row at P= 0.05, ns= not significant. Data on the number of eggs was modified by square root transformation.

3.3.3 Multiple choice oviposition preference

There were some significant differences between the number of eggs laid by *C. partellus* females in a multiple-choice oviposition preference experiment (Table 14). When *C. partellus* was reared on sorghum, the number of eggs laid on maize, sorghum, *S. arundinaceum* and *S. versicolor* showed no significant differences. Similarly, there were no significant differences between the number of eggs laid on maize, sorghum, *S. arundinaceum* and *S. versicolor* when *C. partellus* was reared on maize. However, the number of eggs laid on *P. purpureum* was significantly lower than the number of eggs laid on either maize or sorghum. When *C. partellus* was reared on *S. arundinaceum*, the number of eggs laid on maize, sorghum, *S. arundinaceum* and *S. versicolor* showed no significant differences but they were significantly higher than those laid on *P. purpureum*. When *C. partellus* was reared on *S. versicolor* and *P. purpureum*, the number of eggs laid on all the test hosts showed no significant differences.

There were no significant differences between the number of eggs laid by female *B. fusca* in a multiple choice oviposition preference experiment (Table 15).

Table 14: Mean number of eggs laid in a multiple-choice oviposition preference by 5th generation *C. partellus* females reared on various host plants.

Rearing host	Test host	\bar{X} Eggs (No.)
<i>Sorghum</i>	Maize	11.59 ± 0.610a
	<i>Sorghum</i>	11.01 ± 1.355ab
	<i>S. arundinaceum</i>	10.05 ± 0.619ab
	<i>S. versicolor</i>	10.76 ± 1.130ab
	<i>P. purpureum</i>	6.37 ± 1.441b
Maize	Maize	11.03 ± 1.053a
	<i>Sorghum</i>	9.98 ± 0.786ab
	<i>S. arundinaceum</i>	7.77 ± 1.823ab
	<i>S. versicolor</i>	10.34 ± 0.961ab
	<i>P. purpureum</i>	5.31 ± 2.019b
<i>S. arundinaceum</i>	Maize	10.37 ± 0.570a
	<i>Sorghum</i>	10.53 ± 0.591a
	<i>S. arundinaceum</i>	11.05 ± 0.615a
	<i>S. versicolor</i>	10.80 ± 0.978a
	<i>P. purpureum</i>	5.33 ± 1.932b
<i>S. versicolor</i>	Maize	11.22 ± 1.193a
	<i>Sorghum</i>	9.91 ± 0.936a
	<i>S. arundinaceum</i>	8.68 ± 2.128a
	<i>S. versicolor</i>	9.76 ± 2.424a
	<i>P. purpureum</i>	8.03 ± 1.846a
<i>P. purpureum</i>	Maize	10.71 ± 0.825a
	<i>Sorghum</i>	9.92 ± 0.921a
	<i>S. arundinaceum</i>	7.28 ± 1.683a
	<i>S. versicolor</i>	8.78 ± 0.982a
	<i>P. purpureum</i>	8.16 ± 1.914a

Means with the same letter within a column are not significantly different at P=0.05. Data on the number of eggs was modified by square root transformation.

Table 15: Mean number of eggs laid in a multiple-choice oviposition preference by 5th generation *B. fusca* females reared on various host plants

Rearing host	Test host	\bar{X} Eggs (No.)
<i>Sorghum</i>	Maize	12.18 ± 0.648a
	<i>Sorghum</i>	13.95 ± 0.923a
	<i>S. arundinaceum</i>	9.99 ± 2.585a
	<i>S. versicolor</i>	13.91 ± 0.937a
	<i>P. purpureum</i>	10.56 ± 1.129a
Maize	Maize	17.03 ± 2.224a
	<i>Sorghum</i>	14.27 ± 1.703a
	<i>S. arundinaceum</i>	12.53 ± 2.063a
	<i>S. versicolor</i>	14.15 ± 3.168a
	<i>P. purpureum</i>	10.99 ± 0.705a
<i>S. arundinacium</i>	Maize	12.13 ± 0.480a
	<i>Sorghum</i>	10.86 ± 0.553a
	<i>S. arundinaceum</i>	10.89 ± 0.499a
	<i>S. versicolor</i>	11.24 ± 1.024a
	<i>P. purpureum</i>	11.34 ± 0.808a
<i>S. versicolor</i>	Maize	10.30 ± 0.765a
	<i>Sorghum</i>	10.82 ± 0.329a
	<i>S. arundinaceum</i>	8.54 ± 1.362a
	<i>S. versicolor</i>	12.66 ± 0.967a
	<i>P. purpureum</i>	8.98 ± 1.647a
<i>P. purpureum</i>	Maize	10.85 ± 0.748a
	<i>Sorghum</i>	10.22 ± 0.625a
	<i>S. arundinaceum</i>	9.26 ± 1.055a
	<i>S. versicolor</i>	10.92 ± 0.951a
	<i>P. purpureum</i>	8.99 ± 2.223a

Means with the same letter within a column are not significantly different at P=0.05. Data on the number of eggs was modified by square root transformation.

3.4 Discussion

Results on the performance of *B. fusca* showed that larval development was longest on *P. purpureum* followed by *S. arundinaceum* while the shortest larval periods which were not significantly different were on *S. versicolor*, sorghum and maize. The pupal weights of *B. fusca* reared on *P. purpureum* were significantly lower than those of insects reared on maize, sorghum, *S. versicolor* and *S. arundinaceum* which showed no significant differences. Therefore, *B. fusca* had a faster larval development on *S. versicolor*, sorghum and maize followed by *S. arundinaceum* while the slowest development was on *P. purpureum*. The poor performance of *B. fusca* on *P. purpureum* could have been due to the presence of antibiotic factors or poor nutrient contents. Saxena (1990) reported that poor survival and slow development of insects reared on resistant maize cultivar MP 704 reflected the involvement of antibiotic factors.

Results on the performance of *C. partellus* similarly showed that, the larval development was longest on *P. purpureum* while the shortest larval period was on maize, *S. arundinaceum*, *S. versicolor* and sorghum and these were not significantly different from each other. The pupal weights of this species reared on *S. arundinaceum* was significantly higher than those of the insects reared on maize, *S. versicolor*, *S. arundinaceum* and *P. purpureum* which showed no significant differences. Therefore, *C. partellus* had a better performance on maize, *S. versicolor*, Sorghum followed by *S. arundinaceum* while the poorest performance was on *P. purpureum*. Similar findings that revealed a poor

performance of *C. partellus* reared on *P. purpureum* in comparison to that reared on maize, sorghum and *S. versicolor* were reported by Mohamed (1997). According to the same author, the poor performance of *C. partellus* on the resistant plant (including *P. purpureum*) may be attributed to antibiotic properties, or lack of nutrients necessary for optimal growth. Renwick and Chew (1994) reported that structure, colour, growth habit and stages, and pubescence of plants, in addition to chemical characteristics, moisture and nutrient status, affect acceptability of plants as potential food for insects. Within a given plant, various parts may also vary in the amount of associated allelochemicals. Reese and Beck (1976) working on the effects of allelochemicals on the black cut worm *Agrotis ipsilon* Hufnagel reported that certain allelochemicals could exert chronic effects on the growth, ingestion of food, utilisation of food and pupation. Growth and pupation were inhibited by P-benzoquinone (reduced form of hydroquinone which is commonly found in plants) through reduced ingestion.

Results on two the choice oviposition preference of *B. fusca* showed that the number of eggs laid on the "test hosts" were not significantly different from those laid on the "rearing host" when it was reared on *S. versicolor*, *S. arundinaceum* and *P. purpureum*. However, when it was reared on maize and sorghum, some significant differences were observed. The number of eggs laid on sorghum was significantly higher than those laid on either maize or on *P. purpureum* while that laid on maize was significantly higher than that laid on *P.*

purpureum. In this study, it has been demonstrated that *B. fusca* reared on sorghum and tested for oviposition alternately against maize and sorghum preferred to lay more eggs on sorghum than on maize. Similarly *B. fusca* reared on sorghum and tested for oviposition against *P. purpureum* preferred to lay more eggs on sorghum than on *P. purpureum*. As regards *B. fusca* reared on maize and tested for oviposition against *P. purpureum*, more eggs were also laid on maize than on *P. purpureum*.

The number of eggs laid by *C. partellus* on the test host were not significantly different from the number of eggs laid on the rearing host when it was reared on sorghum, *S. arundinaceum*, *S. versicolor* and *P. purpureum*. However, when it was reared on maize and tested for oviposition on either sorghum or *S. versicolor*, there were some significant differences. The number of eggs laid on maize were significantly higher than those on either sorghum or *S. versicolor*. Consequently, *C. partellus* reared on maize and tested for oviposition against sorghum and *S. versicolor* laid more eggs on maize than on either sorghum or *S. versicolor*.

These findings revealed that, in some instances *B. fusca* and *C. partellus* reared on a given host preferred to lay more eggs on the same host during a two-choice oviposition preference experiment. This oviposition preference in favour of the plant already experienced by the insect's larva during feeding might be Hopkins' host selection principle. It postulates that a memory of the larval food

predisposes the adult female of phytophagous insects to oviposit on the same species as that upon which they themselves had fed as larvae.

The multiple-choice oviposition preference results revealed that at no instance did *B. fusca* or *C. partellus* reared on a given host plant prefer to lay more eggs on the same host plant. Therefore, Hopkins' host selection principle which was found in two choice test was not evident.

The above studies suggest that little concrete evidence is available to unequivocally state that Hopkins' host selection principle is operative in adult oviposition preferences of *B. fusca* and *C. partellus*. It is only in a few tests in two-choice that the memory of the larval food predisposed the adult female insects to oviposit on the same species as that upon which they themselves had fed as larvae. In majority of the tests, oviposition preferences of the females was not substantially influenced by the larval food. This conforms to the findings by Papaj and Rausher (1983) who pointed that experimental support of the principle has been limited and there is actually much evidence against it. Van Emden *et al.* (1996) showed that plant-odour preference of adult female parasitoids (*Aphidius rhopalosiphi* De Stef.) was not established during larval development, but at the time, the emerging adult cut its exit hole in the skin of the mummy. These results contradict Hopkins' host selection principle, but support Corbet's (1985) chemical legacy hypothesis which postulates that "larval learning" displayed by adult insects arises from contact with the chemical

in or on the organism at the time the insect emerges. Wiklund (1974) investigating oviposition preferences in *Papilio machaon* (L.) in relation to the host plants of the larvae showed that in no case was the oviposition preferences of the females influenced substantially by the larval food. Therefore, existence of a larval memory of host plant characteristics affecting the oviposition preferences of the adult females was not found. However, their experiments showed that the host plants that were tested formed a hierarchy of larval host suitability, which was in close agreement with the hierarchy of adult oviposition preference. Thompson and Parker (1928), Takata (1961) and Palmitter (1966) found no evidence for Hopkins' host selection principle in oviposition preferences of *Ostrinia nubilalis*, *Helicoverpa zea* and *Pieris rapae* respectively. Similarly, de Wilde *et al.* (1960), Hsiao and Fraenkel (1968) and Wenhua and Logan (1994), working with *Leptinotarsa decemlineata* reported that neither larval nor preovipositional feeding on potato induced ovipositional preference. They postulated that oviposition preference is innate and not a consequence of larval or adult feeding preference.

In most of the cited experiments showing evidence in support of Hopkins' host selection principle (Yammamoto *et al.*, 1969; Yammamoto and Jenkins, 1972; Kuznetzov, 1952; Hovanitz and Chang, 1963b; Hsiao, 1978) the experiments lacked test protocols and statistics and hence the interpretation of the results may not be convincing. Therefore, this principle based on a memory of larval

food, which would perpetuate modified oviposition behaviour in both *B. fusca* and *C. partellus* has yet to be convincingly demonstrated.

4 MOVEMENT AND EGG DEPOSITION PATTERNS OF *BUSSEOLA FUSCA* AND *ORULO PARTELLUS*

4.1 introduction

Nonsocial insects need to search for the many and varied resources they require to survive and reproduce. The fitness of an animal was dependent on its movement patterns or searching behaviour. This is the ability to interpret and act upon internal and external pieces of information, so as to enhance the animal's chance of survival and to minimize the damage done to it, such as predator (Jander, 1975).

Insects move about in search for food, mates, shelter, oviposition sites, to avoid predators or for some other reasons. Whatever the reasons for their movements, their success in achieving their affairs their survival and reproductive rate. Thus, the population dynamics of a species may depend on its movement patterns and cannot be completely understood without the study. The type of insect movement patterns investigated moves from a central point towards a central point which are usually of a central point. An assumption of dispersal from a central point is a necessary simplification for the investigation of insect movement patterns, but cannot completely predict the behaviour of insects dispersing from a fixed area (Fletcher, 1971). This is a simplification of the dispersal of insects and egg deposition patterns.

CHAPTER FOUR

4 MOVEMENT AND EGG DEPOSITION PATTERNS OF *BUSSEOLA FUSCA* AND *CHILO PARTELLUS*

4.1 Introduction

Non-sessile animals need to search for the many and varied resources they require to survive and reproduce. The fitness of an animal will depend on its movement patterns or searching behaviour. This is the ability to interpret and act upon internal and external pieces of information, so as to minimize the animal's distance from resources and maximize the distance from stress sources such as predators (Jander, 1975).

Insects move about to seek for food, mates, shelter, oviposition sites, to avoid predation or for some other reasons. Whatever the reasons for their movements, their success in achieving them affects their survival or reproductive rate. Thus, the population dynamics of a species may depend on its movement pattern: one cannot be completely understood without the other. The type of insect movement commonly investigated relates to diffusion or dissemination of insects, which are initially at a central point. The assumption of dispersal from one central point is a necessary simplification for the derivation of a model of the insects movement; but cannot wholly reflect the real situation of the insects dispersing from a finite area (Freeman, 1977). This work was conducted to understand the dispersal and egg deposition patterns of

internally marked *B. fusca* and *C. partellus* released from a central release point within a maize field. At the same time, sampling was done to recover eggs and larvae from wild *B. fusca* and *C. partellus* populations.

4.2 Materials and methods

A farm measuring about 12,100m² was ploughed at Ungoye field site. The farm was situated in an area surrounded by wild host plants that had been colonized by both *B. fusca* and *C. partellus*. Susceptible maize variety was planted at a spacing of 65cm along the circumferences of five concentric circles placed at 10, 20, 30, 40 and 50m away from the central release point (Fig. 1). When the maize plants were three weeks old, Calco Red internally marked and mated *B. fusca* and *C. partellus* moths were released at the central point at evening (7.30 p.m after sunset) and allowed to disperse. The distance of dispersal was investigated the following day by inspecting all the plants to detect the red coloured eggs. The total number of eggs and eggs batches (clusters) recovered per every insect species and at every concentric circle were recorded. Within the same field, sampling was done to recover eggs and larvae from the wild *B. fusca* and *C. partellus* populations. Three separate experiments were conducted at different times within the same field and the results were pooled for statistical analysis.

4.3 Results

4.3.1 Non-linear analysis

Non-linear regression of the mean density per distance from the central release point was used. The data were fitted with a non-linearly modified kernel density function and a series of kernel density functions of practical importance

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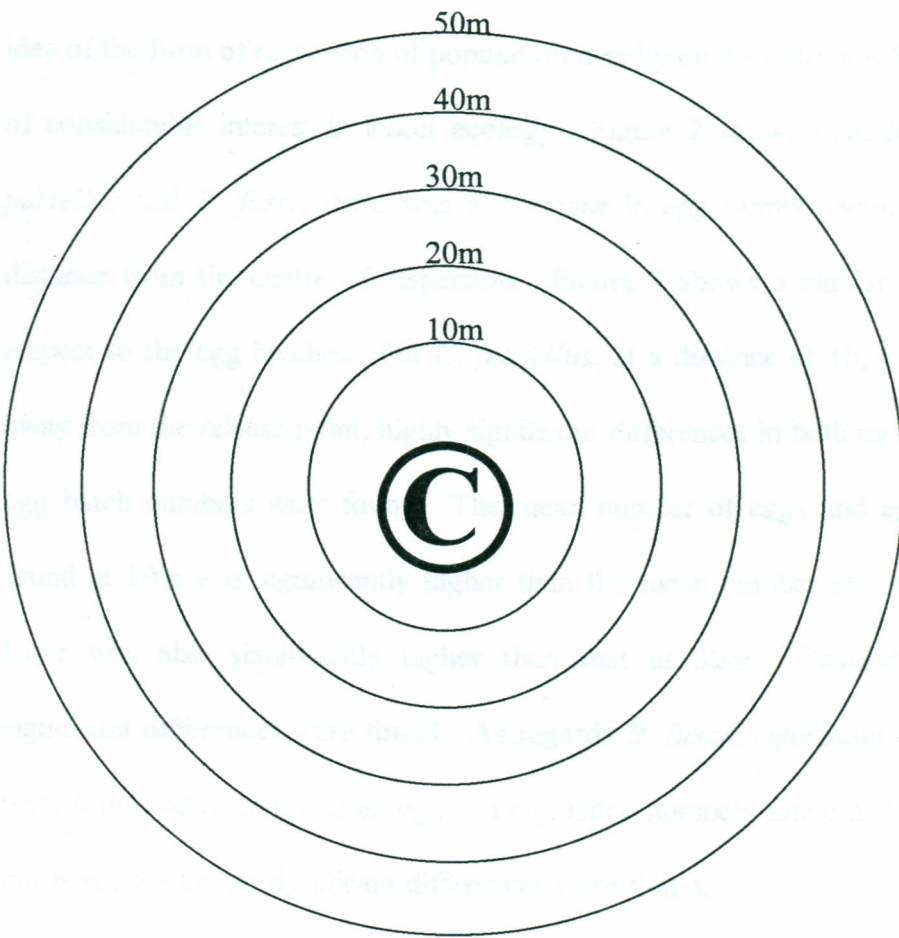


Fig. 1. Arrangement of concentric circles away from the central release point ©.

4.3 Results

4.3.1 Non-linear analysis

Non-linear regression of the insect density on distance from the central release point was done. The number of eggs laid by internally marked female moths was used as a measure of insect density. The results are of practical importance from the standpoint of control in indicating distance of spread and also give an idea of the form of regression of population density on distance, a subject that is of considerable interest in insect ecology. Figure 2 shows that, for both *C. partellus* and *B. fusca* there was a decrease in egg number with increasing distance from the centre of dispersion. Figure 3 shows a similar trend with respect to the egg batches. For *C. partellus*, at a distance of 10, 20 and 30m away from the release point, highly significant differences in both mean egg and egg batch numbers were found. The mean number of eggs and egg batches found at 10m was significantly higher than the mean number at 20m and the latter was also significantly higher than that at 30m. Beyond 30m, no significant differences were found. As regards *B. fusca*, significant differences were found between the mean egg and egg batch numbers found at 10 and 20m but beyond 20m, no significant differences were found.

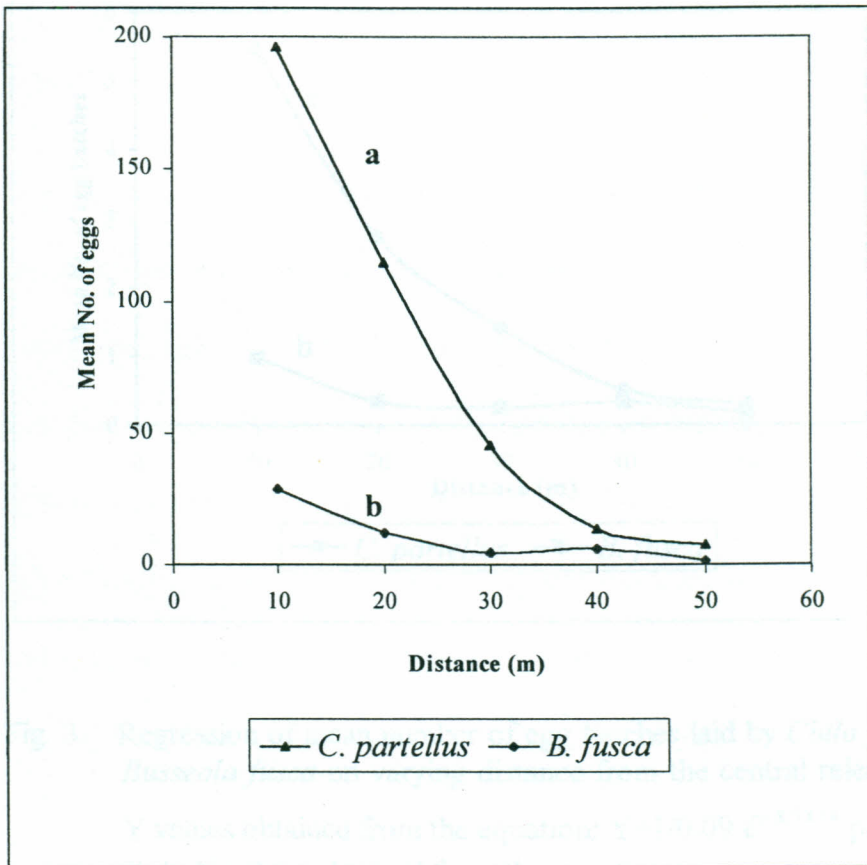


Fig. 2. Regression of mean number of eggs laid by *Chilo partellus* and *Busseola fusca* on varying distance from the central release point. a, Y values obtained from the equation: $Y=75.56 - 1/26.08 e^{-X/0.5}$ plotted against X; b, Y values obtained from the equation: $Y=10.63 + 1/1.75 e^{-X/0.5}$ plotted against X.

4.2.2 Linear analysis

To test the significance of the differences between the

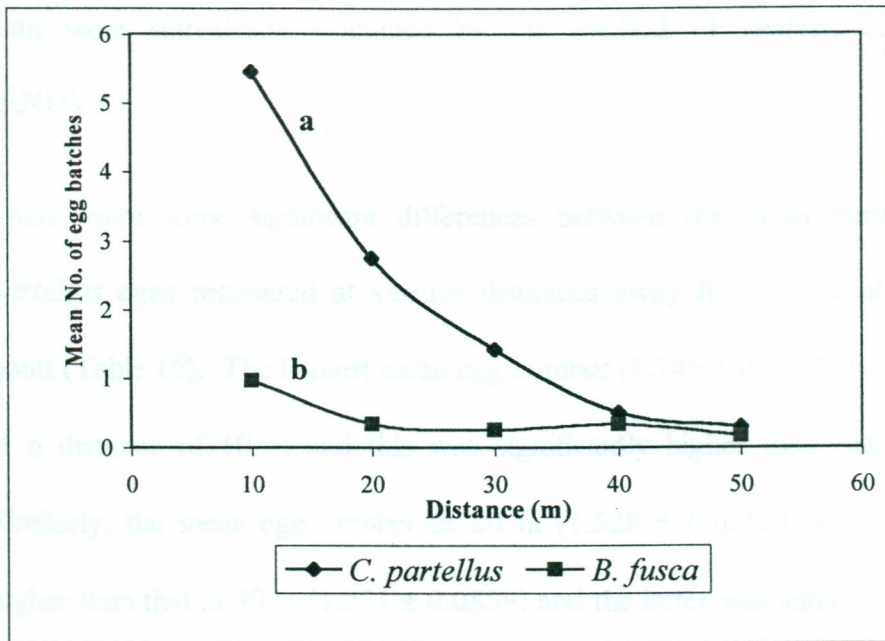


Fig. 3. Regression of mean number of egg batches laid by *Chilo partellus* and *Busseola fusca* on varying distance from the central release point. a,

Y values obtained from the equation: $Y=1/0.09 e^{-X/14.14}$ plotted against X; b, Y values obtained from the equation:

$Y=0.4 + 1/194815408.9 e^{-X/16234702.1}$ plotted against X.

4.3.2 Linear analysis

To test the significance of the dispersional differences between distances, the data were statistically examined by the method of analysis of variance (ANOVA).

There were some significant differences between the mean number of *C. partellus* eggs recovered at various distances away from the central release point (Table 16). The highest mean egg number (1.746 ± 0.0282) was recorded at a distance of 10 m and this was significantly higher than that at 20 m. Similarly, the mean egg number at 20 m (1.528 ± 0.0282) was significantly higher than that at 30 m (1.271 ± 0.0859) and the latter was significantly higher than that at 40 and 50 m. However, there were no significant differences between the mean egg numbers at a distance of 40 and 50 m.

There were some significant differences between the mean number of *C. partellus* egg batches recovered at various distances away from the central release point (Table 17). The highest mean egg batch was recorded at a distance of 10 m (1.298 ± 0.0215) and this was significantly higher than that at 20 m (1.470 ± 0.040). Similarly, the mean egg batch at 20 m was significantly higher than that at 30 m (1.029 ± 0.0399) and the latter was significantly higher than that at 40 and 50 m. However, there were no significant differences between the mean egg batches at a distance of 40 and 50 m.

Table 16: Mean number of *C. partellus* eggs recovered at various distances away from a central release point.

Distance (m)	\bar{X} egg batch (\pm S.E)
10	1.746 \pm 0.0282a
20	1.528 \pm 0.0282b
30	1.271 \pm 0.0859c
40	0.952 \pm 0.0719d
50	1.004 \pm 0.0627d

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $=\sqrt{\log_{10}(X+0.5) + 1}$.

Table 17: Mean number of *C. partellus* egg batches (cluster) recovered at various distances away from a central release point.

Distance (m)	\bar{X} egg batch (\pm S.E)
10	1.298 \pm 0.0215a
20	1.47 \pm 0.0401b
30	1.029 \pm 0.0399c
40	0.927 \pm 0.0304d
50	0.902 \pm 0.0242d

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $=\sqrt{\log_{10}(X+0.5) + 1}$.

There were no significant differences between the mean number of *B. fusca* eggs and egg batches recovered at various distances away from the central release point (Tables 18 and 19).

Table 18: Mean number of *B. fusca* eggs recovered at various distances away from a central release point.

Distance (m)	\bar{X} egg No. (\pm S.E)
10	1.143 \pm 0.0837a
20	1.049 \pm 0.0709a
30	1.033 \pm 0.0556a
40	0.954 \pm 0.0644a
50	0.912 \pm 0.0421a

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $=\sqrt{\log_{10}(X+0.5) + 1}$.

Table 19: Mean number of *B. fusca* egg batches (cluster) recovered at various distances away from a central release point.

Distance (m)	egg batch (\pm S.E)
10	0.968 \pm 0.0376a
20	0.913 \pm 0.0252a
30	0.913 \pm 0.0234a
40	0.886 \pm 0.0252a
50	0.871 \pm 0.0197a

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $=\sqrt{\log_{10}(X+0.5) + 1}$.

There were some significant differences between the mean number of *C. partellus* eggs recovered at various distances away from the source (wild hosts) (Table 20). The highest mean egg number (1.492 \pm 0.0637) was recorded at a distance of 50 m from the centre (fifth concentric circle) and this was significantly higher than that at 40 m (1.278 \pm 0.0729). The mean egg number

at 40 m was not significantly different from that at 30 and 20 m. Similarly, the mean egg numbers at 30, 20 and 10 m showed no significant differences.

Table 20: Mean number of *C. partellus* eggs recovered at various distances away from the source (wild hosts).

Distance (m)	\bar{X} egg No. (\pm S.E)
50 (fifth circle)	1.492 \pm 0.0637a
40 (fourth circle)	1.278 \pm 0.0729b
30 (third circle)	1.184 \pm 0.0741bc
20 (second circle)	1.205 \pm 0.0728bc
10 (first circle)	1.013 \pm 0.0644c

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $\sqrt{\log_{10}(X+0.5) + 1}$.

There were some significant differences between the mean number of *C. partellus* egg batches recovered at various distances away from the source (Table 21). The highest mean egg number (1.129 \pm 0.0315) was recorded at a distance of 50 m from the centre (fifth concentric circle) and this was significantly higher than that at 40, 30 and 20 m. The mean egg number at 40 m was not significantly different from that at 30 and 20 m. Similarly, the mean egg number at 30 and 10 m showed no significant differences.

Table 21: Mean number of *C. partellus* egg batches recovered at various distances away from the source (wild hosts).

Distance (m)	\bar{X} egg batch (\pm S.E)
50	1.129 \pm 0.0315a
40	1.027 \pm 0.0327b
30	0.972 \pm 0.0291bc
20	1.005 \pm 0.0342b
10	0.902 \pm 0.0242c

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $=\sqrt{\log_{10}(X+0.5) + 1}$.

There were no significant differences between the mean number of *B. fusca* eggs recovered at various distances away from the source (Table 22). Similarly, there were no significant differences between the mean number of *B. fusca* egg batches recovered at various distances away from the source (Table 23).

Table 22: Mean number of *B. fusca* eggs recovered at various distances away from the source (wild hosts).

Distance (m)	\bar{X} egg No (\pm S.E)
50	1.044 \pm 0.0682a
40	1.003 \pm 0.0607a
30	0.899 \pm 0.0437a
20	0.956 \pm 0.0565a
10	0.867 \pm 0.0308a

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $=\sqrt{\log_{10}(X+0.5) + 1}$.

Table 23: Mean number of *B. fusca* egg batches recovered at various distances away from the source (wild hosts).

Distance (m)	\bar{X} egg batch (\pm S.E)
50	0.917 \pm 0.0267a
40	0.902 \pm 0.0242a
30	0.861 \pm 0.0174a
20	0.877 \pm 0.0193a
10	0.846 \pm 0.1035a

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $= \sqrt{\log_{10}(X+0.5) + 1}$.

There were some significant differences between the mean number of *C. partellus* larvae recovered at various distances away from the source (Table 24). The mean number of larvae at 50, 40, 30 and 20 m were not significantly different. However, the mean egg numbers at 50, 40 and 30 were significantly higher than that at 10 m. The latter was also not significantly different from that at 20 m. There were some significant differences between the mean number of *C. partellus* larval clusters recovered at various distances away from the source (Table 25). The mean larval clusters at 50, 40, 30 and 20 m were not significantly different. However, the mean larval clusters at 50, 40 and 30 m were significantly higher than that at 10 m. The latter was also not significantly different from that at 20 m.

Table 24: Mean number of *C. partellus* larvae recovered at various distances away from the source (wild hosts).

Distance (m)	\bar{X} larval No. (\pm S.E)
50	1.261 \pm 0.0507a
40	1.246 \pm 0.0481a
30	1.211 \pm 0.0516a
20	1.081 \pm 0.0544ab
10	0.989 \pm 0.0478b

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $=\sqrt{\log_{10}(X+0.5) + 1}$.

Table 25: Mean number of *C. partellus* larval clusters recovered at various distances away from the source (wild hosts).

Distance (m)	\bar{X} cluster No. (\pm S.E)
50	1.111 \pm 0.0335a
40	1.110 \pm 0.0302a
30	1.077 \pm 0.0318a
20	0.999 \pm 0.0333ab
10	0.935 \pm 0.0305b

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $=\sqrt{\log_{10}(X+0.5) + 1}$.

There were some significant differences between the mean number of *B. fusca* larvae recovered at various distances away from the source (Table 26). The mean larval numbers at 50, 40 and 30 m were not significantly different. Similarly, the mean larval numbers at 40, 30, 20 and 10 m were not significantly different. However, the mean larval numbers at 50 m (1.067 ± 0.0525) was significantly higher than that at 10 m (0.906 ± 0.0337). There were also some

significant differences between the mean number of *B. fusca* larval clusters recovered at various distances away from the source (Table 27). The mean larval clusters at 50, 40 and 30 m were not significantly different. Similarly, the mean larval clusters at 40, 30, 20 and 10 m were not significantly different. However, the mean larval cluster at 50 m (0.988 ± 0.0333) was significantly higher than that at 10 m (0.882 ± 0.0215).

Table 26: Mean number of *B. fusca* larvae recovered at various distances away from the source (wild hosts).

Distance (m)	\bar{X} larval No. (\pm S.E)
50	$1.067 \pm 0.0525a$
40	$1.023 \pm 0.0534ab$
30	$0.944 \pm 0.0407ab$
20	$0.875 \pm 0.0229b$
10	$0.906 \pm 0.0337b$

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $= \sqrt{\log_{10}(X+0.5) + 1}$.

Table 27: Mean number of *B. fusca* larval clusters recovered at various distances away from the source (wild hosts).

Distance (m)	\bar{X} cluster No. (\pm S.E)
50	$0.988 \pm 0.0333a$
40	$0.959 \pm 0.0354ab$
30	$0.917 \pm 0.0305ab$
20	$0.867 \pm 0.0171b$
10	$0.882 \pm 0.0215b$

Means having the same letter within a column are not significantly different at $P=0.05$. Data transformed using $= \sqrt{\log_{10}(X+0.5) + 1}$.

4.4 Discussion

The type of dispersal which was being investigated here relates to diffusion or dissemination of flying insects which were all initially at a central release point. The assumption of this type of dispersal is a necessary simplification for derivation of a model of insect movement. A non-linear regression analysis was carried out to establish the general model that describes distribution of eggs and egg batches of *B. fusca* and *C. partellus* along the dispersal distance. The best fitting regression equations for describing the decline of egg batch and egg numbers with distance from the centre of dispersal are: -

a. $E(Y) = \beta_0 + 1/\beta_1 e^{-X/\beta_2}$ for eggs of *C. partellus* and *B. fusca* eggs and egg batches of *B. fusca*

b. $E(Y) = 1/\beta_0 e^{-X/\beta_1}$ for egg batches of *C. partellus*.

Where $E(Y)$ = expected value of Y (mean egg or egg batch number)

X = distance, β_0 , β_1 and β_2 = parameters

Indications from the results show that for both insect species, individual moths might travel for more than 50 m and the downward slope of the plotted curve tended to level off as the distance increased. The steep (sharp) fall in numbers of eggs and egg batches up to a distance of 30 m from the release point observed for *C. partellus* was largely due to the short distance flying nature of the pest. Similarly, the higher recovery rate of *C. partellus* eggs was a good evidence for low dispersal rates. On the other hand, *B. fusca* seemed to be

more of a long distance flier as evidenced by its lower egg recovery rate and the more or less uniform distribution of eggs through out the dispersal distance.

Linear analysis of the experiment investigating changes in insect density with increasing distance from a central release point using oviposition by internally marked female moths as a measure of insect density showed that, for *C. partellus* there was a profound falling off in egg batch and egg density with increasing distance. The mean egg batches and egg numbers recorded on maize plants at various concentric circles was in the following decreasing order: - 10 m > 20 m > 30m > 40=50m. This implies that maize plants which were nearer to the release point (at 10 m) received the highest number of eggs and egg batches while those that were far away (at 40 and 50 m) received the least number of eggs and egg batches. This could have been brought about by a situation whereby a large proportion of *C. partellus* female moths preferred to disperse horizontally away from the source as opposed to a vertical dispersal which would have taken them high up and possibly even outside the sampling area. Similar results showing a falling off in insect density with increasing distance from the centre of dispersion have been reported by (Freeman, 1977; Wadley and Wolfenberger, 1944; Rose, 1973). As regards *B. fusca*, the mean egg batches and egg numbers recorded on maize plants at various concentric circles showed no significant differences and were more or less uniform throughout the dispersal distance. This could have been brought about by a situation whereby a large proportion of *B. fusca* female moths preferred to

disperse vertically away from the source, thus distributing the eggs and egg batches more or less uniformly throughout the dispersal distance as opposed to a horizontal dispersal.

Results also showed that at any distance more eggs of *C. partellus* were recovered than those of *B. fusca*. The higher recovery rate for *C. partellus* eggs is usually associated with very low dispersal rates. On the other hand, the lower recovery rate for *B. fusca* eggs is associated with high dispersal rates. Consequently, the results give further evidence to implicate *B. fusca* as a higher flier whereas *C. partellus* is a lower flier.

Results of the experiment investigating changes in insect density with increasing distance from the source (wild host) by using eggs and larval counts as a measure of insect density also showed that, for *C. partellus* there was profound falling off in the number of eggs, egg batches, larvae and larval clusters with increasing distance. The mean egg numbers recorded on maize plants at various concentric circles was in the following decreasing order:- 50 m > 40 m ; 40 m = 30m and 20 m; 30 m = 20 m and 10 m. This implies that maize plants which were nearer to the source of the insect (i.e.) closer to the wild hosts (or at fifth concentric circle) received the highest number of eggs.

The mean egg batches recorded on maize plants at various concentric circles was in the following decreasing order: - 50 m > 40 m; 40m = 30m and 20 m;

30m = 20; 20 m > 10 m and 10 m = 30 m. This implies that maize plants which were nearer to the source of the insect (i.e.) closer to the wild hosts (or at fifth 50 m concentric circle) received the highest number of egg batches. The above two observed results are cases of a commonly observed phenomenon called "edge effect" whereby an insect prefers to lay more eggs on the plants they first encounter i.e. (in a cultivated field insects will prefer to lay more eggs on plants situated at the edge of the plot than in the centre). In a situation where dispersal of insects is from a central release point, "edge effect" could bring about a situation whereby the insect prefers to lay more eggs on the plants nearest to the release point. Similar results showing a preferential oviposition on edges of experimental plots have been reported by (Wright and Ashby, 1949; Harcourt, 1961; Kobayashi, 1965; Kirk, 1965; Kieckhefer and Medler, 1966; Courtney and Courtney, 1982; Cappuccino and Martin, 1997). Edge effect could also be brought about by a situation whereby a large proportion of *C. partellus* female moths preferred to disperse horizontally away from the source as opposed to a vertical dispersal which would have taken them high up and possibly even outside the sampling area. Alternatively, it has been reported that choice of oviposition site by *C. partellus* females seems to be mediated by tactile stimuli rather than by chemical stimuli. Female *C. partellus* prefers to oviposit in creases anywhere on the host plant (Roome *et al.*, 1977) and is more fecund than *B. fusca* (pers. observation). Roome *et al.* (1977) suggested that oviposition site choice is for egg survival rather than for a suitable host for larvae, as larvae are able to disperse. Therefore, in a situation like this where

the insect is more fecund and oviposition site choice is for egg survival rather than for a suitable host for larvae, little time is used in search and *C. partellus* females will prefer to lay more eggs on the plants they first encounter.

As regards *B. fusca*, the mean egg batch and egg numbers recorded on maize plants at various concentric circles showed no significant differences and were more or less uniform throughout the dispersal distance. Therefore, "edge effect" was not evident. This could have been brought about by a situation whereby a large proportion of *B. fusca* female moths preferred to disperse vertically away from the source as opposed to a horizontal dispersal. Alternatively, it has been reported that *B. fusca* females prefer to lay their eggs beneath the leaf sheaths of the youngest fully unfolded leaf. This implies that more search time is required and hence females will not necessarily prefer to lay more eggs on the plants they first encounter.

CHAPTER FIVE

5 GENERAL DISCUSSION AND CONCLUSIONS

5.1 General discussion

Calco Red N-1700 and Sudan Blau-670 dyes added to the larval diet were shown to be effective internal markers for *C. partellus* and *B. fusca*. Both dyes successfully marked the larvae, adults, eggs and first stage F1 larvae. However, the dyes prolonged development time for both borer species but had no effect on pupal weights except in *B. fusca* whereby insects reared on a normal diet were heavier than those reared on a diet containing Sudan Blau. This conforms to the findings by Brewer (1982) who reported a delayed development time when Calco Red was mixed with the larval diet of *Heliothis virescens*. Nevertheless, the differences in development time were not considered sufficient to prevent the use of the dyes for marking insects during dispersal studies.

In another experiment, *B. fusca* could still be internally marked if the larvae were reared on a normal diet for 18 days then transferred to a diet containing Calco Red dye. This technique was found to be advantageous because the larval period was significantly reduced and was equal to that of insects reared on a normal diet. Similarly by larval transfer, the time the insects were exposed to the possible deleterious effects of the dye was reduced. This method is however cumbersome and the insects might be injured or contaminated during

transfer. However as regards *B. fusca* rearing, the technique was found to be the most appropriate but a lot of care had to be taken during transfer.

Externally, moths obtained from dyed diets showed no distinct colour differences from those obtained from normal diet. However, on removing the scales on the abdomen using a brush or by wetting the insect, the colour was clearly seen and it was bright red. This implies that, during dispersal studies the internally marked moths would not be more exposed to the predators than the normal ones. Similar findings showing no external colour differences between normal and Calco Red dyed insects were reported by Pats (1989). The same author reported that after dissection of the moths, the fat body, the ovaries and the reservoir for the accessory glands were also coloured red.

Apparently, the dyes did not affect pheromone production because successful mating occurred in all the groups that were tested. Graham and Mangum (1971) and Lindig *et al.* (1980) reported that Calco Red N-1700 does not affect pheromone production in *Anthonomus grandis* and *Pectinophora gossypiella* respectively and this was also proved to be true for *B. fusca* and *C. partellus* in this study.

When the marked first stage F1 larvae were introduced to feed on a normal diet or on maize leaves, they retained the internal mark for about two days after which they lost it (presumably through excretion).

Calco Red dye had no effect on fecundity and longevity of the two stem borer species. The mean fecundity and longevity of the insects reared on a normal diet were not significantly different from those reared on a diet containing Calco Red dye. Similarly for both species, the dye did not effect tethered flights. The mean flight duration of mated female insects reared on a normal diet were not significantly different from those reared on a diet containing Calco Red dye. These findings further showed that the dye could be used effectively for marking insects during dispersal studies.

Results on the performance of *B. fusca* and *C. partellus* reared on different host plants showed that, the slowest larval development occurred on *P. purpureum*. Similarly, *B. fusca* had a slower larval development on *S. arundinaceum* than on *S. versicolor*, sorghum and maize which showed no significant differences. The lowest pupal weights of *B. fusca* and *C. partellus* were also recorded on *P. purpureum*. The pupal weights of *B. fusca* reared on *S. arundinaceum* were significantly higher than those reared on maize, sorghum and *S. versicolor* which showed no significant differences. These findings revealed that both *B. fusca* and *C. partellus* had a poor performance on *P. purpureum* than on sorghum, maize, *S. versicolor* and *S. arundinaceum*. This poor performance on *P. purpureum* could have been due to presence of antibiotic factors or to poor nutrient contents. It is known that insect feeding and metabolism are components of insect-plant relationship (Kumar, 1993). Growth and development of an insect on its host plant is usually one of the means used to

determine the suitability of the plant and the mechanisms of resistance of plant to the insect. Larval growth is related to the physical characteristics of the plant, lack of nutrients or presence of feeding stimulants, toxins or deterrents which influence food intake and digestion by the insect (Soo Hoo and Fraenkel, 1966; Saxena, 1985; 1990).

Randriamananoro (1996) reported a similar poor performance of *B. fusca* reared in *P. purpureum* and attributed it to presence of antibiotic factors or poor nutrient contents. He actually demonstrated that quality of nutrients had a role to play in the development of *B. fusca* on susceptible (Inbred A, IS18363, *S. arundinaceum* and *S. versicolor*) and resistant test plants (IS 1044, MP 704, *H. rufa*, *P. purpureum* and *E. pyramindalis*). The analysis of leaf tissues showed that the susceptible plants that favoured the performance of *B. fusca* had a higher nitrogen content than the resistant plants. Soo Hoo and Fraenkel (1966) reported that even though all the necessary nutrients required for growth might be present, it is conceivable that the insect may still grow poorly as a result of improper nutrient proportions.

Alternatively, feeding rates may be influenced by anatomical characters such as hairiness (presence of trichomes) or presence of high concentrations of waxes (Painter, 1951; Norris and Kogan, 1979; Bernays and Chapman, 1994). Mohamed (1997) reported presence of high densities of trichomes on the leaf surface of resistant wild grasses and postulated that they adversely affected

larval feeding by *C. partellus*. Kumar *et al.* (1993) reported that resistant maize cultivar MP 704, V-37 and Poza Rica 7832 retarded the development of *C. partellus* larvae due to resistance through antibiosis. The same authors reported that larvae feeding on resistant plant would require a longer period to complete a generation than those feeding on susceptible plants. Any plant characteristic which slows development or causes larvae to leave the plant, exposes them to the dangers of increased predation and adverse environmental factors such as heavy rain, excessive wind and/or heat (Singh *et al.*, 1974). According to Mc Naughton *et al.* (1985) and Setamou *et al.* (1993), a high silica content may be one of the factors responsible for stem borer resistance in wild grasses. Mohamed (1997) reported that, leaf tissue toughness found on some of the wild grasses was a physical factor which could adversely affect *C. partellus* larval feeding.

On the other hand, the better performance of *B. fusca* and *C. partellus* on some of the hosts could be attributed to either the better quality of nutrient contents or the absence of antibiotic factors.

The two wild sorghum species which supported growth and development of *B. fusca* and *C. partellus* may therefore act as important reservoir or alternate hosts, which help in sustaining the wild populations of the two pests during the off season. They could also be integrated as a component of pest management of stem borers and used for intercropping or as a trap crop. The latter could be

planted a few weeks before the maize or sorghum crop and cut as fodder a month after crop emergence. This practice could eliminate a big portion of the stem borer eggs.

Results on the two choice oviposition preference showed that *B. fusca* reared on sorghum and tested for oviposition alternately against maize and sorghum preferred to lay more eggs on sorghum than on maize. Similarly *B. fusca* reared on sorghum and tested for oviposition alternately against *P. purpureum* and sorghum preferred to lay more eggs on sorghum than on *P. purpureum*. Likewise *B. fusca* reared on maize and tested for oviposition alternately against *P. purpureum* and maize laid more eggs on maize than on *P. purpureum*. These findings revealed that in some instances, *B. fusca* reared on a given host plant will prefer to lay more eggs on the same plant during a two-choice oviposition preference test.

Results on the two choice oviposition preference of *C. partellus* showed that when its was reared on maize and tested for oviposition alternately with either sorghum or *S. versicolor*, there were some significant differences. The number of eggs laid on maize were significantly higher than those on either sorghum or *S. versicolor*. Therefore *C. partellus* reared on maize and tested for oviposition against maize and *S. versicolor* preferred to lay more eggs on maize than on either sorghum or *S. versicolor*. These findings revealed that similarly in some instances, *C. partellus* reared on a given host will prefer to lay more eggs on the

same host during a two-choice oviposition preference experiment. This oviposition preference in favour of the plant already experienced by the insect's larva during rearing which was also observed with *B. fusca* is in agreement with Hopkins' host selection principle. Results on multiple-choice oviposition preference showed that at no instance did *B. fusca* or *C. partellus* reared on a given host plant prefer to lay more eggs on the same host plant. Therefore, Hopkins' host selection principle which was found in the two-choice oviposition test was not evident. (Singer, 1944; Rose, 1973; Fries, 1977).

On the other hand, the mean egg batch and egg numbers of *B. fusca* reared

Considering the above reported results, it is evident that not in all the cases was the oviposition preference in *B. fusca* and *C. partellus* substantially influenced by the larval food. Hence, one cannot generalise that Hopkins' host selection principle is operational during choice of oviposition hosts by the two stem borer species. Therefore, an alternative explanation must be sought to account for how adult oviposition and larval feeding preferences are interrelated. There is strong evidence that different genetic preferential systems are operating in larval host plant suitability and adult oviposition preferences. This implies that there is an existence of two separate gene complexes regulating them.

Results of the experiment investigating changes in insect density with increasing distance from a central release point using oviposition by internally marked female moths as a measure of insect density showed that, for *C. partellus* there was a profound falling off in the number of eggs and egg batches with

increasing distance. Hence the maize plants which were nearer to the release point received the highest number of eggs and egg batches. This could have been brought about by a situation whereby a large proportion of *C. partellus* female moths preferred to disperse horizontally away from the source as opposed to a vertical dispersal which would have taken them high up and possibly even outside the sampling area. Similar results showing a falling off in insect density with increasing distance from the centre of dispersion have been reported by (Wadley and Wolfenberger, 1944; Rose, 1973, Freeman, 1977). On the other hand, the mean egg batch and egg numbers of *B. fusca* recorded on maize plants at various concentric circles showed no significant differences and there was a more or less uniform distribution throughout the dispersal distance. This could have been brought about by a situation whereby a large proportion of *B. fusca* female moths preferred to disperse vertically away from the source distributing the eggs and egg batches more or less uniformly as opposed to a horizontal dispersal. The results also showed that at each concentric circle, more eggs of *C. partellus* were recovered than those of *B. fusca*. The higher recovery rate for *C. partellus* eggs is a phenomenon associated with very low dispersal rates. On the other hand, the lower recovery rate for *B. fusca* eggs is associated with high dispersal rates. Consequently, it implies that *B. fusca* may be a higher flier whereas *C. partellus* is a lower flier.

Results of the experiment investigating changes in insect density with increasing distance from the source (wild host) by using egg and larval counts as a

measure of insect density also showed that, for *C. partellus* there was a profound falling off in the number of eggs and egg batches with increasing distance. Hence maize plants on the edges of the field (i.e.) bordering the wild hosts (or at fifth concentric circle) received the highest number of eggs. This is a commonly observed "edge effect" phenomenon whereby insects colonising cultivated fields from the outside prefer to lay more eggs on the plants situated at the edge of the plot than in the centre. Edge effect could also have been brought about by a situation whereby a large proportion of *C. partellus* female moths preferred to disperse horizontally away from the source as opposed to a vertical dispersal which would have taken them high up and possibly even outside the sampling area. An important implication of edge effect is that the insect can be controlled by use of trap crops or by applying insecticides only on the margins of the field where infestation is severe. Edge effect was not evident in *B. fusca* because the mean egg batch and egg numbers recorded on maize plants at various concentric circles showed no significant differences and were more or less uniform throughout the dispersal distance. This could have been as a result of a large proportion of *B. fusca* female moths preferring to disperse vertically away from the source.

5.2 Conclusions

1. Adding Calco Red N-1700 and Sudan Blau-670 to the artificial larval diet was shown to be an effective method for marking adult *C. partellus* and *B. fusca* for mark-release experiments. Both dyes successfully marked the larvae, adults, eggs and first stage F1 larvae. Calco Red dye was found to be more appropriate for further marking experiments because marked moths laid red eggs which can easily be detected on maize plants. Experiments on longevity, fecundity, pupal weights and tethered flight revealed that marked and unmarked insects showed no significant differences.

2. Results on growth and development showed that both *C. partellus* and *B. fusca* performed better on sorghum, maize and the two wild sorghum species (*S. versicolor* and *S. arundinaceum*) while the poorest performance was on napier grass (*P. purpureum*). Therefore, the two wild sorghum species may act as important reservoir or alternate hosts, which help in sustaining the wild populations of the two pests during the off season. They may also act as trap crops.

3. Two-choice oviposition preference experiments revealed that at some instances for both species, moths which were reared on a given host preferred to lay more eggs on that host. This oviposition preference in favour of the plant species upon which the larvae were reared on is a phenomenon referred to as Hopkins' host selection principle (HHSP). However, this phenomenon was not

evident in multiple-choice oviposition preference experiments indicating that the validity of this phenomenon as a general principle operating in oviposition preferences of *B. fusca* and *C. partellus* still remains to be proved.

4. During a study of changes in insect density with increasing distance away from a central release point using oviposition by internally marked female moths as a measure of density, it was found that for *C. partellus* there was a profound falling off in egg batch and egg numbers with increasing distance. At a distance of 10, 20 and 30 m away from the release point, highly significant differences in mean egg batch and egg numbers were found and they showed a decreasing order. This implies that maize plants which were near the release point received the highest number of eggs. Beyond 30 m (at 40 and 50 m) away from the release point no significant differences were found. However, with respect to *B. fusca*, the mean egg batches and egg numbers were more or less uniform through out the dispersal distance.

Similar studies were conducted within the same field and involved sampling to recover eggs and larvae from the wild population of *B. fusca* and *C. partellus*. Results showed that for *C. partellus* more eggs and egg batches were recovered on the edge of the plot (fifth concentric circle, bordering the wild host plants), a phenomenon referred to as "edge effect". In contrast, for *B. fusca* egg batches, eggs and larvae showed a more or less uniform distribution and therefore "edge effect" was not evident. Therefore *B. fusca* and *C. partellus* behave quite

differently and the former distributes its eggs more or less uniformly whereas *C. partellus* lays more eggs on the nearest host plants. Therefore, most *C. partellus* outbreaks in crops could be prevented by planting trap crops or by applying insecticides on the plants on the margins. Most eggs of *C. partellus* will be laid on the trap crop, which can be destroyed or cut as fodder after crop emergence. However, trap crops unless very attractive may have little value for the protection of crops against invasion by *B. fusca* because the latter is capable of dispersing its eggs in a more or less uniform manner and even more widely i.e. (*B. fusca* is a higher and long flier).

5.3 Recommendations

1. Large scale work to determine the maximum distances *B. fusca* and *C. partellus* are capable of dispersing in the field is needed. This calls for a larger field.
2. More work is needed on the effect of the internal marking dyes on the parasitoids of *B. fusca* and *C. partellus*. The problem to be investigated is whether the dyes can be transferred to the parasitoids and their effects on their biology.
3. Because the results showed little evidence in support of Hopkins' host selection principle (HHSP), it is suggested that more research on the mechanisms regulating larval feeding and oviposition preference in *B.*

- fusca* and *C. partellus* is critical. Further experiments to investigate Hopkins' host selection principle need to be carried out using insects reared for many generations and large sample sizes. Further work also needs to be carried out on the degree of the retention of the induced preference (if there will be any) and the length of exposure required to induce a new preference.
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