Interspecific competition between *Xanthopimpla stemmator* Thunberg and *Dentichasmias busseolae* Heinrich (Hymenoptera: Ichneumonidae) pupal parasitoids of *Chilo partellus* Swinhoe (Lepidoptera: Crambidae).

By: Benjamin Kimwele Muli

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Department of Zoology

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DECLARATIONS

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

Benjamin Kimwele Muli

Signature _____ Date 15/7/05

This thesis has been submitted with our approval as supervisors.

Dr. Rosebella O. Maranga

Jomo Kenyatta University of Agriculture and Technology (JKUAT)

Signature..... Date 15/7/05

Dr. Helen L. Kutima

Jomo Kenyatta University of Agriculture and Technology (JKUAT)

Signature..... Date 15/07/05

Dr. Schulthess Fritz

International Centre of Insect Physiology and Ecology (ICIPE)

Signature..... Date 15/7/05

Dedication

This thesis is dedicated to Florence, my parents, my brothers and sisters.

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Abstract

Chilo partellus Swinhoe (Lepidoptera: Crambidae) is an exotic cereal stem borer that was accidentally introduced into Africa from South Eastern Asia early 20th century. It is now widespread in most of the lowland areas of the eastern and southern parts of the African continent. The invasive stem borer *C. partellus*, has proved to be a highly competitive colonizer in many of the areas it has invaded in eastern and southern Africa, often becoming the most serious stem borer. Due to its status as an introduced pest, *C. partellus* has been a primary target of classical biological control. In 1991, a larval parasitoid, *Cotesia flavipes* (Hymenoptera: Braconidae), was introduced from Pakistan and later from India against *C. partellus*. However, the level of control provided by this natural enemy varies from area to area since *C. flavipes* is not able to complete development in *B. fusca* since the eggs are encapsulated. An exotic pupal parasitoid, *Xanthopimpla stemmator*, which exploits a broad range of hosts within the same niche, was imported by ICIPE in 2001 for classical biological control of *C. partellus*. Since it is an exotic parasitoid, careful evaluation is necessary as biological control introductions can impact the environment negatively.

The objectives of this study were to (i) determine whether the parasitoids will discriminate between parasitized and unparasitized host pupae; (ii) investigate the effect of interspecific competition on *X. stemmator* and *D. busseolae* (iii) the host searching efficiency of the parasitoids on different parts of maize plant.

For interspecific host discrimination and competition studies, host pupae were given to *X. stemmator* and *D. busseolae* in paper straws and artificial pupal chambers respectively. Two time intervals (0 and 48 hour) were used between ovipositions by the

two parasitoids. Sequences Db-Xs (*D. busseolae* then *X. stemmator*) and Xs-Db (*X. stemmator* then *D. busseolae*) were used for each time interval. For searching efficiency, pupae which pupated in stems/cobs were offered to the parasitoids in 1000cc clear plastic jar and observed for parasitization. In all cases, 30 pupae were used where a pupa was considered a replicate.

The study on interspecific host discrimination showed that both *X. stemmator* and *D. busseolae* lacked the ability to discriminate between parasitized and unparasitized pupae as indicated by oviposition in both types of hosts. For instance, oviposition time for *D. busseolae* did not vary with the parasitized and unparasitized pupae at both 0 hr and 48 hr time intervals ($t=0.40$; $P= 0.694$ and $t=0.79$; $P= 0.432$ for 0 and 48 hr intervals respectively). Interspecific competition study revealed that *X. stemmator* is competitively superior to *D. busseolae* irrespective of the sequence and time interval except when *D. busseolae* parasitized *C. partellus* pupae 48 hours before *X. stemmator*. For instance, there was a significant difference between percentage of pupae yielding *D. busseolae* from Db-Xs sequence and the control (Db alone) ($\chi^2=28.18$; $P=0.0001$). At 48 hr interval, there was no significant difference between the percentage of pupae yielding *D. busseolae* in the Db-Xs sequence and the control (Db alone) ($\chi^2 =0.287$; $P= 0.592$). Studies on the searching efficiency of *D. busseolae* and *X. stemmator* indicated that *D. busseolae* is able to search and successfully attack hosts in both stems and cobs as opposed to *X. stemmator* which is successful in stems only. For instance, there was a highly significant effect by the part of plant used on the parasitization efficiency of *X. stemmator* ($\chi^2 =11.2946$; d.f. $=1$; $P=0.0008$). From the current study, although *X. stemmator* seems to be competitively superior to *D. busseolae*, there is a possibility that

the two can co-exist due to some differences in their host niche. However, further studies using experienced female parasitoids; at different temperatures, humidities and host ages and at screen houses are required to validate the authenticity of the current findings before release of the exotic *X. stemmator* since such factors determine the outcome of interspecific competition.

CHAPTER ONE

1.0. GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1. Introduction

Agricultural production in developing countries is seriously hindered by pests. The use of pesticides dominates crop protection efforts and reliance on them is growing due to their ability to control short-term pest problems and their potential for replacing labour intensive work in some situations like weeding. However, chemicals are hazardous to man and other non-target organisms as well as promoting resistance in target pests to insecticides if used for a long time or in sub-lethal quantities (Minja, 1990).

Cereals are extremely important crops grown in Africa primarily for human consumption, with surpluses being used as livestock feeds (Sibanda, 1985). Of the various insect pests attacking cereal crops in Africa, lepidopteran stem borers are by far the most injurious (Kfir *et al.*, 2002). Estimates of losses vary greatly, but are typically about 20-40% of the potential yield (Youdeowei, 1989). Methods currently used to manage stem borers include among others: chemical control, early planting and intercropping with non cereals (Minja, 1990). Chemical control of borers is expensive and often unsatisfactory due to the cryptic feeding behaviour of stem borers (Kfir, 1990, 1992b). Cultural control methods such as intercropping and early planting have been practised by farmers but studies show that their impact on stem borer populations is limited (Oloo, 1989; Skovgård and Päts, 1996). There have been several attempts over the past 50 years to introduce exotic parasitoids for biological control of stem borers in Africa particularly for suppression of the invasive exotic stem borers, *C. partellus* on the mainland Africa and *C. sacchariphagus* on the Indian Ocean islands (Overholt, 1998). For instance, the gregarious koinobiont larval parasitoid *Cotesia flavipes* Cameron

(Hymenoptera: Braconidae), was introduced in eastern and southern Africa for the control of *C. partellus* (Overholt, 1998). The emphasis on classical biological control of stem borers may be due to high costs associated with pesticides, which makes their use uneconomical. Furthermore, insecticidal control is difficult to achieve, due to the cryptic feeding behaviour of stem borers (Overholt, 1998). A compelling motivation for adoption of biological control is potentially a permanent return to ecological conditions similar to those seen before the arrival of the invasive pest and reduced ongoing expenditure for pesticides, labour, and specialised equipment (Hoddle, 2004). However, decisions as to whether to attempt the use of biological control agents must weigh the risks of it creating problems against the risks associated with not using it (e.g. diminished crop yields or use of chemical pesticides instead). Hoddle (2004) skirts the essential ecological issue: predicting the magnitude of the outcome of new interactions in a new environment. This is because biological control introductions can cause a decrease of native parasitoids through competition for food (Elliot *et al.*, 1996) and can also feed on non-target natives (Louda *et al.*, 2003). Biological introductions have also disrupted key ecological functions in many systems, with far reaching implications for economic activities supported by those systems (Heywood, 1995). However, intentionally introduced species are likely to establish in the environment since they are selected for their ability to survive in the environment where they are introduced (Lonsdale, 1994; Smith *et al.*, 1999). Due to the potential risks associated with biological introductions, it is therefore, necessary to elucidate whether the target species is actually a pest; evaluate the effect of natural enemies on non-target organisms before massive releasing followed by elaborate post-releasing monitoring, and hence the aim of this study.

1.2. Literature review

1.2.1. Stem Borers

Stem borers feed in communities of wild and cultivated grasses which have stems sufficiently large to accommodate their feeding behaviour (Harris, 1990). Feeding and stem tunnelling by the borer larvae leads to crop losses through destruction of the growing point, early leaf senescence, interference with translocation of metabolites and nutrients that result to malformation of grains, stem breakage, plant stunting, lodging and direct damage to the ears. Infestations by stem borers also increase the incidence and severity of stalk rots (Bosque-Pérez and Mareck, 1991). Various wild host plants of these stem borers have been documented (Ingram, 1958; Nye, 1960; Harris, 1962; Gebre-Amlak, 1988). Among the wild hosts, native grasses, sedges (*Cyperacea*) and cat's-tails (*Typacea*) are important host plants for the borers (Jepson, 1954; Conlong, 1990) and are presumably the aboriginal host plants for the indigenous stem borers in Africa. However, stem borer densities in wild hosts do not reach nearly the levels observed in cultivated crops (Mathez, 1972). Wild hosts may have certain antibiotic properties, are physically less suitable for oviposition or lack essential nutrients necessary for optimal stem borer growth. High silica content may be a factor responsible for stem borer resistance in wild grasses (Sétamou *et al.*, 1993).

The introduction and widespread cultivation of maize and sugarcane has undoubtedly had an impact on the abundance of graminaceous stem borers by providing a highly nutritious and readily available source of food and little inherent resistance to stem borers (Overholt, 1998). Stem borer larvae occur in large numbers in maize fields but some of the adult stem borers migrate to alternative hosts and wild grasses close to the

fields after harvest of the crop where they survive throughout the non-cropping dry season. In East Africa, injurious stem borer species include the indigenous pyralid *Chilo orichalcociliellus* Strand, and *Eldana saccharina* Walker (Lepidoptera: Pyralidae), and the Noctuids *Busseola fusca* (Fuller) and *Sesamia* species (Lepidoptera: Noctuidae) (Nye, 1960; Mohyuddin and Greathead, 1970; Seshu Reddy, 1983; Minja, 1990).

Chilo orichalcociliellus occurs in the Coastal region of East Africa, Malawi and Madagascar at altitudes below 600m (Nye, 1960; Mathez, 1972). Of the *Sesamia* species, *S. calamistis* is probably the most widely distributed and economically important species but others, including *Sesamia cretica* Lederer and *Sesamia botanephaga* Tams and Bowden which occur in east and West Africa are also important. *Eldana saccharina* is widely distributed and has been reported from several grasses and sedges in Africa (Ingram, 1958; Conlong, 1990) where it is considered to be a pest of both maize and sugarcane in West Africa (Bosque-Pérez and Mareck, 1990). *Busseola fusca* is the most damaging indigenous stem borer of maize and sorghum in sub-Saharan Africa (Harris, 1989). In addition to the native stem borers, two introduced species, *C. partellus* and *Chilo sacchariphagus*, are important pests. Despite being exotic, *C. partellus* is the dominant and most economically important stem borer in many parts of East and Southern Africa (Mohyuddin and Greathead, 1970; Harris, 1990; Overholt *et al.*, 1994).

Chilo partellus Swinhoe (Lepidoptera: Crambidae) is an exotic cereal stem borer that was accidentally introduced into Africa from South Eastern Asia early in the 20th century and was first recorded from Malawi in 1932 (Tams, 1932). Since then, *C. partellus* has been recorded in several other countries and is now found in most of the lowland areas of the eastern and southern parts of the African continent (CABI, 1989). In east Africa, *C.*

partellus was first recorded in Tanzania in 1952 (Duerden, 1953) and has since spread to the other east African countries.

Maize and sorghum are the major host plants of *C. partellus*, but it has been observed damaging pearl millet, finger millet, wheat, rice, and sugarcane in the field. Wild host plants include such grasses as *Andropogon* spp., *Sorghum halepense*, *Sorghum verticilliflorum* and *Panicum maximum* (Sithole, 1990). Recent surveys indicated that *C. partellus* was by far the most abundant stem borer species of maize and sorghum in the coastal area of Kenya and typically accounted for more than 80% of the stem borer population (Overholt *et al.*, 1994) with 18% yield losses in maize being attributed to *C. partellus* and *C. orichalcociliellus* (Warui and Kuria, 1983). In Southern Mozambique, *C. partellus* accounted for 50% yield loss in maize and sorghum (Sithole, 1990). Losses differ from one farm to another and range from 0-100% (Sithole, 1990). Recent evidence suggests that *C. partellus* is also increasingly becoming a pest of higher elevation areas (Sithole, 1990). The invasive stem borer, *C. partellus*, has proved to be a highly competitive colonizer in many of the areas it has invaded in eastern and southern Africa, often becoming the most serious stem borer (Seshu Reddy, 1983; Kfir, 1997a) and is displacing native species (Kfir, 1997b; Overholt, 1998). The high prevalence of *C. partellus* may be due to the fact that it is a good colonizer of new habitats (Overholt *et al.*, 1994; Kfir, 1997b). It is possible that *C. partellus* emerges earlier in the season than the other stem borer species, hence colonizing the suitable feeding niches in the maize crops and thus reducing the early season colonization and infestation by other stem borers (Songa *et al.*, 2002). *Chilo partellus* completes a generation in less time than *C. orichalcociliellus* (Ofomata *et al.*, 2000), which may result in higher population growth

rate. Moreover, *C. partellus* terminates diapause more rapidly than *C. orichalcociliellus* (Ofomata *et al.*, 1999) or *B. fusca* (Kfir, 1997 b), which may allow *C. partellus* to colonize host plants before the two native species at the beginning of growing seasons. Finally, more neonate *C. partellus* larvae disperse greater distances than *C. orichalcociliellus*, which may allow *C. partellus* to colonize more plants than the native borer (Ofomata, 1997).

Chilo partellus females are active in the evening and mate soon after emergence and oviposit for two to three subsequent nights in batches of 10-80 overlapping eggs on the upper and undersides of the leaves, mainly near the midribs. Adults live for about 2-5 days and do not normally disperse far from emergence sites. In the late planted maize, eggs may be laid on cobs (Sithole, 1990). Eggs hatch 4-8 days after being laid and young larvae ascend plants and enter leaf whorls and start feeding gregariously on leaves for some time prior to dispersion. The first two instar larvae spin silk threads which enable them to disperse from one plant to another with the help of wind (van Hamburg, 1980). Older larvae tunnel into the stem tissue and after feeding for 2-3 weeks, pupate in the stems for 5-12 days and the life cycle is completed in 25-50 days.

Towards the end of the growing season, some of the stem borer larvae enter diapause which they spend as fully grown larvae in dry crop residues left in the field after harvest (Warui and Kuria, 1983; Unnithan and Seshu Reddy, 1989). In Kenya, *C. partellus*, *S. calamistis* and *C. orichalcociliellus* enter diapause for several months in the dry season (Scheltes, 1978; Ofomata *et al.*, 1999). In West Africa, *B. fusca* enters diapause during the dry season which takes up to six months and the larvae pupate within the stems with initiation of rains and adult moths emerge 10-12 days later (Harris, 1962). Among the

factors inducing diapause, increase in carbohydrates, decrease in protein and water of the food plant and general deterioration of the nutritive environment have been cited for different stem borers (Nye, 1960). During diapause, the larvae of *B. fusca* and *C. partellus* decrease in weight and emerging moths have reduced eggs compared to those emerging from non-diapausing larvae (Kfir, 1991a). A combination of temperature and photoperiod play an important role in termination of diapause in *B. fusca* in South Africa, and water is important as a stimulus for morphogenesis following diapause (Kfir, 1993).

1.2.2. Management of stem borers

Methods currently used in the management of stem borers include: chemical control; cultural control; habitat management; host plant resistance and biological control. Chemical control is usually recommended by national extension agencies, and research has shown that it can indeed be effective in reducing stem borer numbers (Mathez, 1972; Warui and Kuria, 1983). However, the relatively short time larvae are exposed (i.e. before they enter the stems) makes it necessary to apply pesticides on regular basis. This time consuming and expensive technology may not be feasible for majority of poor resource, small scale farmers in Africa (Bonhof *et al.*, 1997). Furthermore, chemicals are hazardous to man and other non-target organisms as well as promoting resistance in target pests to insecticides if used for a long time or in sub-lethal quantities (Minja, 1990).

Cultural control is the most relevant and economic method of stem borer control for resource poor farmers in Africa. It includes destruction of crop residues, intercropping, crop rotation, manipulation of planting dates and tillage methods (Polaszek, 1998). Destruction of crop residues by burning can create problems in farms where the organic

matter is low and soil erosion from wind and rains is severe (Polaszek, 1998). For cultural control to be effective, the co-operation of farmers in a region is required because moths emerging from untreated fields can infest adjacent crops (Kfir, 1992a). In subsistence farming systems in Africa where farmers normally intercrop cereals with other crops and lack of water is a major constraint, manipulation of sowing dates and management of plant densities is not always practical as farmers often plant after first rains (Polaszek, 1998).

Host plant resistance provide an inherent control that involves no environmental problems and they are generally compatible with other insect control methods (Kfir *et al.*, 2002). Efforts are underway in Africa to identify sources of stem borer resistance in cereal crops, but high levels of resistance have not been found (Kfir *et al.*, 2002).

Another useful tactic for stem borer control is planting an outer encircling row of some highly preferred host to act as trap crop. Napier grass, *Pennisetum purpureum*, and Sudan grass, *Sorghum vulgare sudanese,* are reported from Kenya to provide natural control to stem borers by acting as trap plants (Khan *et al.*, 1997; 2000). For the control of stem borers in resource-poor maize farming systems in eastern Africa, novel habitat-management strategies have been developed using "push-pull" techniques (Khan *et al.*, 2000). This involves use of intercropping and trap crop systems. Stem borers are trapped on highly susceptible trap plants (pull) and are driven away from maize crop by repellent intercrops (push). Napier grass and Sudan grass are used as trap plants, whereas molasses grass and silver leaf desmodium repel ovipositing stem borers (Khan *et al.*, 1997). However, it has also been reported that molasses grass when intercropped with maize

increases stem borer parasitism by, *Cotesia sesamiae* Cameron (Hymenoptera: Braconidae) (Khan *et al.*, 1997).

Biological control involves the use of parasitoids, predators, pathogens, antagonists or competitors to suppress a pest population (van Driesche and Bellows, 1996), and give a promising alternative to the use of chemical pesticides in pest management yet are safer to public health than chemical control (Pimentel and Andow, 1984). Information on the impact of pathogens in east Africa is limited. However, laboratory and screen house experiments show that the bacteria *Bacillus thuringiensis*, fungi and protozoa of genus *Nosema*, have high potential for controlling stem borers (Bonhof *et al.*, 1997). The impact of predators on stem borers in east Africa has not been well studied but, there seems to be a consensus that predators play an important role (Mohyuddin and Greathead, 1970; Oloo, 1989; Greathead, 1990; Oloo and Ogeda, 1990). A complex of native parasitoid species attack stem borers in Africa but do not seem to be able to maintain stem borer populations at economically acceptable levels (Oloo, 1989). There have been attempts to increase natural mortality of stem borers by using Classical biological control which targets exotic pests and involves importation and release of an organism outside its natural range from the pest's native home into an area where the pest is invasive (Howarth, 1991). For instance, *C. partellus* and *C. sacchariphagus* have been targets of biological control (Overholt, 1998).

1.2.3. Parasitoids and stem borer control

A survey of indigenous natural enemies of stem borers has been carried out in Kenya, and the number of species recovered was reported to be more than 40 (Table 1.1) (Bonhof *et al.*, 1997). A wide range of egg, larval and pupal parasitoids of stem borers

has been identified. Parasitoids of holometabolous insects are classified by the stage they attack. The most abundant and widespread parasitoids in the east African region are the egg parasitoids *Telenomus* spp., and *Trichogramma* spp., the larval parasitoids *C. sesamiae* and *Sturmiopsis parasitica* Curran (Hymenoptera: Tachnidae), and the pupal parasitoids *Pediobius furvus* Gahan (Hymenoptera: Eulophidae) and *D. busseolae* (Oloo and Ogeda., 1990; Bonhof *et al.*, 1997).

Table 1.1 Primary parasitoids of common cereal stem borers in Kenya

Parasitoid	Host species	Host stage
HYMENOPTERA		
Bethylidae		
**Goniozus* sp.	C. sp	L
Goniozus indicus Ashmead	Co, Cp	L
Odontepyris transvaalensis De Buyson	?	L
Braconidae		
Amyosom nyanzaense Quicke and Wharton	Bf, Cp	L
**Apanteles* sp. (ater group)	Cp	L
**Apanteles* sp. Nr laevigatus (Ratzeburg)	Co	L
Bassus sublevis (Granger)	Cp, Es	L
**Bracon* (*Glabrobracon*) sp.	Co, Cp	L
Bracon chinensis Szépligeti (*Myosoma chinensis*)	Cp	L
Bracon sesamiae Cameron	Bf, Cp, C. sp.	L
Chelous sp.	?	P
Chelonus curvimaculutus Cameron	Co, Cp	E / L
Cotesia flavipes Cameron (*Apanteles flavipes*)	Cp	L
Cotesia ruficrus Haliday	?	L
Cotesia sesamiae Cameron (*Apanteles sesamia*)	Co, Cp	L
**Dolichogenidae fuscivora* Walker	Bf, Cp	L
Dolichogenidae polaszeki Walker	Bf, Cp	L
Euvipio rufa Szépligeti	Cp	L
Glytapanteles africanus Cameron (*Apanteles africanus*)	Cp	L
Glytapanteles maculitarsis Cameron (*Apanteles maculitarsis*)	Bf	?
Glyptomorpha spp.	Co, Cp	L
Macrocentrus sesamivorus van Achterberg	Cp, Sc	L
**Meteorus* sp.	Bf	L
Myosoma nyanzaensis Quicke and Wharton	Cp	L
Phanerotoma leucobasis Kriechbaumer	Bf	E / L
Rhaconotus sp.	Cp	L
Rhaconotus scirpophagae Wilkinson	Cp	L
Stenobracon rufus Szépligeti	Bf, Co, Cp, C. sp., Es, Sc, S. Sp.	L
Chalcididae		
Anthrocephalus mitys Walker	Cp	P
**Brachimeria* spp.	Co, C. sp. Bf, Cp, Es	P
Psilochalchis soudanensis Steffan	Bf, Cp, Es	P
Eulophidae		
Pediobius furvus Gahan	Bf, Cp, S. spp.	P
**Tetrastichus* sp. A	C. sp.	?
Eurytomidae		
Eurytoma oryzivora? Delvare	Cp	P
Ichneumonidae		
Dentichasmias busseolae Heinrich	Cp, Co, B.sp.	P
Pristomerus sp.	C.sp.	?

Table 1.1 continued

Parasitoid	Host species	Host stage
Procerochasmias nigrimaculatus Cameron	Bf, Sc	P
Syzeuctus ruberrimus Benoit	Co, Cp	L
Xanthopimpla sp.	Cp	P
Pteromalidae		
Norbanus sp.	Cp	L
Scelionidae		
**Telenomus busseolae* Gahan	Bf	E
Telenomus sp.	Cp	E
Telenomus applanatus Bin and Johnson	Es	E
T. Nemesis Polaszek and Kimani	Co, C.Sp.	E
**Trichogramma* sp.	Co, Cp, Sc	E
DIPTERA		
Chrolopidae		
**Polyodaspis* sp.? *robusta* Lamp	Co, Cp	L
Muscidae		
**Antherigona* sp.	C.sp.	L
Tachinidae		
Sturmiopsis parasitica Curran	Co	L

Bf= *Busseola fusca*
B.sp. = *Busseola species*
Co= *Chilo orichalcociliellus*
Cp= *Chilo partellus*
C.Sp. = *Chilo species*
Es= *Eldana saccharina*
Sc= *Sesamia calamistis*
S.Sp. = *Sesamia species*

E= egg
L= larva
P= pupa
?= unknown
* = incidental parasitoid or species of doubtful status

(Table adopted from Bonhof *et al.*, 1997)

1.2.4. Pupal parasitoids

Pupal parasitoids attack the pupa stage of the host. Those that attack stem borers include several genera of the Eulophidae, Ichneumonidae and Chalcidae (Smith *et al.*, 1993). In contrast to the parasitization of early host life stages, the indispensable contribution of mortality by pupal parasitoids could contribute more to intergenerational mortality of the stem borers (Rodriguez-Del-Bosque and Smith, 1997). Parasitoids which attack non-feeding host stages like pupae use cues from other stages of the host (Vet and Dicke, 1992; Gohole *et al.*, 2003). Pupal parasitoids respond to cues associated with plant

damage or the pupal chamber and use different strategies to attack the host. For instance, the gregarious endoparasitoid *P. furvus*, the solitary endoparasitoid *Psilochalcis soudanensis* Steffan (Hymenoptera: Chalcidae) and the solitary endoparasitoid *D. busseolae* use ingress-and-sting strategy (Smith *et al.*, 1993) whereas *X. stemmator*, an exotic pupal parasitoid, uses drill-and-sting attack strategy (Smith *et al.*, 1993).

Dentichasmias busseolae is a solitary pupal endoparasitoid endemic in East Africa and attacks graminaceous stem borer *Chilo* spp. in east Africa (Mohyuddin, 1972). In semi arid areas of Kenya, *D. busseolae* is responsible for most parasitism (Songa *et al.*, 2002). In western Kenya, parasitism by *D. busseolae* is quite variable ranging from 0 to 58 % (Oloo and Ogeda, 1990), whereas on the Kenyan coast, it ranges from 0 to 26% (Mathez, 1972). In *C. partellus, D. busseolae* takes about 17.4 days to develop and slightly longer in other hosts averaging 18.0 in *S. calamistis*, 19.5 in *B. fusca* and 20.0 in *E. saccharina*. Although discrepancies exist in literature concerning the host range of *D. busseolae,* it is primarily a parasitoid of *C. partellus* (Zwart, 1998). *Sesamia calamistis, B. fusca* and *E. saccharina* are suitable laboratory hosts and are not parasitized in the field therefore *D. busseolae* seems to be mono-phagous in the field (Mohyuddin, 1972; Bahana, 1990; Zhou *et al.*, 2003). Mohyuddin (1972) showed that *D. busseolae* parasitized *B. fusca* pupae when placed in *C. partellus* pupal tunnels but not when they are in their own tunnels. *Dentichasmias busseolae* does not discriminate between volatiles from *B. fusca* infested and *C. partellus* infested maize. The parasitoid however, prefers volatiles from the infested sorghum to those from the infested maize (Gohole *et al.*, 2003).

Mating occurs immediately after emergence and oviposition starts a few hours after emergence. The optimum reproductive age is 5-7 days. Newly emerged females are more attractive to males than older ones and the adults mate repeatedly with the first mating taking an average of one and half minutes. *Dentichasmias busseolae* enters the pupal chambers through the moth emergence window (Mohyuddin, 1972). The female inserts the antennae through the moth exit and searches the tunnel for pupa for few seconds and if a host is present, the female raises the lid with her mandibles, enters the tunnel and oviposits in the pupa. Time spent in the tunnel varies from a few seconds to 1½ minutes but oviposition only takes about 10 seconds. The female inserts the ovipositor into the pupa while staying on one side parallel to it. Mohyuddin (1972) observed that the female cannot parasitize a host if it cannot reach it from outside or enter the tunnel. However, the females prefer to enter the tunnel to oviposit.

Xanthopimpla stemmator is a solitary pupal endoparasitoid and has a broad geographic distribution having been reported from many areas in Asia, including India, Indonesia, Malaysia, the Philippines, Sri-Lanka and Taiwan (Hailemichael *et al.*, 1994). The parasitoid has a broad host range that encompasses approximately 15 species of lepidoptera in Pyralidae and Noctuidae families. It was introduced into South Africa from Mauritius for biological control of the lepidopteran stem borer *C. partellus* but it failed to establish due to differences in climatic factors (Moore and Kfir, 1996). In Asia, *X. stemmator* is an important parasitoid of graminaceous Noctuid, Pyralid, and Crambid stem borers (Moutia and Courtois, 1952). Gitau (2002) found that the parasitoid would attack and develop in *C. partellus*, *B. fusca* and *S. calamistis* which are stem borers found in Eastern and Southern Africa.

Mating takes place immediately after emergence from the host with females mating only once but males can mate with several females in succession (Moore and Kfir, 1996). The females can also produce parthenogenetically, but unmated females give rise to male progeny only (Moore and Kfir, 1996). Adult female parasitoids are attracted by grass stems and when they alight on the stems, they move rapidly up and down palpating the surface with their antennae, apparently searching for the cues that denote a host is present (Hailemichael *et al.*, 1994). The female is stimulated by the presence of larval frass, odour associated with the host and sound vibrations of the host. Attraction of *X. stemmator* females to larval frass helps guide female to the microhabitat of the host pupa and stimulates ovipositor drilling. Pupal odour and pupal movement further restricts local searching to help pinpoint the location for ovipositor drilling (Hailemichael *et al.*, 1994).

Xanthopimpla stemmator attacks its host by "drill-and-sting" attack strategy (Smith *et al.*, 1993), in which the parasitoid drills with the stout ovipositor through the stalk wall or leaf sheath enclosing the host and parasitizes the pupa constrained in the cryptic micro-habitat. Moore and Kfir (1996) noted that pre-oviposition period is normally 3 to 6 days and the duration of development decreases with increasing temperature. Hailemichael *et al.* (1994) observed that host acceptance was not influenced by the age of the pupae but host suitability was influenced by the age. The proportion of emerging female progeny increases with host pupae age and females live longer than males.

1.3 Problem statement and justification

Cereals are important crops grown in most parts of the world for human consumption and surpluses are used for livestock feeds (Sibanda, 1985). Among the major production constraints are pests, and stem borers are by far the most destructive

(Kfir *et al.*, 2002). An exotic borer species, *C. partellus*, is a serious stem borer in many parts of eastern and southern Africa. Due to its status as an introduced pest, *C. partellus* has been a primary target of classical biological control. In 1991, the International Centre of Insect Physiology and Ecology (ICIPE) introduced a larval parasitoid, *Cotesia flavipes* (Hymenoptera: Braconidae) from Pakistan and later from India against *C. partellus*. However, the level of control provided by this natural enemy varies from area to area (Overholt *et al.*, 1997) since *C. flavipes* is not able to complete development in *B. fusca* which therefore acts as a reproductive sink (Ngi-Song *et al.*, 1998). An exotic pupal parasitoid, *Xanthopimpla stemmator*, which exploits a broad range of hosts within the same niche (Hailemichael *et al.*, 1994), was imported by ICIPE in 2001 for classical biological control of *C. partellus*. Host range studies at ICIPE revealed that *X. stemmator* will attack and develop in all major borer species in eastern and southern Africa (Gitau, 2002). *Xanthopimpla stemmator* uses "drill-and-sting" attack strategy (Smith *et al.*, 1993), a behaviour not shared by any common native pupal parasitoid and therefore can fill a largely vacant niche in Africa. However, biological introductions with tremendous potential to reduce the pest numbers can also have negative impacts on non-target insect populations including indigenous parasitoids (Pimentel and Andow, 1984). Therefore, careful evaluation of natural enemies prior to their release within a geographic area is necessary (Alyokhin, 2000). Previous investigations aiming at addressing this question were conducted in the laboratory using *P. furvus* hence the need to assess the impact of *X. stemmator* on the efficiency of indigenous pupal parasitoid, *D. busseolae,* and whether the parasitoid will co-exist with the local pupal parasitoid.

1.4. Null hypotheses

This study was based on the following hypotheses:

i. *Xanthopimpla stemmator* and *D. busseolae* female parasitoids will not discriminate between a parasitized and unparasitized *C. partellus* host pupae.

ii. *Xanthopimpla stemmator* and *D. busseolae* will not successfully multi-parasitize *C. partellus* pupae.

iii. The searching efficiency of a female parasitoid, *X. stemmator* and *D. busseolae* in parasitizing a host pupa will not depend on the part of the plant in which the pupa is found.

1.5. Objectives of the study

1.5.1. General objective

The overall aim of this study was to assess the impact of *X. stemmator* on the efficiency of indigenous pupal parasitoid, *D. busseolae*.

1.5.2. Specific Objectives

The specific objectives of this study were to:

i. determine whether female *X. stemmator* and *D. busseolae* parasitoids will discriminate between *C. partellus* pupae parasitized by the other species and those that are unparasitized.

ii. investigate the effect of multi-parasitism on *X. stemmator* and *D. busseolae* using *C. partellus* pupae.

iii. determine the host searching efficiency of *X. stemmator* and *D. busseolae* female parasitoids on different parts of the maize plant.

CHAPTER TWO

2.0. GENERAL MATERIALS AND METHODS

2.1. Study site

The study was conducted at the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya.

2.2. Insects

All the insects used were reared in the Animal Rearing and Containment Unit (ARCU) at ICIPE. *Chilo partellus* (Plates 2.1, 2.2 and 2.3) was used in all the experiments. Adults were allowed to mate in Perspex oviposition cages (20x20x25cm) and the eggs laid were used to produce pupae for experiments. In the laboratory *C. partellus* was reared on artificial diet according to the method of Ochieng *et al.* (1985). Two-day old pupae of *C. partellus* were used in the bioassays.

The parasitoids used were *X. stemmator* (Plate 2.5) and *D. busseolae* (Plate 2.4). A colony of *D. busseolae* was established from material collected from western Kenya. It was reared on *C. partellus* following the method by Bahana (1990). Two-day old *C. partellus* pupae were placed in artificial pupal chambers in 10cm-long mature maize stems and were offered to gravid parasitoids in oviposition cages (30 by 30 by 30 cm) at a ratio of 1 female to 1 pupa for at least 24 hours. These were presented in an upright position by placing them on a clay base. Pupal chambers were produced by first splitting the stem longitudinally into two. A 2cm-long, 1cm deep and 1cm wide depression was scooped out of one of the longitudinal sections. Exit holes were bored through the other section of the stem, at the same location as the depression. The depressions were filled

with frass from fifth instar *C. partellus* larvae but leaving enough space for *D. busseolae* female to move freely around the pupa. After placing a pupa in the depression, the two stem sections were joined together using rubber bands. The holes were lightly covered with frass to simulate a natural exit hole. After 24 hours of exposure, the pupae were removed and placed in Petri dishes and maintained in an incubator at 25±1°C and 50-60% relative humidity until either moth or parasitoid emergence. Five-day old mated naïve *D. busseolae* females were used in bioassays. The adults of *D. busseolae* were fed on 20 % honey solution.

A colony of *X. stemmator* initiated with insects imported from India was reared at the ARCU. Mated *X. stemmator* females were offered pupae of *C. partellus* in 10 cm long and 0.5 cm wide paper straws for 4 hours in 15 x 15 x 15cm Perspex cages. The straws were smeared with frass to enhance acceptance (Hailemichael *et al.*, 1994). Exposure of pupae was carried out twice a week and parasitized pupae were kept in petri dishes until adult moths or parasitoids emerged. On emergence, the adult parasitoids were released into clean perspex cages and were fed on 20 % honey solution. The colony of parasitoids was maintained at 25 ± 1°C, 50-60 % RH and 12: 12 (L: D) photoperiod. For all experiments, 6-day old mated naive females were used in bioassays.

Oviposition cages used had two circular openings cut halfway on the front and rear sides. The front opening was fitted with a cylindrical muslin sleeve. This was to allow for hand-insertion during regular inspection, feeding and during experiments. The rear opening was covered with nylon net to allow free air circulation.

Plate 2.1 *Chilo partellus* adult

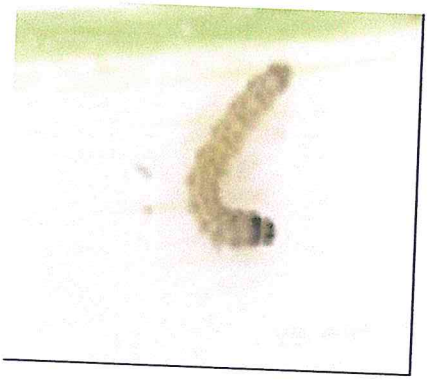

Plate 2.2 *Chilo partellus* larva

Plate 2.3 *Chilo partellus* pupa

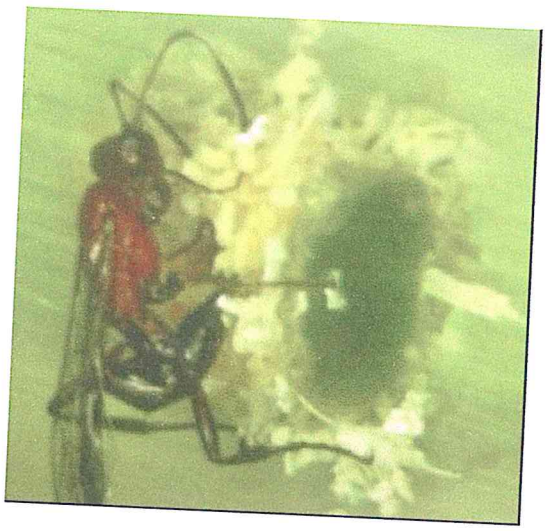

Plate 2.4 ***Dentichasmias busseolae***

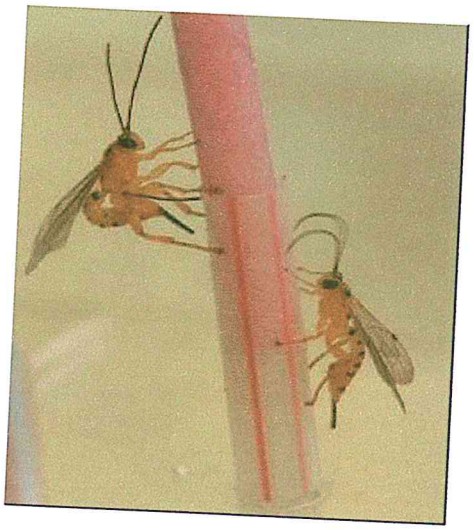

Plate 2.5 *Xanthopimpla stemmator*

2.3. Host plant

The maize variety Katumani was planted at ICIPE in plots measuring 6 by 4 metres every two weeks for at least three months. Three seeds were put per hole and thinned to 2 plants 7 days after emergence of the seedling. Weeding was done 3 weeks after emergence and top dressing was done using Calcium ammonium nitrate when the plants were 45 cm high. Re-weeding was done when appropriate. Sprinkler irrigation was applied during the dry spells at least once a week depending on the weather conditions.

CHAPTER THREE

3.0. INTERSPECIFIC HOST DISCRIMINATION AND COMPETITION BETWEEN *XANTHOPIMPLA STEMMATOR* AND *DENTICHASMIAS BUSSEOLAE*

3.1. Introduction

Discrimination between parasitized and unparasitized hosts has evolved in many species of hymenopterous parasitoids (van Lenteren, 1981; Waage, 1986) as a means to avoid waste of offspring and of search time resulting from parasitization in previously parasitized hosts. Host discrimination can be of three kinds: self, conspecific and heterospecific (= interspecific) discrimination. Interspecific host discrimination is the ability of female parasitoids to distinguish between unparasitized hosts and hosts that have been parasitized by another parasitoid species. The allocation of one or more eggs to a host already parasitized by a conspecific is termed superparasitism (van Dijken and Waage, 1987), and oviposition into a host previously parasitized by another species is termed multiparasitism. Host discrimination cannot be studied directly; what is studied is whether parasitoids show different behavior towards parasitized and unparasitized hosts (Pijls *et al.*, 1995). Interspecific host discrimination and the possible avoidance of multiparasitism are among the determinants of the population dynamics of a species (Pijls *et al.*, 1995).

Parasitoid wasp females have to decide which hosts to accept for oviposition and this decision strongly depends on the characteristics of the hosts (Visser *et al.*, 1992). An important feature is whether the host has been parasitized or not (Ueno, 1994). In solitary parasitoids, only one individual can develop in a host and supernumerary individuals are

eliminated through intra-host competition (Hubbard *et al.*, 1987). Generally, the oldest parasite eliminates all the younger competitors (Mangel, 1987). Therefore, a parasitized host is of lower quality for a female parasitoid (Nelson and Roitberg, 1995). Many studies have reported that parasitoids can discriminate between parasitized and unparasitized hosts (Ueno, 1994), and this ability is generally mediated through host markers present externally or internally. Some solitary parasitoids mark the host they just attacked externally with either a pheromone deposited during oviposition or a physical mark left on the host body (Takasu and Hirose, 1988; Mackauer, 1990). Internal cues for host discrimination can originate either from parasitoid injected substances (Vinson, 1976; Hubbard *et al.*, 1987) or from host quality changes associated with parasitism (Cloutier *et al.*, 1984; Hofsvang, 1988; Mackauer, 1990). In contrast, occasional or total lack of host discrimination has been observed in a few solitary parasitoids (Rosenheim and Mangel, 1994).

Competition between species of insect parasitoids or predators can influence the size and the structure as well as the stability of insect populations in several trophic levels (Price *et al.*, 1986). In biological control, competition between species of introduced natural enemies or between introduced and native natural enemies of a pest has been used to explain why some species failed to either become established or to control the pest completely (Ehler and Hall, 1982; Jalali *et al.*, 1988). Direct effects of competition are generally thought to result from a reduction in resource availability either by exploitation or by interference. Indirect effects, which are more difficult to prove, include changes in host behaviour in response to parasitoid searching patterns as well as parasitoid-mediated interactions between different host species (Price *et al.*, 1986; Hawkins, 1988). In solitary

species, normally only one larva completes development to the adult stage in each host, with supernumerary larvae being eliminated by some form of physiological suppression or physical combat among the larvae (Mackauer, 1990). The present study aimed to assess whether pupal parasitoids *X. stemmator* and *D. busseolae* will discriminate between a host pupa parasitized by a female parasitoid of the other species hence avoid multiparasitism.

3.2. Materials and methods

3.2.1. Insects

Chilo partellus was reared as described in section 2.2. Two-day-old borer pupae were used in this study. The study was carried out using *X. stemmator* and *D. busseolae* females reared as described in section 2.2.

3.2.2. Bioassays

At two different time intervals (0 and 48hrs) and two sequences [*X. stemmator* (XS) followed by *D. busseolae* (DB) and vice versa] within each interval, 30 two-day old *C. partellus* pupae were individually exposed to individual females of *X. stemmator* and *D. busseolae* for parasitization. Thirty pupae were used for control whereby the parasitoid ovipositing second in the Xs-Db or Db-Xs treatment was allowed to parasitize in order to compare the parasitoid's behaviour on parasitized and unparasitized host pupae. The trials were replicated 30 times in a randomised design and each pupa was considered a replicate. At time interval 1 (0hr interval), the time span between oviposition by the two parasitoids was less than 2 minutes. At time interval 2 (48 hr interval), there were 48±1 hours between oviposition by the two species. In sequence 1, a *C. partellus* pupa was first

parasitized by *X. stemmator* female before offering it to *D. busseolae* (Xs-Db); in the control, 2- or 4-day old pupa was stung by *D. busseolae* alone for 0 and 48 hr intervals respectively. In sequence 2, a *C. partellus* pupa was first stung by *D. busseolae* female and then by *X. stemmator* female (Db-Xs). In the control, 2- or 4-day old pupa was stung by *X. stemmator* alone for 0 and 48 hr intervals respectively. Pupae were exposed to *X. stemmator* in a 5 cm paper straw smeared with its 5th instar larvae frass to enhance acceptance. The paper straw standing on a clay base was supported on a clean bench. A mated naive 6-day old *X. stemmator* female was selected from a rearing cage by placing a straw containing pupa inside the cage and one of the actively searching (an indication that it was ready for oviposition) was collected using a 2.5 by 10 cm vial. The vial with the parasitoid was placed upside down over the paper straw and observed for parasitization. *Chilo partellus* pupa was offered to *D. busseolae* in artificial pupal chamber. Fresh fifth instar larval frass was sprinkled around the pupa to provide simulation of a natural pupal chamber. The depression was covered using a clear glass slide and secured using rubber bands at each end to make it possible to observe the parasitization process. The experimental arena was a clear plastic jar. It was assumed that each probe resulted in oviposition as revealed by a preliminary experiment which involved dissection of parasitized pupae. Observations were made on the parasitization process, foraging time (time from onset of searching to the first attempt of ovipositor insertion) and probing time (time from the first attempt to insert ovipositor until the parasitoid left the host) as well as on host marking. Probed pupae were removed and each incubated in a separate vial which was kept at 25±1°C, 50-60% RH and 12:12 L: D photoperiod. Data on the fate

(parasitoid emergence, moth or pupal death) of parasitized pupae was recorded. The experiment will hereafter be referred to as experiment A).

The experiment was repeated with different controls: in sequence 1 (Xs-Db), in the control, 2-day old *C. partellus* pupa was stung by *X. stemmator* (Xs) alone for both 0 and 48 time intervals and for sequence 2 (Db-Xs), in the control, 2-day old *C. partellus* pupa was stung by *D. busseolae* (Db) alone for both time intervals. Probed pupae were removed and incubated each in separate vial and kept at 25±1°C, 50-60% RH and 12:12 L:D photoperiod. Data on the fate of the parasitized pupae (parasitoid emergence, moth emergence or pupal death) and developmental time were recorded. The experiment will hereafter be referred to experiment B).

3.2.3. Data analysis

Data on foraging time and oviposition time were analysed using t-test. (SAS Institute, 2000). Data on the number of pupae yielding parasitoids were compared using Chi-square test for equal proportions. Data on developmental time in multiparasitized host was subjected to analysis of variance (ANOVA) using the generalised linear models procedure (GLM) of SAS (SAS Institute, 2000). Means were separated using Student-Newman-Keuls test (SNK) when ANOVA was significant.

3.3. Results

3.3.1. Parasitoid foraging behaviour

When *X. stemmator* reached the location with the host, it stopped, antennated and assumed a head down/abdomen in the air/tip toe position and started drilling. While the ovipositor was in the pupa, *X. stemmator* moved the ovipositor lobes up and down, at the same time vibrating the stretched wings. When *D. busseolae* reached an exit hole, it

stopped, inserted the antennae, antennated the pupa and got inside where it parasitized the pupa. On inserting the ovipositor, *D. busseolae* rhythmical contractions of the abdomen were observed. After oviposition, both *X. stemmator* and *D. busseolae* withdrew the ovipositor and left the host without exhibiting any marking behaviour such as dragging or brushing the ovipositor on the host. Some *X. stemmator* females were observed feeding on host haemolymph oozing from the ovipositor wounds onto the surface of the straw.

3.3.2. Foraging time and oviposition time of *X. stemmator* and *D. busseolae* on parasitized and unparasitized hosts.

For both parasitoid species and time intervals (0hr and 48 hr) foraging time did not vary between the parasitized and unparasitized host pupae (Table 3.1). Between the time intervals, there was no significant difference in time taken by *X. stemmator* ovipositing in pupae parasitized first by *D. busseolae* (P=0.328; Table 3.1). At 0hr, oviposition time of *X. stemmator* was significantly shorter on pupae parasitized by *D. busseolae* than unparasitized pupae (P=0.015; Table 3.1). At 48 hr time interval, there was no significant difference in time taken by *X. stemmator* to oviposit in the parasitized and unparasitized pupae (P=0.476; Table 3.1). For *D. busseolae*, oviposition time did not vary with parasitized and unparasitized pupae at both 0 hr and 48 hr time interval (Table 3.1).

Table 3.1. Mean (±SE) foraging and oviposition time (sec) of a) *X. stemmator* (Xs) on unparasitized pupae and pupae parasitized by *D. busseolae* (Db-Xs) and of b) *D. busseolae* (Db) on unparasitized pupae and pupae parasitized by *X. stemmator* (Xs-Db) at two different time intervals (n = 30)

	Foraging time				Oviposition time			
	0 hour	48 hours	t-value	*P*	0 hour	48 hours	t-value	P
a) Db-Xs	19.6±2.3	21.4±1.9	-0.58	0.563	39.3±5.2	3.4±14.3	0.99	0.328
Unparasitized	22.8±3.0	18.2±1.4	1.37	0.177	110.7±28.0	32.2±4.3	2.14	0.037
t-value	-0.85	1.29			-2.51	-0.72		
P	0.401	0.201			0.015	0.476		
b) Xs-Db	95.1±10.2	104.0±8.7	-0.66	0.510	67.0±12.9	66.2±8.5	0.05	0.963
Unparasitized	98.2±11.5	111.2±13.9	-0.71	0.478	59.8±12.6	82.2±18.3	-1.01	0.317
t-value	0.20	0.43			-0.40	0.79		
P	0.842	0.665			0.694	0.432		

3.3.3. Competition in the multi-parasitized hosts

Pupae successfully parasitized by both parasitoids yielded either *D. busseolae* or *X. stemmator* and none yielded both parasitoids. Pupae, which were not successfully parasitized, yielded adult moth or died. In experiment A, in the 0hr interval, the percentage of pupae yielding *D. busseolae* was significantly lower in the Db-Xs sequences than in the control (Db alone): a higher percentage of the pupae in the Db-Xs yielded *X. stemmator* (Table 3.2). In the Db-Xs, there was a significant difference in the percent pupae producing *X. stemmator* and *D. busseolae* between the two time intervals (Table 3.2): a higher percentage of pupae in Db-Xs sequence 48 hr interval yielded *D. busseolae* as opposed to the 0 hr interval where a higher percentage yielded *X. stemmator* (Table 3.2). In Xs-Db sequence there was no significant difference in the percentage pupae yielding *X. stemmator* between the time intervals (Table 3.2).

Table 3.2. Percent pupae producing *D. busseolae* or *X. stemmator* in multiparasitism situation when the second parasitoid did not discriminate pupae 0 or 48 hours after parasitization by the first parasitoid (pupae which produced moths or died are not included in the analysis).

Sequence	0-hour	48-hour	χ^2	*P*
	% pupae *producing X. stemmator*			
Xs-Db	90.0	73.3		
Db only	-	-	2.87	0.090
Db-Xs	80.0	10.3		
Xs only	83.3	90.0	33.05	0.0001
χ^2	0.11	44.17	0.58	0.445
P	0.74	0.0001		
	% pupae producing *D. busseolae*			
Xs-Db	3.3	10.0		
Db only	90.0	63.3	1.12	0.290
χ^2	54.64	19.92	6.26	0.012
P	0.0001	0.0001		
Db-Xs	10.0	79.3		
Xs only	-	-	30.01	0.0001

In experiment B, there was no difference in the percentage of pupae producing *X. stemmator* between the Xs-Db sequence and the control (Xs alone) (Table 3.2). Besides, there was no difference in the percentage of pupae producing *X. stemmator* between the two time intervals in the Xs-Db sequence (Table 3.2). Similarly, there was no significant difference in percentage of pupae yielding *D. busseolae* between the time intervals in the Xs-Db sequence. However, there was a significant difference in the percentage of pupae producing *D. busseolae* between Db-Xs sequence and the control (Db alone) (Table 3.2). Similarly, there was a significant difference in percentage of pupae yielding either X. stemmator or D. busseolae between the time intervals in the Db-Xs sequence (Table 3.2)

Table 3.3. Percent of multiparasitized pupae yielding *D. busseolae* (Db) or *X. stemmator* (Xs) when *D. busseolae* or *X. stemmator* parasitized first at two different time intervals (0 and 48 hours) between parasitism (pupae which produced moth or died were not included in the analysis)

	% pupae producing *X. stemmator*			
Sequence	0-hour	48-hour	χ^2	P
Xs-Db	80.0	76.7	0.10	0.754
Xs only	70.0	90.0	3.89	0.049
χ^2	0.81	1.97		
P	0.370	0.161		
Db-Xs	83.3	16.7	29.11	0.0001
Db only	-	-		
χ^2				
P				
	% pupae producing *D. busseolae*			
Xs-Db	10.0	13.3	0.16	0.687
Xs only	-	-		
χ^2				
P				
Db-Xs	3.3	60.0	25.77	0.0001
Db only	63.3	66.7	0.073	0.787
χ^2	28.18	0.287		
P	0.0001	0.592		

3.3.4. Effect of multiparasitism on the developmental time of *D. busseolae* and *X. stemmator*

With the 0hr interval, there was no significant difference in the immature development time of *D. busseolae* progeny between the Db-Xs sequence and the control (Db alone) (F=0.63; d.f. =1, 21; P=0.4379; Table 3.4). With the 48 hrs interval, development time of D. *busseolae* was slightly longer on multiparasitized pupae than in the control (F=9.00; d.f. =1, 36; P=0.0049; Table 3.4). There was no significant difference in development time of *D. busseolae* progeny between the two time intervals in the Db-Xs sequence (Table 3.4). In the Xs-Db sequence, there was no significant

difference in the development time fo

between the Xs-Db sequence and the Xs

Table 3.4. Mean (±SE) deve
multiparasitism situations where
parasitized first followed by the o
by either species only, at two diff
parasitism

	0 hour			
		D. busseolae		
Host type	n		n	
Db-Xs	4	17.0±0.41Aa	18	17
Db alone	19	17.2±0.13Aa	20	16.
Df		1,21		
F-value		0.63		
p		0.4379		
		X. stemmator		
Xs-Db	24	18.9±0.17Aa	23	18.
Xs alone	21	18.8±0.10Aa	27	18.
Df		1,43		
F-value		0.08		
p		0.773		

Means within the same row followed by th
same column followed by the same uppe
$P>0.05$ (SNK).

3.4. Discussion

For parasitoids attacking the cryptic larvae and pupae of stem borers in tunnels of graminaceous plants, the cues for locating the host appear to be derived from the host plant, or host by-products, such as frass and plant damage (Smith *et al.*, 1993; Potting *et al.*, 1995). Gustatory or contact chemical cues are assessed through the use of the antennae and the ovipositor (Mackauer *et al.*, 1996). The present findings are in agreement with the above observations since both *X. stemmator* and *D. busseolae* located their host microhabitat with ease and searched using their antennae before the onset of probing using the ovipositor. The two parasitoids use different attack strategies and different behaviours were observed when the parasitoids attempted to reach the host. *Dentichasmias busseolae*, which uses "ingress-and-sting" attack tactic (Smith *et al.*, 1993), antennated the pupa in the pupal chamber suggesting that chemicals on the host cuticle stimulated the probing of the host. *Xanthopimpla stemmator*, which uses "drill-and-sting" tactic (Smith *et al.*, 1993), started drilling the straw immediately suggesting that the ovipositor was used to asses the host condition prior to oviposition.

Most parasitoids avoid superparasitism or multiparasitism using interspecific host discrimination to ensure being the primary parasitoid (Pijls *et al.*, 1995). Reports on interspecific host discrimination, or the ability of a wasp to recognize a host parasitized by another species, in contrast, are often scarce (Chow and Mackauer, 1984; Vet *et al.*, 1984; Agboka *et al.*, 2002). Absence of heterospecific discrimination and a consequent lack of oviposition restraint, results in multiparasitism (Smith, 1916). In hymenopteran parasitoids, evidence of an ability to discriminate between parasitized and unparasitized hosts has been gathered for 150 to 200 species and in nearly every family (van Lenteren, 1981). In many cases, marking pheromones (MPs) have been implicated in mediating

host discrimination (van Lenteren, 1976; Hofsvang, 1990; Godfray, 1993). In entomophagous Hymenoptera, females may use, internal or/and external marks to determine if a host has been previously exploited (Salt, 1937; Hofsvang, 1990). According to Bosque and Rabinovich (1979), whether MPs are deposited on the inside or the outside of the host depends on the life stage attacked. Egg parasitoids tend to mark the hosts externally while parasitoids utilizing other host stages tend to mark the host internally. Being pupal parasitoids, it is logical to conclude that *X. stemmator* and *D. busseolae* mark their hosts internally or they don't mark them at all. This may explain why after oviposition, both parasitoids withdrew the ovipositor and left the host without exhibiting any marking behaviour. Most MPs are non-volatile and are detected by contact chemo-receptors (van Baaren and Nenon, 1996). Besides, marking pheromones are chemical signals associated with the host resource that signals occupation of conspecifics (Nufio and Papaj, 2001). According to Turlings *et al.* (1985) and Hagvar (1989), interspecific discrimination is uncommon but it is observed when two species are closely related (Vet *et al.*, 1984; McBrien and Mackauer, 1990; van Baaren *et al.*, 1994). The observation that there was no significant difference in foraging time for both parasitized and unparasitized hosts by both *X. stemmator* and *D. busseolae* therefore, makes sense since *X. stemmator* and *D. busseolae* are pupal parasitoids attacking concealed hosts. Hence, they cannot judge the condition of their hosts before coming into contact with them. In addition, *X. stemmator* and *D. busseolae* are not closely related and therefore their ability to recognize hetero-specific host marking might be absent. This may also explain why there was no significant difference in time taken by *D. busseolae* in ovipositing in pupae parasitized by *X. stemmator* and unparasitized pupae. Oviposition by

entomophagous parasitoids may induce changes in a host's haemolymph composition (Vinson and Iwantsch, 1980a; Ferkovich *et al.*, 1983). The presence of a Mp on or in a host may affect a female in multiple ways, both deterring and enhancing oviposition (Corbet, 1973a; Prokopy, 1981a; Paine *et al.*, 1997). Mayhew (1997) speculated that in nature, parasitized hosts are easy to attack than unparasitized hosts since they are weakened. This may make parasitized hosts more preferable thus the searching and handling efficiency of parasitized hosts may be greater. The shorter time taken by *X. stemmator* to oviposit in pupae parasitized by *D. busseolae* may therefore be attributed to the presence of a MP enhancing oviposition or to the fact that parasitized hosts are easy to attack since they are already weakened

Unlike the preys which are consumed by their predators, hosts attacked by parasitoids remain in their habitat. They can therefore be encountered again by the same or another parasitoid and can be accepted again for oviposition. In solitary parasitoids, only one individual can develop in a host and supernumerary individuals are eliminated by some form of physiological suppression or by physical combat among the larvae (Hubbard *et al.*, 1987; Mackauer, 1990). *Xanthopimpla stemmator* and *D. busseolae* are solitary parasitoids and this explains why in all cases, when *C. partellus* host pupa was parasitized by both *D. busseolae* and *X. stemmator*, either *D. busseolae* or *X. stemmator* emerged and none of the multiparasitized pupa yielded both parasitoids irrespective of the sequence and time interval.

According to Mackauer (1990), the outcome of larval competition depends mainly on; (1) the species of parasitoids that compete for host resources, (2) the sequence in which the different females have attacked the host, and (3) the interval between first and

later ovipositions, since they determine the developmental stage of each potential competitor at the time of interaction and the mechanisms involved in larval competition and elimination. From the current study, time interval between the first oviposition by *D. busseolae* and later oviposition by *X. stemmator* was a crucial factor. *Dentichasmias busseolae* out-competed *X. stemmator* only when *X stemmator* parasitized 48 hrs later. When *X. stemmator* parasitized immediately after *D. busseolae* (0hr interval), it out-competed *D. busseolae*. However, the length of time between oviposition by *X. stemmator* and later by *D. busseolae* did not affect the competitiveness of *X. stemmator*. Hence, it's logical to conclude that *X. stemmator* is competitively superior to *D. busseolae* only when time interval between ovipositions is short.

Various mechanisms have been identified which enable "intrinsically superior" parasitoid species to kill or otherwise eliminate the eggs and larvae of the potential competitors. Suppression can result from some action or process between the immature stages or from some action of the adult wasp that affects larval survival (Salt, 1961; Fisher 1961, 1971; Vinson and Iwantsch, 1980b). Salt (1961) noted that aggression is common among the first-instar larvae of many species of solitary hymenopterous parasitoids. In contrast to later stages, which often are amandibulate or have reduced or non-functional mandibles, most first instars have large and commonly sickle shaped mandibles (Clausen, 1962) that can be used to bite and physically attack other larvae in the same host. Work by Conlong and Graham (1988) showed that egg of *X. stemmator* hatches within a day. At 25°C, the eggs of D. busseolae also hatch within a day (Mohyuddin, 1972). According to Hailemichael *et al.* (1994) *X. stemmator* first instar larvae are cannibalistic. Since eggs of both species hatch within the same period, physical

combat might be the most plausible explanation for competition between *X. stemmator* and *D. busseolae* and the current findings indicate that *X. stemmator* is "intrinsically superior" to *D. busseolae*. Although fighting usually takes place among larvae that are approximately of the same age, in some species first-instar larvae will attack and kill older stages that are amandibulate and hence unable to defend themselves (Chow and Mackauer, 1984, 1986). Results from the current study don't agree with these finding since the parasitoid which parasitized 48 hrs earlier always won and therefore it had a competitive advantage over the other. Fisher (1961, 1971) concluded from an experimental study of heterospecific superparasitism involving two species of endoparasitic Ichneumonidae that asphyxiation was a more likely cause for the suppression of a younger larva by an older one than physical combat. Changes in the physiology of the host due to venom or virus-like particles injected by the ovipositing female (Sroka and Vinson, 1978) can result in an environment unsuitable for the younger competing parasitoids. This may explain why *D. busseolae* won when it parasitized the host 48 hrs before *X. stemmator* and vice versa. Each of the several mechanisms that have been identified as being involved in the elimination of the potential competitors appears to be specific to a particular period of immature development. Physical combat generally occurs early during the first instar stage, whereas physiological suppression is thought to occur either after the eclosion of the oldest embryo to the first instar (by a "toxic secretion") or late during larval development (by starvation or asphyxiation) (Mackauer, 1990). The oldest larva almost always survives in competition with a younger one, except when there is a substantial age difference. However, when there are only minor differences, in larval age, the outcome is indeterminate because developmental variations

may enable a chronologically younger larva to reach the "window" earlier and eliminate a chronologically older competitor (Mackauer, 1990). From the current study, it is logical to conclude that naive *X. stemmator* and *D. busseolae* lack the ability to discriminate between a *C. partellus* pupae parasitized by the other species and unparasitized pupae hence multiparasitized the host pupae. The study also indicates that when both parasitoid species multiparasitize, *X. stemmator* is competitively superior to *D. busseolae* except when *D. busseolae* parasitizes 48 hours before *X. stemmator*.

CHAPTER FOUR

4.0 HOST SEARCHING EFFICIENCY OF *XANTHOPIMPLA STEMMATOR* AND *DENTICHASMIAS BUSSEOLAE* FOR *CHILO PARTELLUS* PUPAE IN DIFFERENT PARTS OF MAIZE PLANT.

4.1 Introduction

Parasitoid reproductivity and survival depends mainly on their ability to locate their potential hosts. According to Vinson (1984), successful parasitoidism depends on host habitat location, host location, host acceptance, host suitability and host regulation. Female parasitoids have to search for hosts in different plants or in a varied plant habitat. There are many strategies that parasitoids use to locate their potential host most efficiently, and this depends on the type of cues provided by the host or its environment (Vinson 1984; Tumlinson *et al.*, 1993). Parasitoids may use olfactory, visual, and host vibrational-stimuli as cues to narrow the search for hosts (Vinson 1984). Successful parasitism of concealed pupae depends on the efficiency of the host location strategy employed, the morphology of the parasitoid and the physical characteristics of the substrate covering the host (Fischer *et al.*, 2003). Parasitoid wasps in the "drill-and-sting" guild pierce through the substrate with the ovipositor to reach their larval or pupal host while those in the "ingress-and-sting" guild have to get into the pupal or larval chamber (Smith *et al.*, 1993). The ability to detect and attack the hosts in different solid substrates is determined by the level of specialization that is reflected in behavioural and morphological adaptation. Coexistence of parasitoid populations of different species requires that some differences exist in niches between the species (Gause, 1934; Hardin, 1960). This study was undertaken to investigate whether there are differences in

searching efficiencies between *X. stemmator* and *D. busseolae* for pupae located in different parts of the host maize plant.

4.2. Materials and methods

4.2.1. Insects

Fifth instar Larvae of *C. partellus* reared as described in section 2.2 were given 8 cm long pieces of stem or cobs (one pupa per stem or cob) in a 1000cc plastic transparent jars, to tunnel and pupate. Maize stems were cut from the upper part of pre-tasselling maize and cobs were harvested at the soft dough stage. Imminent pupation was indicated by formation of moth emergence windows. Thereafter, the parts were observed daily against a strong light from 70Watts bulb to determine the presence of pupa. Two-day old borer pupae were used in this study. The study was carried out using 5-day old mated *D. busseolae* and 6-day old mated *X. stemmator* female parasitoids reared as described in section 2.2.

4.2.2. Bioassays

Searching efficiency for each parasitoid on both stems and cobs was conducted concurrently using 30 pupae for each. Prior to each test, the parasitoids were fed a 20% honey water solution and females were randomly selected from the colony. A stem or cob (for each respective part used) with a pupa was introduced into a cage and one of the actively searching females was carefully removed from the cage using a vial and was introduced in a 1000cc clear plastic jar placed upside down on a clean bench and allowed to settle for 5 minutes before the pupa in stem or cob was introduced into the 1000cc plastic jar. The stem or cob was supported on clay base to maintain it in upright position. The set up was observed for 20 minutes and if the parasitoid did not start searching, the

experiment was cancelled and another female parasitoid was used. If the parasitoid started searching, the following parameters were recorded: for *D. busseolae*, searching time, time taken to open the exit window and time taken while the parasitoid was inside the pupal chamber were determined using a stop watch and recorded; for *X. stemmator*, searching time, time taken from the onset of probing until the parasitoid left, and number of probes made were recorded. Parasitized pupae were removed by splitting the stems or removing the ear husks carefully. Each pupa was placed in a vial and incubated at 25±1°C, 50-60% RH 12:12 L: D photoperiod until emergence. Time (in days) taken from the date of parasitization to emergence, identity of the emergence, and progeny were recorded.

4.2.3. Data analysis

Data on foraging time, time taken opening the exit window, time taken inside the pupal chamber (for *D. busseolae*), foraging time, probing time and number of ovipositor insertions per substrate (for *X. stemmator*) were log transformed and then analysed using t-test. Data on the outcome of parasitization on different parts of maize plant was subjected to logistic regression analysis followed by chi-square to test for differences.

4.3. Results

4.3.1. Searching efficiency and parasitism behaviour by *D. busseolae* for pupae in stems and cobs of maize plant

Dentichasmias busseolae searched by walking up and down antennating the substrate until it reached a moth exit window. There was no significant difference in the foraging time between stems and cobs (P=0.3057; d.f. =58; t=1.03; Table 4.1). Being a parasitoid in the "ingress-and-sting" guild, *D. busseolae* accessed the pupal chamber by

opening the moth exit window using its mandibles. Since the experiment was done under laboratory conditions, some female *D. busseolae* attempted to open the ingress route used by the larva. However, access to the pupal chamber was not possible since the tunnel was already filled with frass from the larval activity. There was no significant difference between the time taken to open the exit window on stems and cobs (P=0.2097; d.f. =49; t=1.27; Table 4.1). There was a significant difference in time the parasitoid spent in the pupal chambers in stems and cobs and it was longer in the cobs than in the stems (P=0.02097; d.f.=58; t=2.25; Table 4.1). The development time of *D. busseolae* progeny from pupae from stems and cobs did not differ significantly (P=0.5172; d.f. =41; t=0.65; Table 4.1).

Table 4.1. Mean (±SE) foraging time (Sec.), time to open exit window (Sec.), time spent inside pupal chamber (Sec.) and developmental time (days) for *Dentichasmias busseolae* parasitizing *Chilo partellus* pupae in different parts of maize plant.

	stem		cob				
	n		n		Df	t-value	p
Foraging time	30	131.23±20.74	30	117.40±18.83	58	1.03	0.3057
Time opening exit window	30	257.33±56.60	30	120.77±35.20	49	1.27	0.2097
Time inside pupal chamber	30	94.37±22.98	30	229.87±65.28	58	2.25	0.02097
Developmental time	26	17.12±0.10	17	17.00±0.17	41	0.65	0.5172

4.3.2. Searching efficiency and parasitization behaviour by *X . stemmator* for pupae in maize stems and cobs

Xanthopimpla stemmator searched by walking up and down and antennating the substrate. On reaching a moth exit window it stopped and drilled with its ovipositor through or near the exit window. Time taken to search for hosts in both stems and cobs did not vary significantly (P=0.7921; d.f. =58; t=0.26; Table 4.2). On stems, probing was concentrated on or near the moth exit window while on cobs it was not specific. Though time taken probing on stems was slightly higher than on the cobs, there was no statistically significant difference (P=0.4028; d.f. =58; t=0.84; Table 4.2). The number of probes did not differ significantly between the two substrates (P=0.3163; d.f. =58; t=1.01; Table 4.2). Development time for *X. stemmator* progeny from pupae from stems and cobs did not differ significantly (P=0.40; d.f. =17; t=0.86; Table 4.2).

Table 4.2. Mean (±SE) foraging time (Sec.), probing time (Sec.), number of ovipositor insertions and developmental time (days) of *Xanthopimpla stemmator* parasitizing *Chilo partellus* pupae in different parts of maize plant.

	stem		cob				
	n		n		Df	t-value	P
Foraging time	30	43.20±7.39	30	39.90±6.77	58	0.26	0.7921
Probe time	30	443.00±78.74	30	272.77±43.91	58	0.84	0.4028
Ovipositor insertions	30	5.67±1.02	30	5.9±0.81	58	1.01	0.3163
Developmental time	18	19.78±0.21	1	19.00	17	0.86	0.4040

4.3.3. Parasitization efficiency for *X. stemmator* and *D. busseolae* on pupae in different parts of maize plant

Xanthopimpla stemmator searched and attacked pupae in both stems and cobs (Fig. 1). However, there was a highly significant difference since parasitism of pupae in cobs was only 3.33% as opposed to 56.67% in stems (χ^2=11.2946; d.f. =1; p=0.0008). *Dentichasmias busseolae* searched and attacked pupae in both stems and cobs (Fig. 1). However, the organ of maize plant in which pupae was found had some effect on the searching efficiency of *D. busseolae* or the mortality of the immature parasitoid since only 56.67% of pupae parasitized in cobs produced parasitoid as opposed to 86.67% in stems (χ^2=6.06; d.f. =1; p=0.0138).

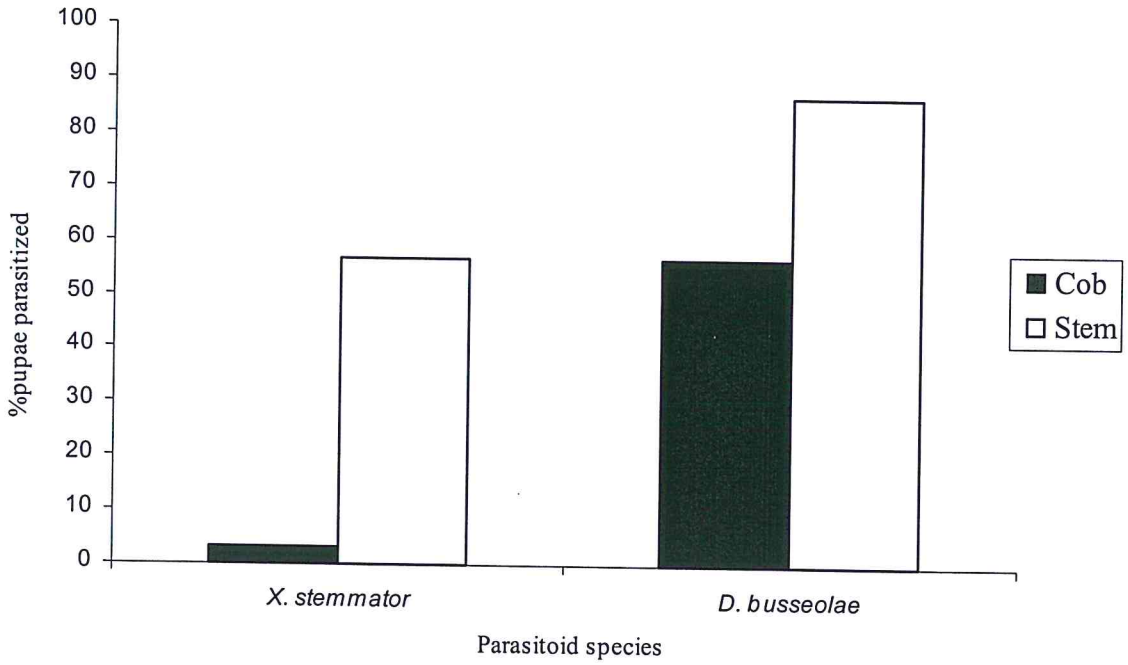

Figure 1: Percent pupae successfully parasitized by *X. stemmator* and *D. busseolae* in different organs of maize plant (n=30).

4.4. Discussion

Plants provide both olfactory and visual signals that are used as cues by foraging parasitoids and predaceous arthropods (Nordlund *et al.,* 1988; Dicke, 1994; Potting *et al.,* 1995). Not only do plants generally influence a parasitoid, but a female may be oriented to and search only parts of a plant (Varley, 1941). The present findings indicate that foraging for host by *D. busseolae* and *X. stemmator* does not depend on the part of maize plant the host pupae is located hence there was no significant difference in the foraging time by both parasitoids on both host plant parts.

Successful parasitism of concealed pupae depends on the efficiency of the host location strategy employed, the morphology of the parasitoid and the physical characteristics of the substrate covering the host (Fischer *et al.*, 2003). *Dentichasmias busseolae* in the drill-and-sting guild, (Smith *et al.,* 1993), has to get into the pupal chamber to parasitize its host. In the current study, *D. busseolae* opened and got into the pupal chamber where it parasitized *C. partellus* pupae. Moth exit window prepared by the last instar larva just before pupation is made of a thin epidermis. This may explain why there was no difference in the time taken to open the exit window in both stems and cobs. The difference in time spent inside the pupal chamber may be explained by the fact that some pupae in cobs were located deep within the cob pith (Muli, personal observation) while in the stems, *C. partellus* pupa is located about 12.9mm from the exit window (Mohyuddin, 1972).

According to Fischer *et al.* (2003), hymenopteran species in the drill and sting guild locate immobile hosts by vibrational sounding, i.e., echolation on solid substrate. Work by Fischer *et al.* (2003), showed that substrate density had a significant negative effect on the number of ovipositor insertions and the host location efficiency of *X. stemmator.* It is assumed that vibrational sounding is influenced by the physical properties of the substrate that supports the produced waves. Attenuation of vibration increases with distance and the density of the substrate (Dusenbery, 1992) and might be impaired in wet wood (Vilhelmsen *et al.*, 2001). This may explain why *X. stemmator* was more successful in parasitizing pupae in maize stems compared to the cobs with only one pupa from the cobs producing a parasitoid. This concurs with work by Hailemichael *et al.* (1994) and Moore and Kfir (1996) that *X. stemmator* parasitizes mainly lepidopteran pupae concealed in

stems of graminaceous plants such as maize, sugarcane or sorghum. Moreover, Muli (personal observation) found that *X. stemmator* often attacks pupae in maize stems through the moth exit window and most of the ovipositor drillings on the stems are on or near the soft exit window. This may explain why there was no significant difference in the number of ovipositor insertions between the stems and cobs despite their differences in hardness.

In the present study, there was no significant difference in the developmental time for progeny produced by both parasitoids from both plant parts. According to Barbosa *et al.* (1982), Duffey and Bloem (1986), and van Emden (1995), plant quality influences the suitability of herbivores as hosts or prey for natural enemies. Toxic allelochemicals occurring in plants are often sequestered in the herbivores' haemolymph and the presence of these chemicals can affect the development and survival of parasitoid progeny. This does not seem to be the case in the present study. The current study indicates that *D. busseolae* successfully searches for and attacks *C. partellus* host pupae in both stems and cobs as opposed to *X. stemmator* which is successful in attacking pupae in stems only. This indicates that there exists some difference in the extent of niches in which the two parasitoids, *X. stemmator* and *D. busseolae*, can successfully search for and attack *C. partellus* pupae.

CHAPTER FIVE

5.0. GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

5.1 General discussion and Conclusions

A compelling motivation for adoption of biological control is potentially a permanent return to ecological conditions similar to those seen before the arrival of the invasive pest and reduced ongoing expenditure for pesticides, labour, and specialised equipment (Hoddle, 2004).The most fundamental question in considering deliberate introductions of exotic species is whether the outcomes can be predicted precisely enough from the known causes to imagined effects to know with certainty that the benefits will outweigh the environmental costs (Louda and Stiling, 2004). In biological control, competition between species of introduced natural enemies or between introduced and native natural enemies of a pest has been used to explain why some species failed to either become established or to control the pest (Jalali *et al.*, 1988). To avoid competition and possible wastage of offspring, many species of hymenopterous parasitoids have developed the ability to discriminate between a parasitized and unparasitized hosts (Waage, 1986). If this ability is lacking, then the parasitoids are likely to exploit a common host resource and consequently, enter into some form of competition which might have negative impacts on the losing parasitoid species since the population dynamics of a given parasitoid species depends on its interaction with the others (Pijls *et al.*, 1995). However, the ability by the parasitoids to attack hosts depends on the efficiency of the parasitoid in locating the host (Fischer *et al.*, 2003) and this might determine the nature of interaction between any two species of parasitoids since co-existence of the parasitoids requires that some differences exist in niches they exploit

(Hardin, 1960). Gitau (2000) found that *X. stemmator*, a valued candidate in the classical biological control of the invasive Crambid stemborer, *C. partellus* successfully attacks and develops in all the major stemborers indigenous in eastern and southern Africa and hence, could be used as a biological control agent in eastern and southern Africa if it could co-exist with the major indigenous pupal parasitoids.

From the current study it can be concluded that:

(i) *Xanthopimpla stemmator* and *D. busseolae* lacked the ability to discriminate unparasitized from parasitized host pupae and therefore multiparasitized the host pupae;

(ii) in multiparasitized host, *X. stemmator* was competitively superior to *D. busseolae* only when time interval between ovipositions was short; and

(iii) although *X. stemmator* was competitively superior to *D. busseolae,* it could not attack pupae in maize cobs which can therefore act as refuge niche for *D. busseolae*. Consequently, there is a possibility that the two parasitoids can co-exist in nature. This adds weight to the work by Muturi *et al.* (2005) in that cobs can also act as a refuge niche for *P. furvus* which like *D. busseolae*, uses ingress and sting attack strategy (Smith et al., 1993). Given this possibility, if the parasitoid is released, the farmers will realise increased yields due to stem borer suppression. Reduced use of pesticides will translate to reduction in production costs and health problems associated with use of pesticides. In addition, shift from pesticide use, which impact negatively on insect fauna will be an added advantage to the ecosystem since ecological processes like pollination which depend on such insects will least be affected.

5.2. Recommendations

However, despite the findings above, this study recommends:

(i) a similar study using experienced females to confirm whether the parasitoids can discriminate between hetero-specifically parasitized host pupae and unparasitized pupae since host discrimination in some parasitoids is a learned behaviour and can improve with experience;

(ii) an interspecific competition study between *X. stemmator* and *D. busseolae* at different temperatures and humidities so as to have the right picture of the expected outcome of competition since factors such as host age and environmental temperature affect the outcome of interspecific competition, and

(iii) semi-field trials in screen houses are required to validate the authenticity of the current findings before initiating the parasitoid release programme.

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