EFFECT OF TEMPERATURE ON THE SYNCHRONY OF STEM BORER PESTS AND THEIR ASSOCIATED LARVAL PARASITOIDS

BY

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DECLARATION

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

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Signature…….. Date…….

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We confirm that the work reported in this thesis was carried out by the candidate under our supervision and has been submitted with our approval as supervisors

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DEDICATION

This thesis is dedicated to my father Morogo Sambai and my late mother Jane Sambai for their love, support and encouragements throughout my work. I also dedicate it to my wife Rose and son Curtis who had to abide with the profound time load of this work.

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ABSTRACT

This study was undertaken to establish the effect of temperature on the development and survival of *B. fusca*, *S. calamistis* and *C. partellus* and their larval parasitoids The stem borers and the larval parasitoids were reared at 20^0C, 25^0C, 28^0C and 30^0C and their development time, survival, fecundity and longevity were recorded. These parameters were subjected to analysis of variance (ANOVA) in General Linear Model (GLM). Results showed that development of stem borer larvae varied among different temperature regimes ($F_{3,367}$=105.3; P<0.0001), *B. fusca* ($F_{3,451}$=66.43; P<0.0001), *S. calamistis*($F_{3,540}$=887.8; P<0.0001).*C. partellus*. Development time of *B. fusca* larvae decreased with increase in temperature with the longest and shortest time recorded at 20^0C (78.30 days) and 30^0C (36.8 days) respectively. In *S. calamistis* larvae, the development time reduced with increase in temperature with mean larval duration ranging between 34.6 days (30^0C) to 48.1 days (20^0C). In *C. partellus* there was a decrease in larval development time (days) as the temperature increased. The longest development time, 57.4 days, was observed at 20^0C while the shortest, 22.2 days, was recorded at 30^0C. There was a significant influence of temperature on the development of *C. sesamiae* Kitale ($F_{3,139}$=125.6; P<0.001), *C. Sesamiae* Mombasa ($F_{3,148}$=246.1; P<0.001) and *C. flavipes* ($F_{3,187}$=719.7; P<0.001). Among *C. sesamiae* Kitale, mean total development time ranged between 17.8 days (28^0C) to 29.7 days (20^0C), while among *C. sesamiae* Mombasa, the highest and lowest mean total development time varied between 29.4 days (20^0C) and 17.0 days (28^0C) respectively. In *C. flavipes*, mean total development time varied between 15.0 days (30^0C) and 31.4 days (20^0C). Temperature affected the host-parasitoid synchrony between stem borers and their associated larval parasitoids as reflected in the variations in respective life table parameters. Biological control of *B. fusca*, *S. calamistis* and *C. partellus* is likely to be affected by changes in temperature. Due to the increased development rate and survival of the stem borers coupled with reduced survival rates of the parasitoids associated with increase in temperature, biological control is likely to be less effective in areas with higher temperatures ranging between 25^0C to 28^0C.

CHAPTER ONE

INTRODUCTION

1.1. Background information

Lepidopteran stem borers are the most important insect pests that attack maize, sorghum and sugarcane in many areas of Africa (Harris, 1962; Polaszek, 1998 Overholt *et al.*, 2001; Kfir *et al*., 2002). The important species in Eastern and Southern Africa include *Chilo partellus* (Swinhoe), *Busseola fusca* Fuller, *Chilo sacchariphagus* (Bojer), *Sesamia calamistis* Hampson, *Sesamia cretica* Lederer, *Eldana saccharina* (Walker) and *Chilo orichalcociliellus* (Strand) (Seshu Reddy, 1983; Zhou *et al*., 2001a; Overholt *et al.*, 2001). With the exception of *C. partellus*, which was accidentally introduced in Africa from Asia around 1930 (Kfir, 1992), the other species are indigenous to the African continent. Due to their destructive nature and yield losses associated with their infestation, stem borers have been extensively researched (Calatayud *et al*., 2006). Distribution and importance of these pests vary among regions depending on their respective ecological requirements (LeRu *et al.,* 2006). In Kenya, important pests include *B. fusca*, *S. calamistis* and *C. partellus*. The indigenous *B. fusca* is reportedly restricted to mid and high altitude zones above 600m and up to 2600m (Ong'amo *et al.,* 2006). This pest has extended its distribution range from the initial point of concentration to most of the maize growing regions at altitudes below 1500m and occasionally higher (Overholt *et al.*, 1994; Zhou *et al.*, 2001; Songa *et al.*, 2002). The exotic *C. partellus* is the most damaging in lowland areas, the regions characterized with low maize yields (Songa *et al*., 2001) while indigenous *S. calamistis*, is of moderate importance and remains a minor pest.

Due to their importance, different management practices have been initiated to control the cereal stem borers. Some of the management practices initiated include, biological control, intercropping maize with some legumes to reduce pest densities in cropping system (Songa *et al*., 2001), use of synthetic sex pheromones to trap male adult moths (Van Rensburg *et al*., 1985), chemical control and growing of resistant varieties among others.

Braconid larval parasitoids, *Cotesia flavipes* and *Cotesia sesamiae* have been used in biological control of *C. partellus* and *B. fusca* respectively (Overholt *et al.*, 1997; Kipkoech *et al.*, 2008). *Cotesia flavipes* and *C. sesamiae* were present in areas where their appropriate host(s) dominated and where the temperature was favorable (Mailafiya *et al.,* 2009).

The biological controls depend largely on the synchrony of the development, growth and population dynamics of the host and parasitoid population. Adult *Cotesia flavipes* parasitizes *C. partellus* while *Cotesia sesamiae* parasitizes *S. calamistis* and *B. fusca* by laying eggs in the larvae of their respective hosts. Temperature, humidity, photoperiod, availability of plant hosts to pests and availability of insect hosts for parasitoids determine host-parasitoid synchrony as it has a direct influence on insect survival, development and reproduction. Development rate, survival and fecundity as well as population growth rate of the parasitoids must be in synchrony with those of its hosts in order for the biological control to be effective. Temperature increase associated with climate change (Levitus *et al*., 2001) is thus likely to affect this host-parasitoid synchrony.

1.2. Statement of the problem and justification

Changes in environmental conditions especially temperature, affects the ecology, physiology and behavior of insect pests (Bale *et al.*, 2002; Karuppaiah and Sujayanad, 2012). Temperature reportedly influences development by inducing physiological stress and thus affects metabolic rate. Thus, the projected increase in temperature associated with climate change is expected to have a differential influence on the development of the parasitoids and their hosts. If the parasitoids develop faster in high temperatures than its specific host, it may lead to asynchrony in the development times, distribution and voltinism (Godfray 1994; Hance *et al.*, 2007). Studies on the influence of temperature on development, fecundity and longevity of stem borers (Mbapila *et al*., 2002; Khadioli *et al*., 2014) and parasitoids (Mbapila and Overholt, 2001; Jiang *et al*., 2004,) have been undertaken independently. The projected increase in temperature may affect host-parasitoid synchrony between stem borers and associated natural enemies. However, no study has been done to validate this assertion. It is therefore important to investigate how the host-parasitoid synchrony between stem borer pests and their associated parasitoids will be affected by the projected increase in temperature and establish its implication on biological control.

1.3. Hypothesis

Changes in temperature will affect the development and survival of stem borer pests and their associated larval parasitoids and the resultant host-parasitoid synchrony between stem borers and associated parasitoids.

1.4. Objectives of the study

1.4.1. Broad Objective

Assess the effect of temperature on development, survival and host-parasitoid synchrony of stem borer pests and their associated larval parasitoids.

1.4. 2. Specific Objectives

i). To determine the effect of temperature on the development and survival of *B. fusca*, *S. calamistis* and *C. partellus* larvae.

ii). To determine the effect of temperature on development, survival and longevity of *Cotesia sesamiae* and *Cotesia flavipes*

iii). To determine the effect of temperature on the host-parasitoid synchrony between stem borers and their associated larval parasitoids.

CHAPTER TWO

LITERATURE REVIEW

2.1. The biology of stem borers

The most important lepidopteran stem borers in Kenya are *Busseola fusca* (Fuller), *Chilo partellus* (Swinhoe) and *Sesamia calamistis* Hampson (Overholt *et al.*, 2001). Larvae of these moths bore into the stalk of sorghum and maize. Their pest status is defined by their distribution, abundance and level of crop destruction caused

2.1.1. Distribution, yield losses and life cycle of *Busseola fusca*

Busseola fusca (Fuller) is distributed widely throughout sub-Saharan Africa. Populations in Eastern and Southern Africa appear to be adapted to different environments from those in West Africa. In Eastern and Southern Africa, *B. fusca* is restricted to mid and high altitude zones above 600m whereas in West Africa, the same species is found at all elevations, but is most abundant in the drier savanna zone (Overholt *et al.*, 2001). In the mid and high elevation regions of Eastern and Southern Africa, *B. fusca* are frequently the most serious stem borer of maize. Yield losses have been estimated to be about 12% for every 10% of plants infested (Harris and Nwanze, 1992). *Busseola fusca* occasionally caused yield losses of 30-50% in Burundi. In Cameroon the reported grain weight loss as 4.6g per stem borer in lowland fields and 8.7g per stem borer in highland fields (Cardwell *et al*., 1997).

The female lays several hundred eggs in batches of 30-50, inserted between the sheath and the stem. Incubation lasts about 1 week, the larvae forage on the young blades of the leaf whorl after hatching and then, suspended from silk strands, spread to neighboring plants. They penetrate the stems by boring through the whorl base. Generally, they

destroy the growing point and tunnel downward. After passing through six to eight stages in 30 -45 days, they chew an outlet for the adult to emerge from and then pupate in the tunnel. Pupation takes 10-20 days (Overholt *et al.*, 2001).

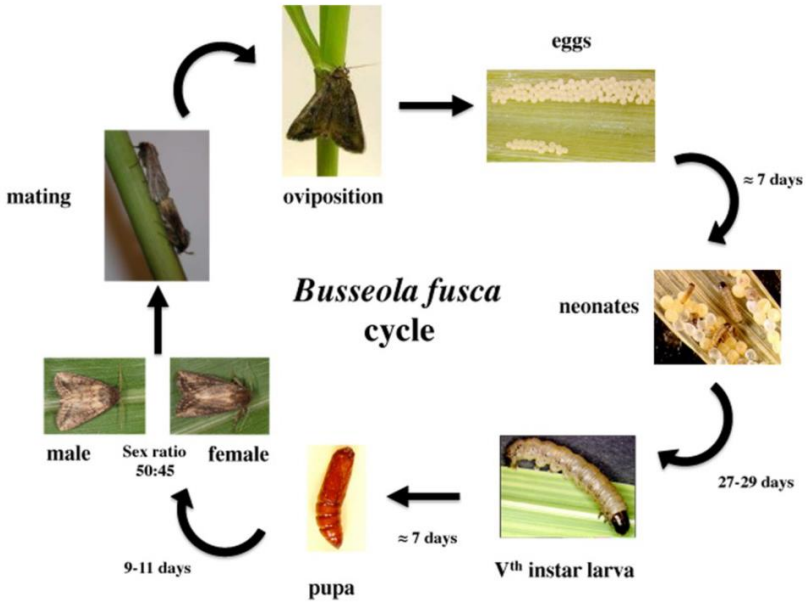

Plate 1. Life cycle of *Busseola fusca* © *Stem borer team icipe*

2.1.2. Distribution, yield losses and life cycle of *Chilo partellus*

Chilo partellus (Swinhoe) is an exotic stem borer species that originated from Asia where it is a pest of sorghum and maize (Zhou *et al.*, 2001). First reports of *C. partellus* in Africa are in Malawi in 1930 and has since extended to other countries in Eastern and Southern Africa (Overholt *et al.*, 2001) including Ethiopia, Malawi, South Africa, Mozambique, Somalia, Uganda, Tanzania, Sudan (CAB 1977) Zimbabwe, Swaziland, Botswana (Sithole, 1990). In Kenya, the first reports were around the early 1950s (Nye, 1960). It has extended to most of the maize growing areas of Kenya at altitudes below 1500m and sometimes higher (Overholt *et al.*, 1994a; Zhou *et al.*, 2001; Ong'amo *et al.*,

2006). It is the most abundant and widely distributed stem borer species and most damaging, mainly in the warmer low-lying areas. In some locations, the exotic stem borer may be displacing native stem borer species (Ofamata *et al.*, 2003). Yield losses in maize of 18% were attributed to *C. partellus* and *C. orichalcocillielus* in the Southern coast of Kenya (Warui and Kuria, 1983) and 50% in Southern Mozambique (Sithole, 1990).

Adults emerge from pupae in the late afternoon and early evening and are active at night. During the day they rest on plants or plant debris. Females mate soon after emergence and oviposit on two to three subsequent nights, in batches of 10-80 overlapping eggs, on the upper and underside of leaves, mainly near the midribs. Some eggs are also laid on the stem. Adults live for about 2-5 days and do not normally disperse from emergence sites. Eggs hatch in the early morning (0600-0800h) 4-8 days after being laid and young larvae ascend plants to enter the leaf whorls, where they start to feed. Older larvae tunnel into stem tissue, and after feeding for 2-3 weeks, pupate in the stems for 5-12 days. Under favorable conditions, the life cycle is completed in 25-50 days, and five or more successive generations may develop during a single maize growing season (Overholt *et al.*, 2001).

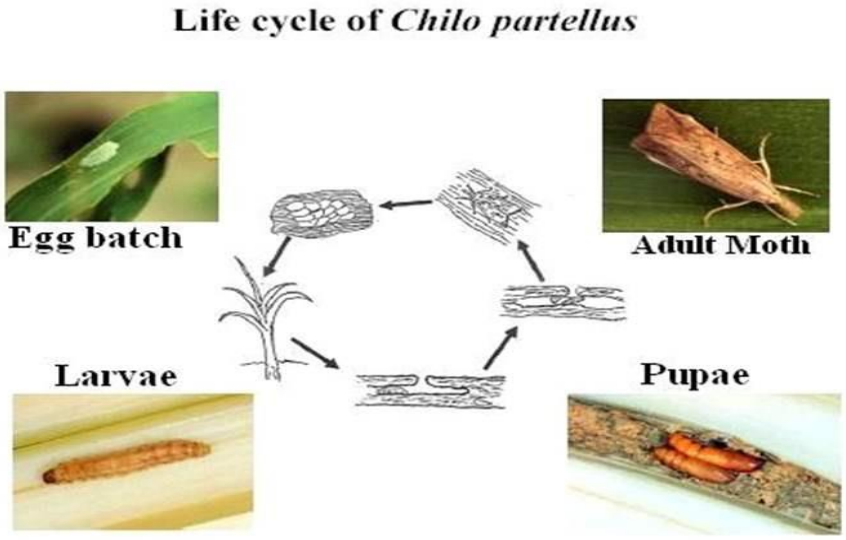

Plate 2. Life cycle of *Chilo partellus* © Stem borer team icipe

2.1.3. Distribution, yield losses and life cycle of *Sesamia calamistis*

Sesamia calamistis Hampson is a native stem borer of most of tropical Africa. In Central and West Africa it's the most common species with densities up to 3-4 larvae per stem which is much higher than most borers in East and South Eastern Africa. In Eastern and Southern Africa, *S. calamistis* is of only moderate importance and though it is widely distributed, densities are typically low (Overholt *et al.*, 2001). *Sesamia calamistis* is considered to be a very damaging borer in West Africa (Bosque-perez and Schulthess, 1998).

In 3-5 days, the female lays up to 350 eggs, deposited in batches of 10-40. The eggs are arranged in two to four contiguous rows and inserted between the lower leaf sheaths and stems. Several hours after hatching, the larvae leave the oviposition site to penetrate the stems either directly or after feeding on the leaf sheath. During the larval stage, which lasts 30-60 days, depending on the climatic conditions, and usually involves five to six

moults, larvae may successively attack a number of young stems. Only one immature larva is observed per young stem or tiller. Pupation generally takes place in the stem, rarely between the sheath and the stem. The pupal period lasts 10-12 days at 25°C. Under tropical conditions five to six generations are completed in a year. *Sesamia calamistis* breeds throughout the year without diapause (Overholt *et al*., 2001).

Plate 3. Larva, pupa and adult *Sesamia calamistis* ©stem borer team icipe

2.2. Stem borer parasitoids

Parasitoids have been introduced to control the stem borers in Kenya. The parasitoids target a specific life stage of the stem borer. *Cotesia flavipes*, an exotic larval endoparasitoid was introduced to control its host *Chilo partellus*. *Busseola fusca* and *Sesamia calamistis* are controlled by *Cotesia sesamiae* which is indigenous to sub-Saharan Africa

2.2.1. *Cotesia sesamiae*

Cotesia sesamiae (Cameron) (Hymenoptera: Braconidae) is a widespread endoparasitoid of B. *fusca* and *S. calamistis* in sub-Saharan Africa. *Cotesia sesamiae* are infected with bacterial symbionts in the genus Wolbachia, which are responsible for reproductive isolation. *Cotesia sesamiae* exists as two biotypes in Kenya. The western biotype completes development in *B. fusca* larvae but the coastal *C. sesamiae* does not complete development in *B. fusca* since its eggs are encapsulated (Mochiah *et al*., 2001). Both biotypes develop successfully in the larvae of *S. calamistis* (Branca *et al*., 2011). Parasitoids have developed a wide array of adaptations to deal with host immunity. Injection of Poly DNA viruses (PDV) is one of them. The viruses are injected into the host along with the parasitoid eggs and are expressed in different tissues and are responsible for host immune suppression (Glatz *et al*., 2004). The difference in virulence between the two biotypes of *C. sesamiae* may perhaps be due to infection by a PolyDNA virus since the injection of virulent wasp calyx fluid in avirulent –wasp-infected host restores parasitoid development (Mochiah *et al*., 2002).

A polydnavirus, *CrV1*, contributes to the suppression of host immunity in *Cotesia* genus parasitoids. In Kenya, the geographic distribution of *CrV1* alleles in *C. sesamiae* was

related to relative abundance of *B. fusca*. The PDV genes evolve through natural selection and are genetically linked to factors of suppression of local host resistance (Dupas *et al*., 2008).

Plate 4. *Cotesia sesamiae* (a) larvae emerging form host to form cocoons (b) Adult (c) cocoons formed outside the host.

2.2.2 *Cotesia flavipes*

Cotesia flavipes (Cameron) (Hymenoptera: Braconidae) is a gregarious endoparasitoid of cereal stem borers. *Cotesia flavipes* has an initial egg load of around 150 eggs and about 40 eggs are laid in each host. The life cycle of *C. flavipes* lasts approximately 22 days, and approximately 40 parasitoids develop in each host larva. Development proceeds through three larval instars in the host's body, and then emerges from the host by biting through the integument. The egg/larval period last about14 days at 25°C. After emergence from the host, the last instar larvae spin cocoons and then pupate. In nature, the cocoons are found inside the host feeding tunnels in cereals. Pupation takes about six days at 25°C, after which adults emerge. The adults are approximately 3 to 4 mm in length. The sexes can be differentiated by their antennae, the antennae of the males is about twice the length of the antennae of the females (Smith Jr *et al*., 1993). Adult lifespan of *C. flavipes* is approximately 35 hours at 25°C if adults are not fed. Provision

of a 20% honey/water solution prolongs the lifespan to about 51 hours. Owing to the short lifespan, *C. flavipes* must quickly mate after emergence and begin searching for hosts. As with many species of Hymenoptera, *C. flavipes* has a haploid-diploid sex determination system. Fertilized eggs develop into females (diploid) while unfertilized eggs develop into males (haploid). Unmated females will thus produce only male offspring. Mated females produce both male and female offspring. Frass produced by the larvae is important in the short range location of the host by *C. flavipes* (Van Leerdam *et al*., 1985; Ngi-song and Overholt, 1997) Stem borer-infested plants have been found to be more attractive to *C. flavipes* females than uninfested plants (Obonyo *et al*, 2008).

Plate 5. *Cotesia flavipes* parasitizing *Chilo partellus* © stem borer team icipe

2.3. Insect phenology

An insect's operative temperature is a range within which most of its physiological activities function optimally. This is represented as the difference between the critical thermal minimum and maximum of a temperature-dependent performance across which a particular level of performance can be measured (Tezze and Botto, 2004). Temperature

has a strong and direct influence on insect development, reproduction and survival (Andrewartha and Birch 1954). Temperature is a key abiotic factor that regulates insect population dynamics, developmental rates, and seasonal occurrence. Changes in temperature would present a challenge to parasitoid species and important impacts are expected in trophic interactions (Hance *et al*., 2007). For example, Tezze and Botto (2004) observed that temperature changes affect the immune system and host resistance among *Trichogramma sp.* Elevated temperatures will thus increase the likelihood of a host to kill its parasitoid by increasing the capacity of hosts to defend themselves against immature parasitoids. Such changes in host-parasite interactions are likely to result in mixed outcome for biological control programs which primarily rely on natural antagonist to control pests. Changes in temperature are also likely to result in a decrease in parasitization success but may also open new possibilities which are yet to be interpreted and thus deserve attention (Tezze and Botto, 2004). A careful analysis on how host-parasitoid systems react to changes in temperature is therefore needed in order to predict and manage the consequences of global change at the ecosystem level.

CHAPTER THREE

MATERIALS AND METHODS

3.1. Rearing insects

This study involved both stem borers *B. fusca*, *S. calamistis* and *C. partellus* and parasitoids *C. flavipes* and *C. sesamiae*. Cultures of stem borers and parasitoids were obtained from established colonies at Animal Rearing and Containment Unit (ARCU) at *Icipe*. The colony of *B. fusca*, *S. calamistis* and *C. partellus*, originated from field-collected individuals from Machakos in 2012. Feral individuals are usually added into colonies after every six months to maintain respective species genetic diversity. Stem borer larvae were reared on artificial diet (Ochieng, 1985). The artificial diet is made using maize leaf powder, bean powder, brewer's yeast, distilled water, sucrose, agar, vitamin E acetate and formaldehyde. The ingredients in powder form, which is maize leaf powder, bean powder and brewer's yeast, are mixed together. Agar is boiled in distilled water until it dissolves completely. The molten agar is then added to the powdery mixture and stirred until uniform viscosity is achieved. Chloramphenicol and 10% formaldehyde are then added to prevent bacteria and fungi growing in the diet. The viscous mixture is then dispensed into glass vials when still hot. The diet solidifies in the vials as it cools down. Stem borer larvae can then be reared on this diet.

Parasitoids were maintained in their respective hosts. *Cotesia flavipes* colony was maintained on *C. partellus* while *C. sesamiae* was maintained on *B. fusca* and *S. calamistis* according to methods described by Overholt *et al*. (1994). The stem borers at larval stage four are exposed to respective parasitoids and the parasitized larvae reared in

artificial diet until cocoons emerge from them. The cocoons are then removed from the diet and kept in clean vials until adult parasitoids emerge.

3.2. Effects of temperature on stem borer development and survival

The stem borers were reared in incubators (Sanyo MLR 350) maintained at temperatures 20, 25, 28 and 30^0C, relative humidity between 60-70% and a photoperiod of 12L12D. For each of the temperatures, two hundred (200) neonates of *B. fusca*, *S. calamistis* and *C. partellus* were transferred individually to glass vials containing artificial diet (Plate 6) and reared until adult insects emerged. Larval and pupal development time, mortality and longevity of adults were recorded daily.

Artificial diet in vials

Artificial diet with stem borers

Plate 6: Artificial diet used in rearing stem borers

3.2.2. Effects of temperature on parasitoids

Cotesia flavipes and *Cotesia sesamiae* were reared at four temperatures 20, 25, 28, and 30^0C. *Cotesia flavipes* was reared in *Chilo partellus* while *Cotesia sesamiae* was reared in S. *calamistis* and *B. fusca*. At larval stage four (L4), stem borer larvae were removed

from artificial diet and fed for 24 hours on pieces of maize stem. This allowed them to develop frass that attracted parasitoids before exposure to the corresponding parasitoids.

During parasitization, stem borer larvae (*B. fusca*, *S. calamistis* and *C. partellus*) were exposed to 24 hour-old mated parasitoid females using the hand-stinging method (Plate 7); only one stinging was allowed per larva. *Busseola fusca* was exposed to *C. sesamiae* Kitale, *S. calamistis* was exposed to *C. sesamiae* Mombasa and *C. partellus* was exposed to *C. flavipes.*

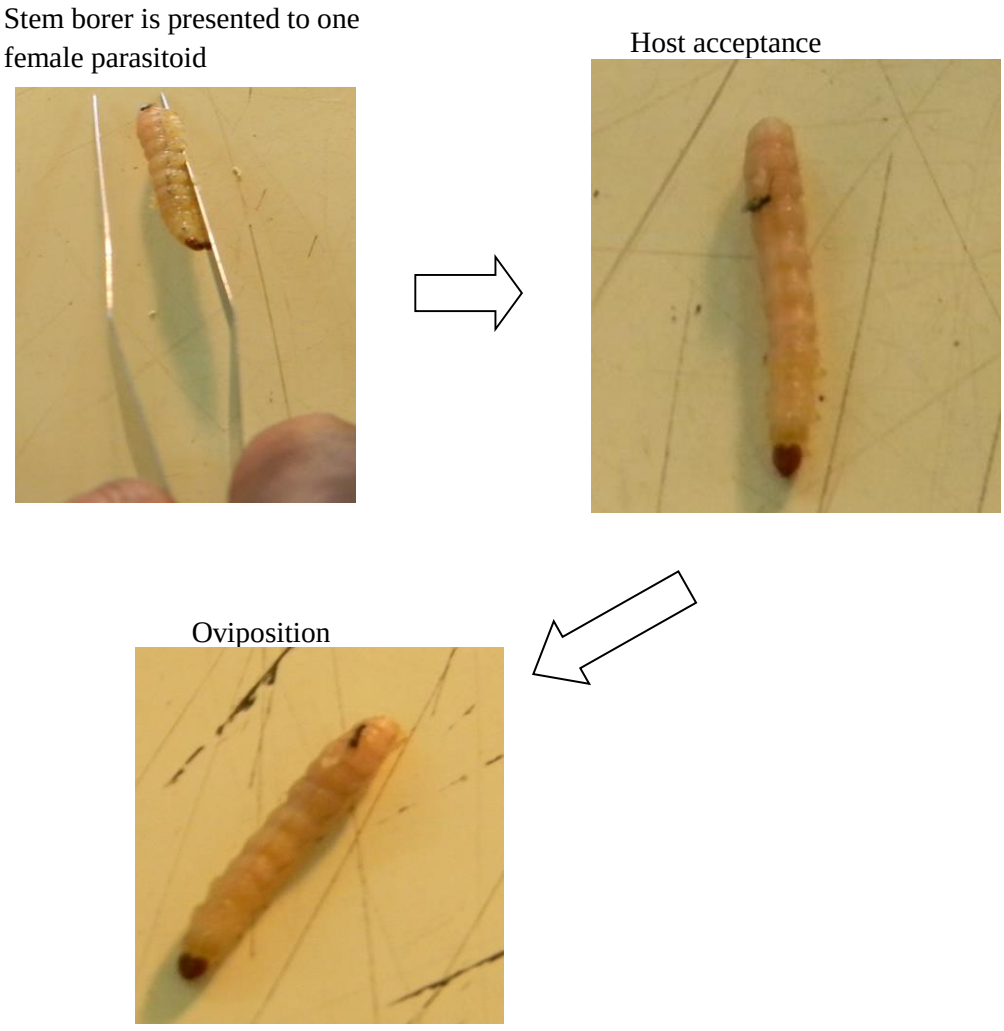

Plate 7. Hand stinging method

In each of the four constant temperatures, 80 of each of the stem borer species (*B. fusca*, *S. calamistis* and *C. partellus*) were reared. Of the 80 larvae reared, 60 larvae each of *C. partellus*, *S. calamistis* and *B. fusca* were parasitized and 20 of each of the stem borer species were left non-parasitized to act as a control. Parasitized and non-parasitized stem borer larvae were thereafter placed individually in glass vials containing artificial diet, and plugged with cotton wool (Plate 6). The 60 parasitized larvae were used to assess larval development by recording larval fate, date of cocoon formation, dead parasitoids (not forming cocoons), cocoon emergence dates, sex ratio, dead adults inside cocoon mass, egg load, and dead parasitoid larvae inside the host were all recorded. Parasitoid survival, calculated as a percentage of parasitoid adults emerging from parasitized stem borers, was estimated for *C. flavipes* and *C. sesamiae* (*C. partellus* for *C. flavipes*, *B. fusca* and *S. calamistis* for *C. sesamiae).*

Plate 8. *Cotesia sesamiae* cocoons forming outside the body of its host *Busseola fusca*.

3.2 Data management and statistical analysis

All data was tested for normality using Shapiro Wilk *W*-test. Development time and survival data failed normality test. Development time data were log transformed and survival data were arcsine transformed. Data on development time, survival, fecundity and sex ratio were subjected to analysis of variance (ANOVA) using the general linear model (GLM) in R. Means were separated using the Student-Newman-Keul's test were ANOVA was significant.

In analyzing development times, individuals who did not complete a specific life stage were excluded in development analysis of that specific life stage. In sex ratio analysis, only hosts that produced mixed sex adults were included in the analysis. Insect Life Cycle Modeling (ILCYM) software was used to calculate the following life table parameters for both the stem borers and parasitoids; Generation Time (T), Net Reproductive Rate (Ro), Intrinsic rate of Increase (r_m) and Finite rate of Increase (λ) at the different temperature regimes.

CHAPTER FOUR

RESULTS

4.1. Effect of temperature on stem borer development

There was variation in development time of *B. fusca* larvae under different temperature regimes ($F_{3,367}$=105.3; P<0.001; Table 1a). Larval development time decreased with increase in temperature with the longest (78.3 days), and the shortest (36.8 days) larval development time recorded at 20 and 30^0C respectively (Table 1a). Variations were also observed in pupal development time at different temperature regimes ($F_{3,290}$=420.99; P<0.001;Table 1b). There was reduced pupal development time with increase in temperature with duration ranging between 13.9 days (28^0C) and 41.9 days (20^0C). Mean pupal development time of 15.3 days was recorded at 30^0C, while 13.9 days was recorded at 28^0C. Temperature significantly affected longevity of *B. fusca* adults ($F_{3,\ 273}$=86.3; P<0.001; Table 1c). Longevity of *B. fusca* adults decreased with increase in temperature with mean longevity ranging between 4.2days at30^0C and 9.1 days at 20^0C.

Results show differences larval development time of *S. calamistis* ($F_{3,420}$=66.43; P<0.001; Table 1a). Larval development time reduced with increase in temperature with mean larval duration ranging from 34.6 days (30^0C) to 48.1 days (20^0C). Variations were also observed among the pupae ($F_{3,420}$; P<0.001; Table 1b). Mean pupal development times ranged between 10.0 days (30^0C) to 18.5 days (20^0C). Mean longevity varied at different temperature regimes ($F_{3,\ 387}$=41.15; P<0.001; Table 1c) with highest (9.1 days) and lowest (7.0 days) mean longevity recorded at 25 and 28^0C respectively. Increase in temperature increased the longevity of *S. calamistis* to an optimum at 25^0C then decreased with further increase in temperature.

Study shows variation in time taken by *C. partellus* larvae to complete development under different temperature regimes ($F_{3,540}$=887.80; P<0.001). In general, there was a decrease in larval development time (days) as the temperature increased with longest (57.4 days) and shortest (22.2 days) larval durations recorded at 20^0C and 30^0C respectively (Table 1a). Temperature significantly affected the time taken by pupae to complete development ($F_{3,506}$=436.40; P<0.001; Table 1b). Pupal development time decreased with increase in temperature with mean pupal duration ranging from 6.9 days (30^0C) to 16.7 days (20^0C). Longevity of *C. partellus* adults was significantly affected by temperature ($F_{3,433}$=31.74; P<0.001; Table 1c). Mean adult longevity ranged between 7.3 days (30^0C) and 10.2 days (20^0C).

Table 1: Effect of temperature on mean development ($\bar{x} \pm SE$) of *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus*.

Temperature	*Busseola fusca*	*Sesamia calamistis*	*Chilo partellus*
(a) Larval duration (days)			
20˚C	78.3 ± 1.03d	48.1 ± 0.93c	57.4 ± 1.11d
25˚C	48.9 ± 1.03c	46.0 ± 0.57c	33.2 ± 0.45c
28˚C	41.3 ± 0.69b	38.4 ± 0.89b	24.3 ± 0.28b
30˚C	36.8 ± 0.99a	34.6 ± 0.61a	22.2 ± 0.27a
F	105.34	66.43	887.8
df	3, 367	3, 451	3, 540
P	<0.0001	<0.0001	<0.0001
(b) Pupal duration (days)			
20˚C	41.9 ± 1.09c	18.5 ± 0.16d	16.7 ± 0.37c
25˚C	14.79± 0.21b	13.9 ± 0.23c	9.3 ± 0.14b
28˚C	13.9 ± 0.23a	10.9 ± 0.13b	9.1 ± 0.16b
30˚C	15.3 ± 0.49b	10.0 0.15a	6.9 ± 0.08a
F	420.99	503.03	436.4
df	3, 290	3, 420	3, 506
P	<0.0001	0.0001	<0.0001
(c) Longevity (days)			
20˚C	9.1 ± 0.45c	8.6 ± 0.17b	10.2 ± 0.44b
25˚C	8.7 ± 0.30c	9.1 ± 0.19b	9.8 ± 0.31b
28˚C	7.1 ± 0.15b	7.0 ± 0.18a	9.7 ± 0.18b
30˚C	4.2 ± 0.16a	7.4 ± 0.20a	7.3 ± 0.15a
F	86.3	41.15	31.74
df	3, 273	3, 387	3, 433
P	<0.0001	<0.0001	<0.0001

*****Means followed by the same lowercase letter are not significantly different (Student Newman Keuls test, $\alpha = 0.05$)

4.1.1. Effect of temperature on survival of *B. fusca, S. calamistis* and *C. partellus* larvae and pupae.

Survival of *B. fusca* larvae increased from 31.0% at 20^0C to 93.5% at 28^0C, and decreased to 58.5% at 30^0C (Table 2). Generally, survival of *B. fusca* pupae varied with increase in temperature with a highest (98.9%), and lowest (55.6%) pupal survival recorded at 28 and 30^0C respectively.

The highest larval survival (65.5%) of *S. calamistis* was recorded at 28^0C while the lowest survival (51.0%) was recorded at 30^0C. Survival of *S. calamistis* pupae increased between 82.2 and 97.7% at 20^0C and 25^0C respectively. This was followed by a decrease to 88.2% at 30^0C.

Survival of *C. partellus* larvae increased with increase in temperature between 20^0C (51.5 and 89.0% at 20 and 28^0C respectively and decreased to 81.5% at 30^0C. Survival of *C. partellus* pupae increased with increase in temperature. The highest pupal survival was 96.9% (30^0C) and the lowest pupal survival was 80.6% (20^0C).

Table 2: Effect of temperature on survival (%) of *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus*.

Temperature	*Busseola fusca*		*Sesamia calamistis*		*Chilo partellus*	
	Larva	Pupa	Larva	Pupa	Larva	Pupa
20˚C	31.0	80.6	53.5	82.2	51.5	80.6
25˚C	87.5	67.4	64.5	97.7	85.0	82.4
28˚C	93.5	98.9	65.5	92.4	89.0	93.3
30˚C	58.5	55.6	51.0	88.2	81.5	96.9

4.2. Effect of temperature on development of *C. sesamiae* Kitale, *C. sesamiae* Mombasa and *C. flavipes*

There was variation in time taken between oviposition and cocoon formation for both *C. sesamiae* and *C. flavipes*. Statistical results reveals that temperature affects time taken between oviposition and cocoon formation of *C. sesamiae* Kitale ($F_{3,139}$=125.6; P<0.001;Table 3a). The time taken from oviposition to cocoon formation decreased with increase in temperature. This trend however, was not same for all the temperature regimes tested as a mean of 11.9 days was recorded at 30˚C which is higher than 11.6 days recorded at 28˚C. Similarly, temperature had an effect on time taken by *C. sesamiae* Mombasa from oviposition to cocoon formation ($F_{3,148}$=143.8; P<0.001; Table 3a). There was a general decrease in time taken from oviposition to cocoon formation with increase in temperature. However, this was not true for all the temperature regimes as a mean duration from egg to cocoon formation of 12.1 days was recorded at 30^0C, which is higher than 10.4 days recorded at 28^0C. Like the two *C. sesamiae* populations tested, there were differences in the time taken by *C. flavipes* from oviposition to cocoon formation ($F_{3,187}$=601.9; P<0.001; Table 3a). There was a general decrease in the time taken from oviposition to cocoon formation. The longest mean duration of oviposition to cocoon formation for *C. flavipes* was 21.4 days (20^0C) and the shortest duration was 8.8 days recorded at 30^0C.

Temperature significantly affected development of *C. sesamiae* Kitale ($F_{3,139}$=125.6; P<0.001; Table 3b) with mean development time reducing with increase in temperature. However, this was not true for all the temperature regimes as a mean total development time of 18.3 days was recorded at 30^0C which was longer than 17.8 days recorded at 28^0C. Similarly, temperature significantly affected development time of *C. sesamiae*

Mombasa ($F_{3,148}$=246.1; P<0.001; Table 3b). Generally, development time decreased with increase in temperature with highest and lowest mean total development time estimated as 29.4 days (20^0C) and 17.0 days (28^0C) respectively. Like the *C. sesamiae* populations tested, development time of *C. flavipes* varied at different temperature regimes ($F_{3,187}$=719.7; P<0.001; Table 3b). Generally, *C. flavipes'* total development time reduced with increase in temperature with mean total development time ranging between 15.0 days (30^0C) and 31.4 days (20^0C).

Table 3: Effect of temperature on mean development ($\bar{x} \pm SE$) of *Cotesia sesamiae* Kitale, *Cotesia sesamiae* Mombasa and *Cotesia flavipes*.

(a) Development time (egg-Cocoon)	Temperature	*C. sesamiae* Kitale	*C. sesamiae* Mombasa	*C. flavipes*
	20˚C	20.7± 0.35c	20.1 ± 0.32d	21.4 ± 0.26d
	25˚C	13.0± 0.20b	13.6 ± 0.35c	14.0 ± 0.22c
	28˚C	11.6± 0.32a	10.4 ± 0.09a	10.0 ± 0.22b
	30˚C	11.9 ± 0.40a	12.1 ± 0.29b	8.8 ± 0.20a
	F	146.2	143.8	601.9
	df	3, 138	3, 148	3, 187
	P	<0.0001	<0.0001	<0.0001
(b) Total Development Time (days)				
	20˚C	29.7 ± 0.44c	29.4 ± 0.38d	31.4± 0.35d
	25˚C	18.1 ± 0.20a	21.6± 0.22c	20.7 ± 0.19c
	28˚C	17.8± 0.45a	17.0 ± 0.10a	16.4 ± 0.15b
	30˚C	18.3 ± 0.60b	19.4 ± 0.50b	15.0 ± 0.34a
	F	125.6	246.1	719.7
	df	3, 139	3,148	3, 187
	P	<0.0001	<0.0001	<0.0001

*Means followed by the same lowercase letter are not significantly different. (Student Newman Keuls Test, α =0.05)

4.2.1. Effect of temperature on longevity and total lifespan of *C. sesamiae* Kitale, *C. sesamiae* Mombasa and *C. flavipes*

Longevity of *C. sesamiae* Kitale varied among different temperature regimes ($F_{3,135}$=7.82; P<0.001; Table 4a) with mean longevity ranging between 1.8 days (30^0C) to 3.6 days (20^0C). Similarly, longevity of *C. sesamiae* Mombasa was significantly affected by temperature ($F_{3,144}$=61.9; P<0.001; Table 4a). Like *C. sesamiae* populations, longevity of *C. flavipes* varied among different temperature regimes ($F_{3,187}$=30.24;P<0.001;Table 4a) with mean longevity ranging from 2.2 days (30^0C) to 4.2 days (20^0C). Generally, longevity decreased with increase in temperature.

The lifespan of *C. sesamiae* Kitale was significantly affected by temperature ($F_{3,139}$=135.5; P<0.001; Table 4b). There was a general decrease in lifespan with increase in temperature. *Cotesia sesamiae* Kitale's lifespan varied between 20.0 days (30^0C) and

33.3 days (20^0C). Temperature significantly affected the lifespan of *C. sesamiae* Mombasa ($F_{3,148}$=210.7; P<0.001; Table 4b) with mean lifespan ranging between 20.8 days (28^0C) and 33.1 days (30^0C). Generally, lifespan of *C. sesamiae* Mombasa decreased with increase in temperature. However, at 30^0C, a mean lifespan of 23.0 days was recorded which was higher than 20.8 days recorded at 28^0C. There was variation in the lifespan of *C. flavipes* at the different temperatures tested ($F_{3,187}$=684.4; P<0.001; Table 4b) with mean lifespan ranging between 17.2 days (30^0C) and 35.6 days (20^0C). The lifespan of *C. flavipes* decreased with increase in temperature.

Table 4: Effect of temperature on longevity and total lifespan ($\bar{x} \pm SE$) of *Cotesia sesamiae* Kitale, *Cotesia sesamiae* Mombasa and *Cotesia flavipes*.

(a) Longevity(days)	Temperature	*C. sesamiae* Kitale	*C. sesamiae* Mombasa	*C. flavipes*
	20˚C	3.6 ± 0.12c	3.6 ± 0.11d	4.2 ± 0.20c
	25˚C	3.4 ± 0.16c	3.0 ± 0.19c	3.2 ± 0.20b
	28˚C	2.8 ± 0.12b	2.5± 0.15b	2.5 ± 0.11a
	30˚C	1.8 ± 0.15a	1.9 ± 0.12a	2.2 ± 0.12a
	F	7.82	61.9	30.24
	df	3, 135	3, 144	3,187
	P	<0.0001	<0.0001	<0.0001
(b) Lifespan(days)				
	20˚C	33.3 ± 0.44c	33.1 ± 0.38d	35.6 ± 0.35d
	25˚C	21.5 ± 0.20b	25.2 ± 0.22c	23.9 ± 0.19c
	28˚C	20.6 ± 0.45a	20.8 ± 0.10a	19.0 ± 0.15b
	30˚C	20.0 ± 0.60a	23.0 ± 0.50b	17.2 ± 0.34a
	F	135.3	210.7	684.4
	df	3, 179	3, 148	3, 187
	P	<0.0001	<0.0001	<0.0001

*Means followed by the same lowercase letter are not significantly different. (Student Newman Keuls Test, α =0.05)

4.2.2. Effect of temperature on fecundity and progeny size of *C. sesamiae* Kitale, *C. sesamiae* Mombasa and *C. flavipes*

There was no significant difference in fecundity of *C. sesamiae* Kitale at the different temperature regimes ($F_{3,139}$=4.45; P=0.1254; Table 5a). Fecundity decreased with increase in temperature between 20^0C (37.1) and 25^0C (35.0) then increased with further increase in temperature to 38.1 at 30^0C. Fecundity was highest at 30^0C (38.1) and lowest at 25^0C (35.0). For *C. sesamiae* Mombasa, there was no significant variation in fecundity at the different temperature regimes ($F_{3,148}$=4.63; P=0.1524; Table 5a). Fecundity of *C. sesamiae* Mombasa decreased with increase in temperature between 20^0C (37.3) and 28^0C (34.1) but increased with further increase to 41.7 at 30^0C. The highest and the lowest fecundity was 41.7 (30^0C) and 34.1 (28^0C) respectively. There was no significant influence of temperature on fecundity of *C. flavipes* ($F_{3,187}$=1.44; P=0.232; Table 5a) with fecundity ranging from 35.4 (30^0C) to 40.7 (25^0C). Fecundity of *C. flavipes* reduced with increase in temperature between 20^0C (38.3) and 25^0C (40.7) then decreased with further increase in temperature to 35.4 at 30^0C.

Temperature significantly influenced progeny size of *C. sesamiae* Kitale ($F_{3,139}$=8.36; P<0.001;Table 5b).The mean progeny size varied from 25.0 (30^0C) to 32.0 (20^0C). For *C. sesamiae* Mombasa, there was no variation in the progeny size at the different temperature regimes ($F_{3,148}$=6.23; *P=0.6725*; Table 5b) with mean progeny size ranging from 26.4 (28^0C) to 33.8 (20^0C). There were differences in progeny size for *C. flavipes* at the different temperature regimes ($F_{3,187}$=2.1;P=0.092; Table 5b) with mean progeny size ranging from 30.9 (28^0C) to 36.8 (25^0C). Progeny size increased between 20^0C (31.0) and 25^0C (36.8) then declined to 30.9 at 28^0C before increasing to 32.7 at 30^0C.

Table 5: Effect of temperature on fecundity and progeny size of *Cotesia sesamiae* Kitale, *Cotesia sesamiae* Mombasa and *Cotesia flavipes*.

(a) Fecundity	Temperature	*C. sesamiae* Kitale	*C. sesamiae* Mombasa	*C. flavipes*
	20˚C	37.1 ± 2.06	37.3 ± 1.85	38.3 ± 1.74
	25˚C	35.0± 2.25	34.7 ±2.61	40.7 ± 2.37
	28˚C	36.5 ± 2.02	34.1 ± 2.25	38.1 ± 1.59
	30˚C	38.1 ± 1.98	41.7 ± 2.06	35.4 ± 1.61
	F	4.45	4.63	1.44
	df	3, 139	3, 148	3, 187
	P	0.1254	0.1524	0.232
(b) Emerged Adults				
	20˚C	32.0 ± 1.99a	33.8 ± 1.89	31.0 ± 1.60
	25˚C	27.3 ±2.02a	29.1± 2.39	36.8 ± 2.44
	28˚C	28.3 ± 1.87a	26.4 ±2.32	30.9 ±1.67
	30˚C	25.0 ± 1.97b	32.9± 1.97	32.7 ± 1.57
	F	8.36	6.23	2.17
	df	3, 139	3, 148	3, 187
	P	<0.0001	0.06725	0.0927

*Means followed by the same lowercase letter are not significantly different. (Student Newman Keuls Test, α =0.05)

4.2.3. Effect of temperature on survival rate and sex ratio of *C. sesamiae* Kitale, *C. sesamiae* Mombasa and *C. flavipes*

Results show variation in survival rate of *C. sesamiae* Kitale at the different temperature regimes ($F_{3,139}$=11.4; P<0.001; Table 6a). Survival rates varied between 68.1 (30^0C) to 85.7 (20^0C) with a general decrease with increase in temperature. For *C. sesamiae* Mombasa, there were differences in survival rates at the different temperature regimes ($F_{3,148}$=16.05; P<0.001; Table 6a). There was a decrease in *C. sesamiae* Mombasa survival rates with increase in temperature between 20^0C (89.4) and 28^0C (71.8) followed by an increase to 80.4 at 30^0C. Similarly, temperature significantly affected survival of *C. flavipes* ($F_{,187}$=12.33; P<0.001; Table 6a), with survival rates varying between 79.4 and 91.7% at 25 and 30^0C respectively.

Temperature significantly affected sex ratios of *C. sesamiae* Kitale ($F_{3,139}$=10.36; P<0.001; Table 6b) with mean sex ratios varying between 0.54 (25^0C) to 0.67(30^0C). Effects were also significant in *C. sesamiae* Mombasa ($F_{3,146}$=11.36; P<0.001; Table 6b) where sex ratios varied between 0.59 (25^0C) to 0.71 (20^0C). Similar significant effect was observed in *C. flavipes* ($F_{3,187}$=12.75; P<0.001; Table 6b). In *C. flavipes*, the sex ratios varied between 0.60 (28^0C) to 0.75 (30^0C).

Table 6. Effect of temperature on survival rate and sex ratio of *Cotesia sesamiae* Kitale, *Cotesia sesamiae* Mombasa and *Cotesia flavipes*.

(a)Survival rate	Temperature	*C. sesamiae* Kitale	*C. sesamiae* Mombasa	*C. flavipes*
	20˚C	85.7 ± 1.52c	89.4 ± 1.44b	80.0 ± 1.53a
	25˚C	77.7 ± 2.67b	83.6 ± 1.60b	79.4 ± 2.21a
	28˚C	76.7 ± 1.73b	71.8 ± 3.46a	87.9 ± 1.87b
	30˚C	68.1 ± 1.11a	80.4 ± 0.97a	91.7 ± 0.87b
	F	11.4	16.05	12.33
	df	3, 139	3, 148	3, 187
	P	<0.0001	<0.0001	0.0001
(b) Sex ratio (Females/Total)				
	20˚C	0.64 ± 0.015bc	0.71 ± 0.020c	0.66 ± 0.004ab
	25˚C	0.54 ± 0.022a	0.59 ± 0.012a	0.69 ± 0.024bc
	28˚C	0.57 ± 0.026ab	0.60 ± 0.015ab	0.60 ± 0.011a
	30˚C	0.67 ± 0.014c	0.65 ± 0.012b	0.75 ± 0.016c
	F	10.36	11.36	12.75
	df	3, 139	3, 146	3, 187
	P	<0.0001	<0.0001	<0.0001

*Means followed by the same lowercase letter are not significantly different. (Student Newman Keuls Test, α =0.05)

4.3. Effect of temperature on host-parasitoid synchrony

4.3.1. Effect of temperature on host-parasitoid synchrony of *Busseola fusca* and *Cotesia sesamiae* Kitale

Generation time (T) decreased with increase in temperature for both *B. fusca* and *C. sesamiae* Kitale (Fig. 1). The generation time ranged between 59.7 days at 28^0C and 107.5 days at 20^0C for *Busseola fusca*. For *C. sesamiae* Kitale, the shortest generation time was 15.2 days recorded at 28^0C and the longest was 32.7 days recorded at 20^0C. However, this trend was not the same for all the temperature regimes in both *B. fusca* and its larval parasitoid, *C. sesamiae* Kitale. Generation time increased at 30^0C for both *B. fusca* and *C. sesamiae* Kitale. The generation time for *B. fusca* increased from 59.7 days (28^0C) to 81.0 days (30^0C) while the generation time of *C. sesamiae* Kitale increased from 18.2 days (28^0C) to 20.5 days (30^0C)

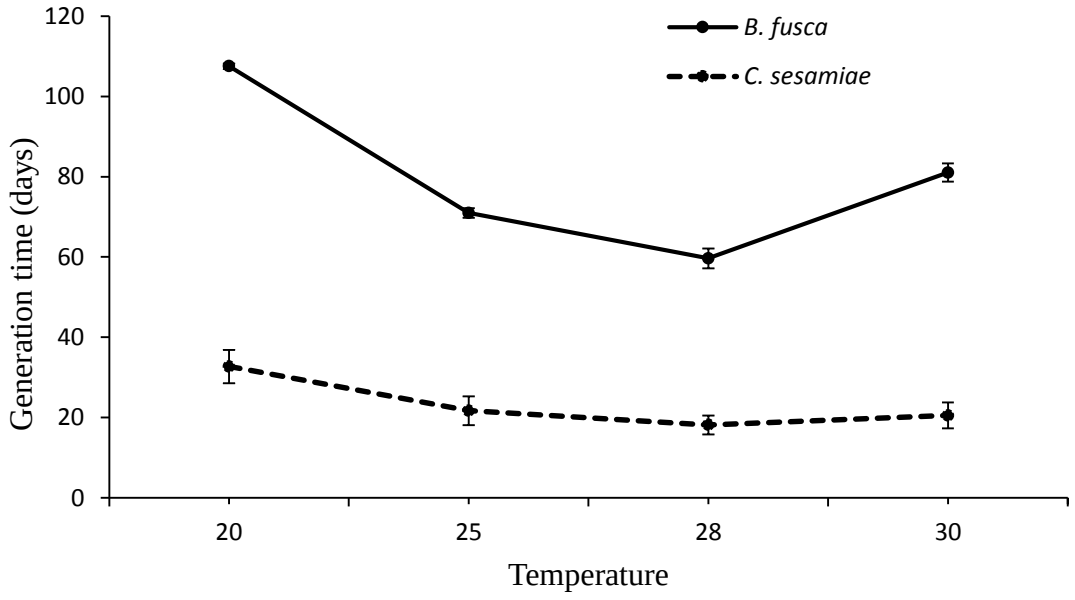

Figure 1: Generation time (T) of *Busseola fusca* and its larval parasitoid *Cotesia sesamiae* Kitale at four constant temperatures.

Net reproductive rate increased sharply with increase in temperature up to an optimum and then declined gradually with further increase in temperature (Fig. 2). *Busseola fusca* showed a steady increase in net reproductive rate between 20ºC (26.6) and 25ºC (29.5) followed by a gradual decline with increase in temperature to 6.9 at 30ºC. *Cotesia sesamiae* Kitale had a similar trend with its host *B. fusca.* The net reproductive rate of *C. sesamiae* Mombasa increased from 20^0C (12.1) to 25^0C (13.8) before reducing to 4.8 at 30^0C. The lowest net reproductive rate for *C. sesamiae* Kitale recorded was 4.8 at 30ºC.

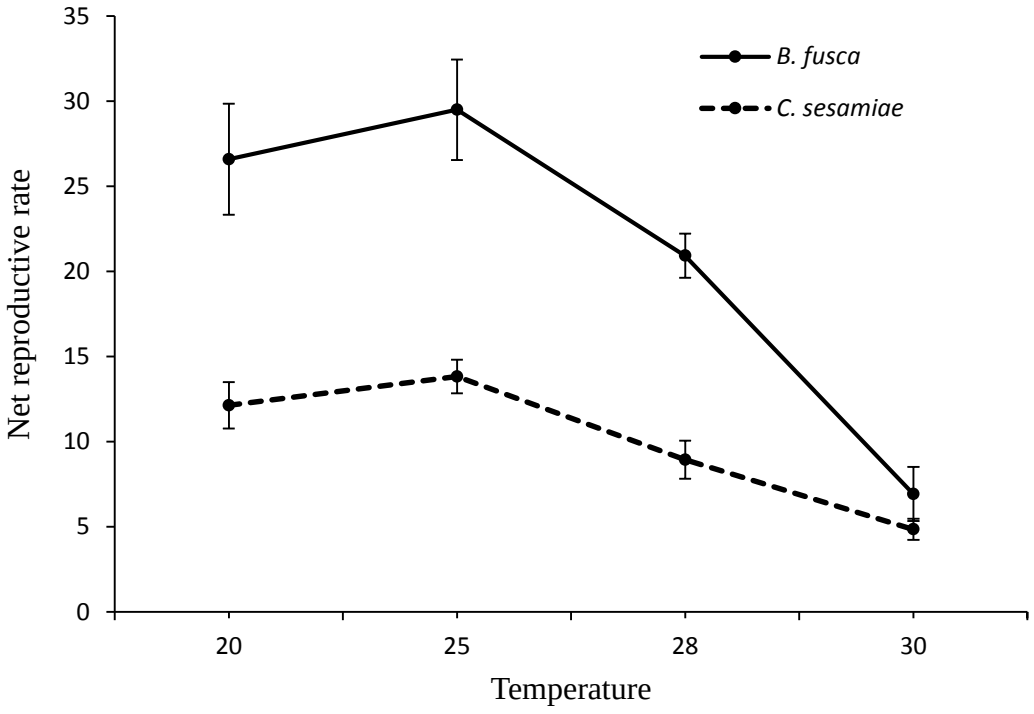

Figure 2. Net Reproductive Rate (Ro) of *Busseola fusca* and its larval parasitoid *Cotesia sesamiae* Kitale at four constant temperatures.

Intrinsic rate of increase rose with increase in temperature to an optimum then decreased with further increase in temperature (Fig. 3). There was a rise in intrinsic rate of increase of *B. fusca* between 20ºC (0.03) and 25ºC (0.13) followed by a steady decrease to 0.02 at 30ºC. *Cotesia sesamiae* Kitale had a similar trend to its host *B. fusca* with a steady rise between 20ºC (0.08) and 25ºC (0.12). Intrinsic rate of increase did not change between 25ºC (0.12) and 28ºC (0.12) and then decreased steadily to 0.08 at 30ºC. At all the temperature regimes except 25ºC, *C. sesamiae* Kitale had higher intrinsic rate of increase than its host, *B. fusca.*

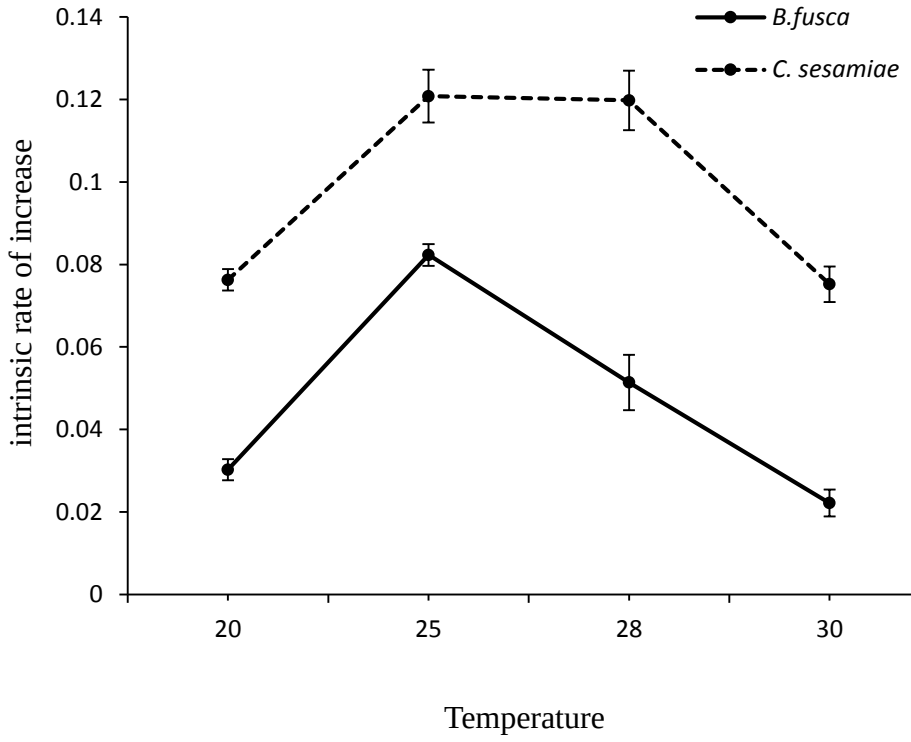

Figure 3. Intrinsic Rate of Increase (r_m) of *Busseola fusca* and its larval parasitoid *Cotesia sesamiae* Kitale at four constant temperatures.

Finite rate of increase rose steadily with increasing temperature up to 25^0C before decreasing with further increase in temperature (Fig. 4). For *B. fusca*, there was a considerable rise in finite rate of increase between 20^0C (1.03) and 25^0C (1.05) then leveled off between 25^0C and 28^0C before a decline to 1.02 at 30^0C. Like its host *B. fusca*, *C. sesamiae* Kitale had a considerable rise in finite rate of increase between 20^0C (1.08) and 25^0C (1.13), then leveled off between 25ºC (1.13) and 28ºC (1.13) followed by a slight decline to 1.08 at 30ºC.

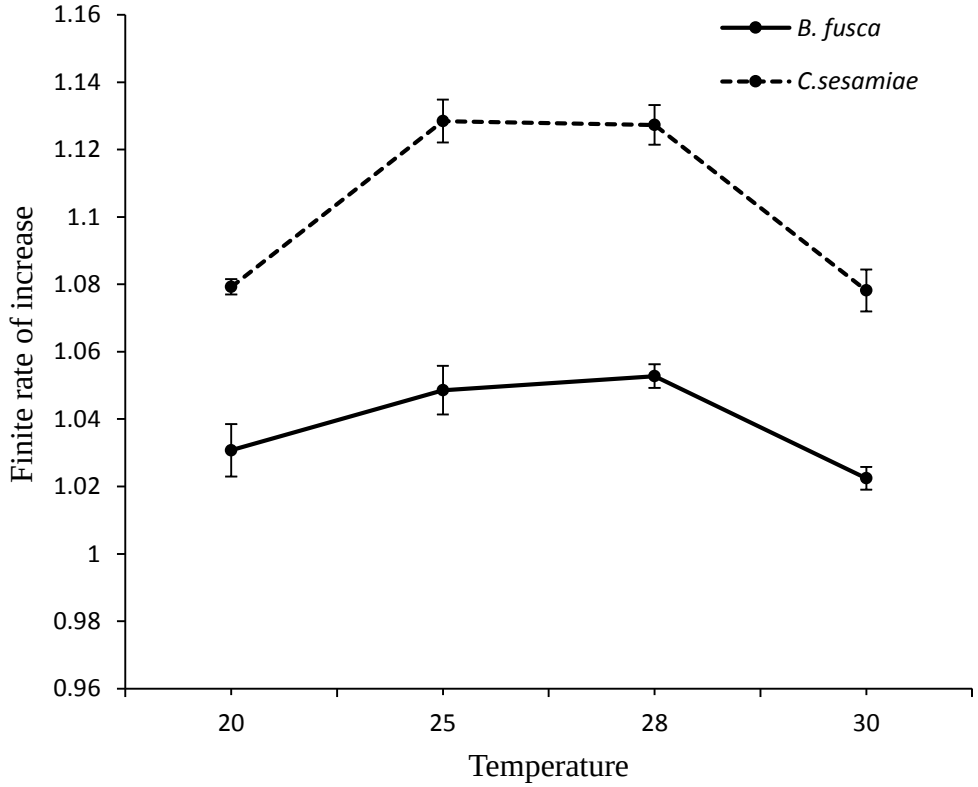

Figure 4: Finite Rate of Increase (λ) of *Busseola fusca* and its larval parasitoid *Cotesia sesamiae* Kitale at four constant temperatures.

4.3.2. Effect of temperature on host-parasitoid synchrony of *Sesamia calamistis* and *Cotesia sesamiae* Mombasa.

Generation time decreased with increase in temperature (Fig 5). The generation time (days) of *S. calamistis* ranged between 51.9 days (30^{o}C) and 88.6 days (20^{o}C). *Cotesia sesamiae* Mombasa showed a similar trend in generation time to its host *S. calamistis* by a decrease with increased temperature. The generation time for *C. sesamiae* Mombasa ranged between 17.0 days (30^{o}C) and 30.0 days (20^{o}C).The highest and lowest generation times were recorded at 20^{0}C and 30^{0}C respectively for both *C. sesamiae* Mombasa and its host *S. calamistis*

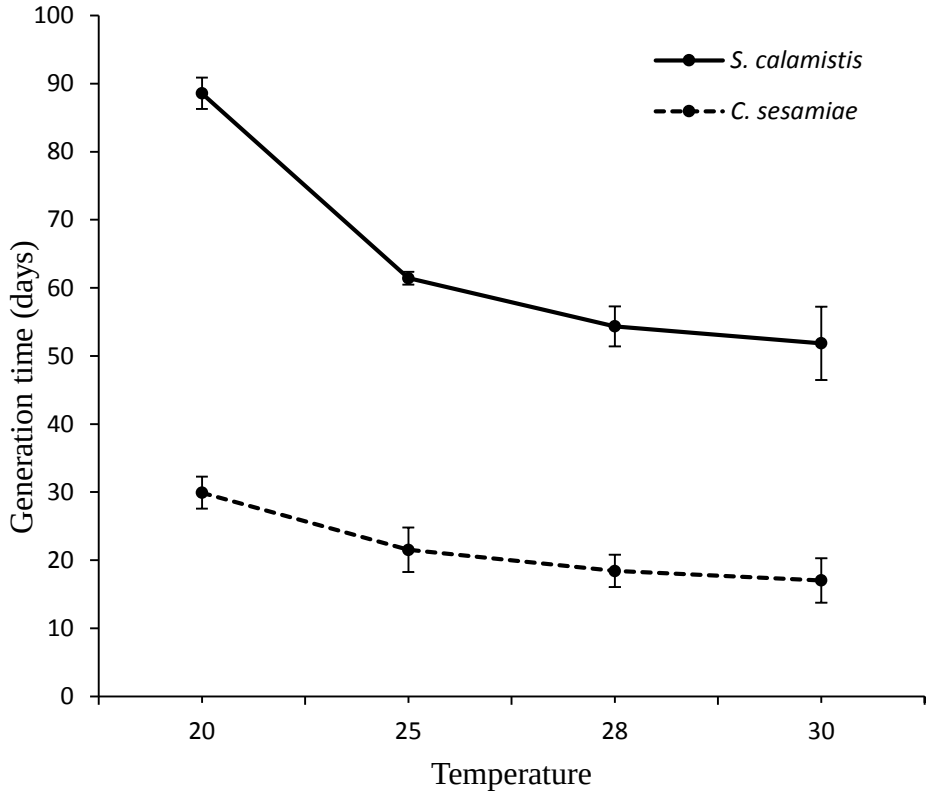

Figure 5. Generation time (T) of *Sesamia calamistis* and its larval parasitoid *Cotesia sesamiae* Mombasa at four constant temperatures.

Net reproductive rate of *S. calamistis* ranged from 7.1 (30ºC) to 28.7 (20ºC) with an optimum of 40.8 at 25ºC. There was a general increase with increase in temperature until the optimum then a decrease with further increase in temperature (Fig. 6). Net reproductive rate of *C. sesamiae* Mombasa showed a similar trend with a gradual increase in net reproductive rate between 20ºC (19.6) and 25ºC (26.2) followed by a steady decline to 15.7 at 30ºC.

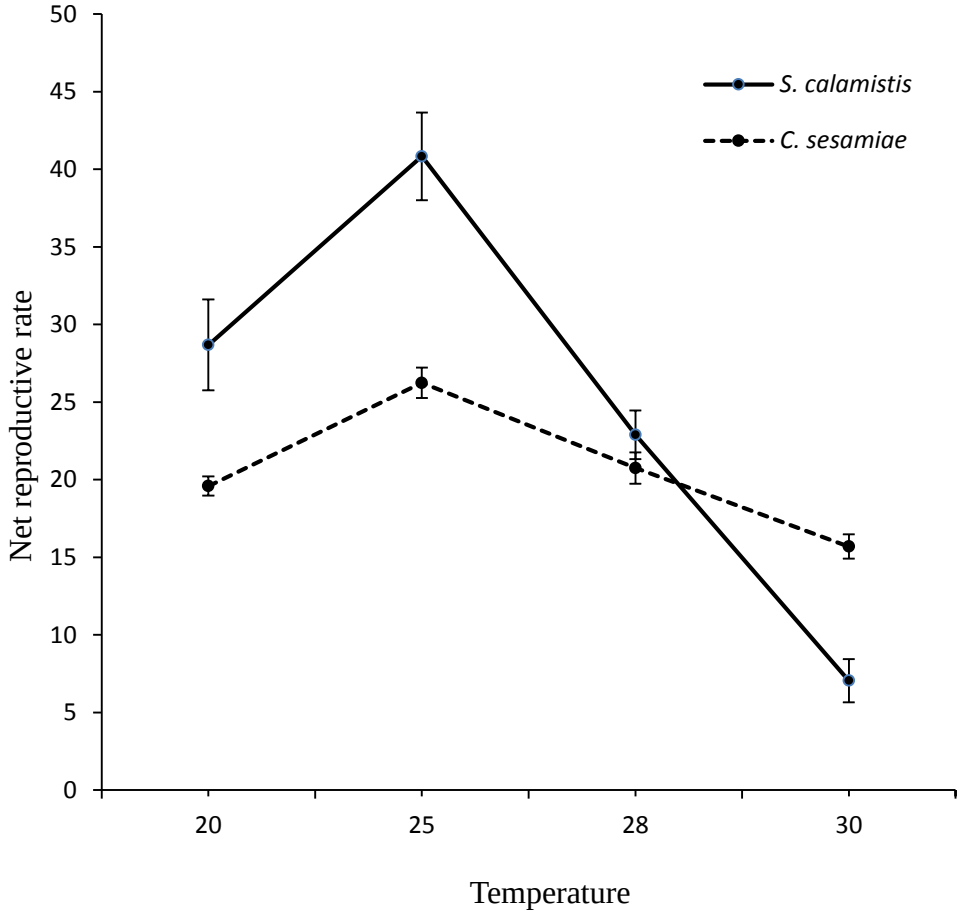

Figure 6. Net Reproductive Rate (Ro) of *Sesamia calamistis* and its larval parasitoid *Cotesia sesamiae* Mombasa at four constant temperatures.

Intrinsic rate of increase of *S. calamistis* and its larval parasitoid *C. sesamiae* Mombasa increased steadily as the temperature increased followed by a decline with further increase in temperature (Fig. 7). For *S. calamistis*, there was a considerable increase in intrinsic rate of increase between 20^{o}C (0.11) and 28^{o}C (0.16) and then declined rapidly to 0.04 at 30^{o}C. For its larval parasitoid *C. sesamiae* Mombasa, intrinsic rate of increase ranged from 0.10 at 20^{o}C increasing to 0.16 at 30^{o}C. At 28^{o}C both *S. calamistis* and *C. sesamiae* Mombasa had an intrinsic rate of 0.16.

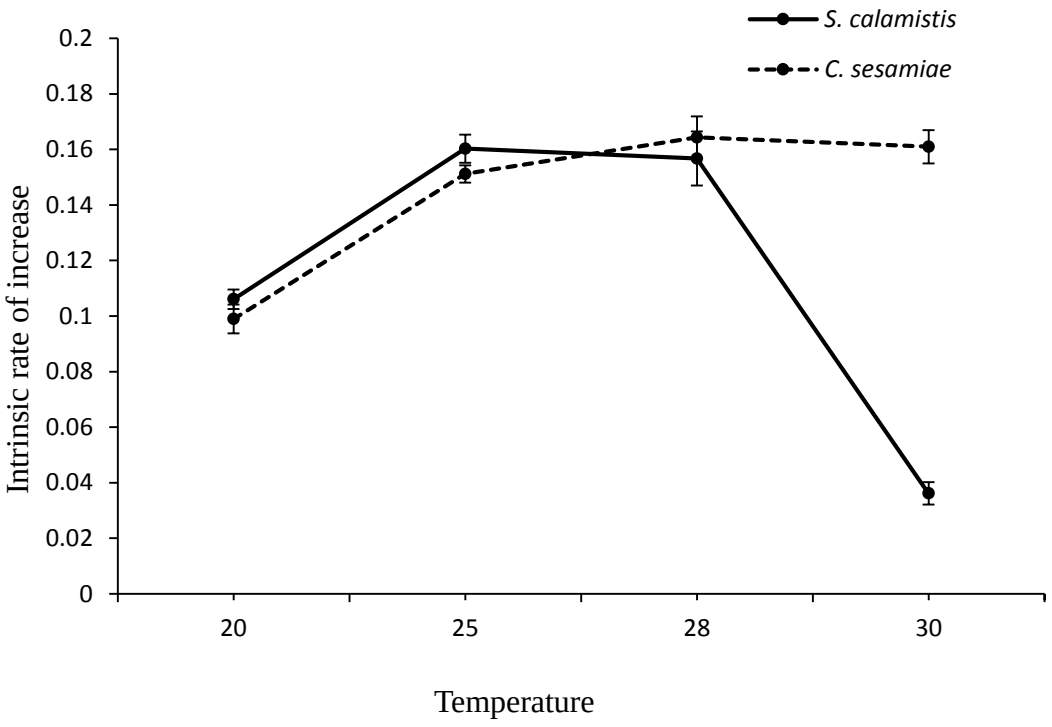

Figure 7: Intrinsic Rate of Increase (r_m) of *Sesamia calamistis* and its larval parasitoid *Cotesia sesamiae* Mombasa at four constant temperatures.

In both *S. calamistis* and *C. sesamiae* Mombasa, the finite rate of increase increased with increase in temperature and reduced steadily with further increase in temperature (Fig. 8). In *S. calamistis*, the finite rate of increase rose gradually between 20^{o}C (λ =1.04) and 28^{o}C (λ =1.06) and decreased to 1.04 at 30^{o}C. Its larval parasitoid *C. sesamiae* Mombasa showed a similar trend with a significant increase from 1.10 at 20^{o}C to 1.18 at 28^{o}C and decreased to 1.17 at 30^{o}C.

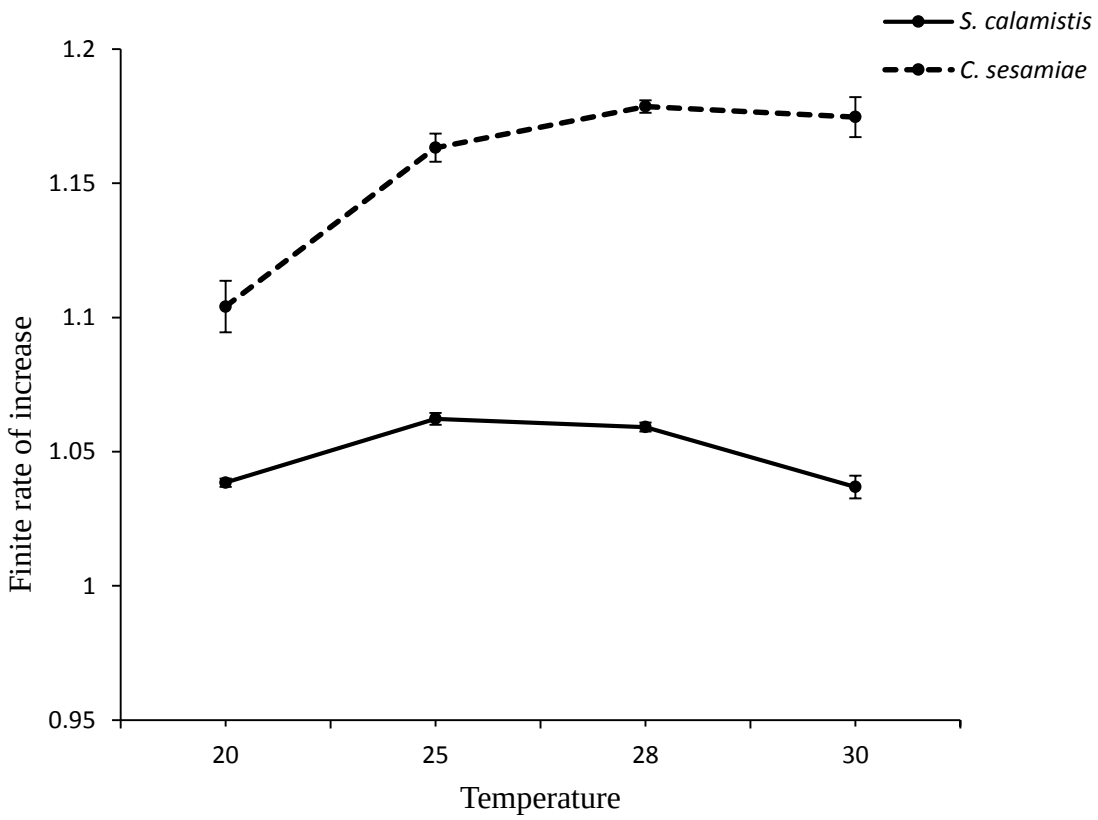

Figure 8: Finite Rate of Increase (λ) of *Sesamia calamistis* and its larval parasitoid *Cotesia sesamiae* Mombasa at four constant temperatures.

4.3.3. Effect of temperature on host-parasitoid synchrony of *Chilo partellus* and *Cotesia flavipes*

Generation time (days) decreased with increase in temperature (Fig. 9). For *C. partellus*, highest generation time (78.1 days) was recorded at 20^0C and decreased to 36.0 days at 30˚C. Its larval parasitoid, *C. flavipes*, had a similar decrease in generation time as the temperature increased. *Cotesia flavipes'* highest generation time (32.6 days) was recorded at 20^0C and lowest (18.8 days) at 30^0C.

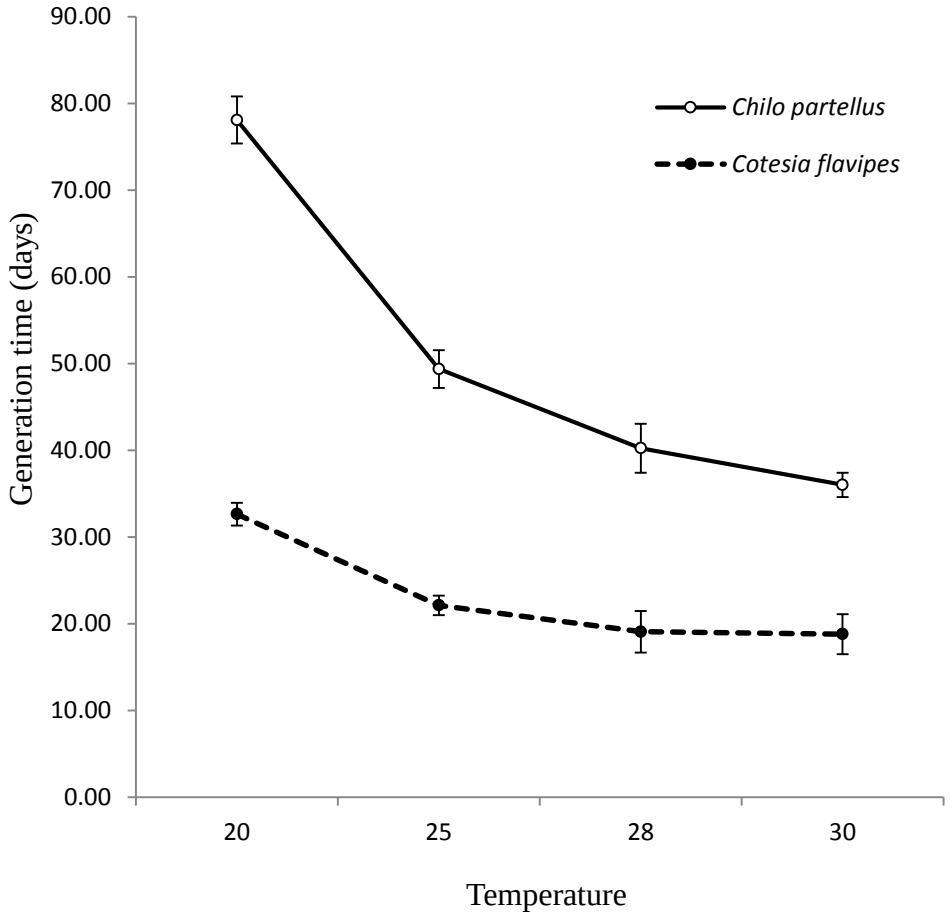

Figure 9:. Generation time (T) of *Chilo partellus* and its larval parasitoid *Cotesia flavipes* at four constant temperatures.

In *Chilo partellus*, net reproductive rate (Ro) increased with increase in temperature between 20°C (R_O=30.4) and 25°C (R_O=56.4) and decreased with further increase in temperature (Fig. 10). The highest net reproductive rate (R_O=56.4) was recorded at 25°C while the lowest (R_O=30.2) was recorded at 20°C. The net reproductive rate for *C. flavipes* showed a similar trend to its host *C. partellus* with an increase between 20°C (R_O=10.1) and 25°C (R_O=11.1) then decreased with subsequent increase in temperature. The highest temperature tested (30°C) had the lowest net reproductive rate (R_O=6.54) for *C. flavipes*.

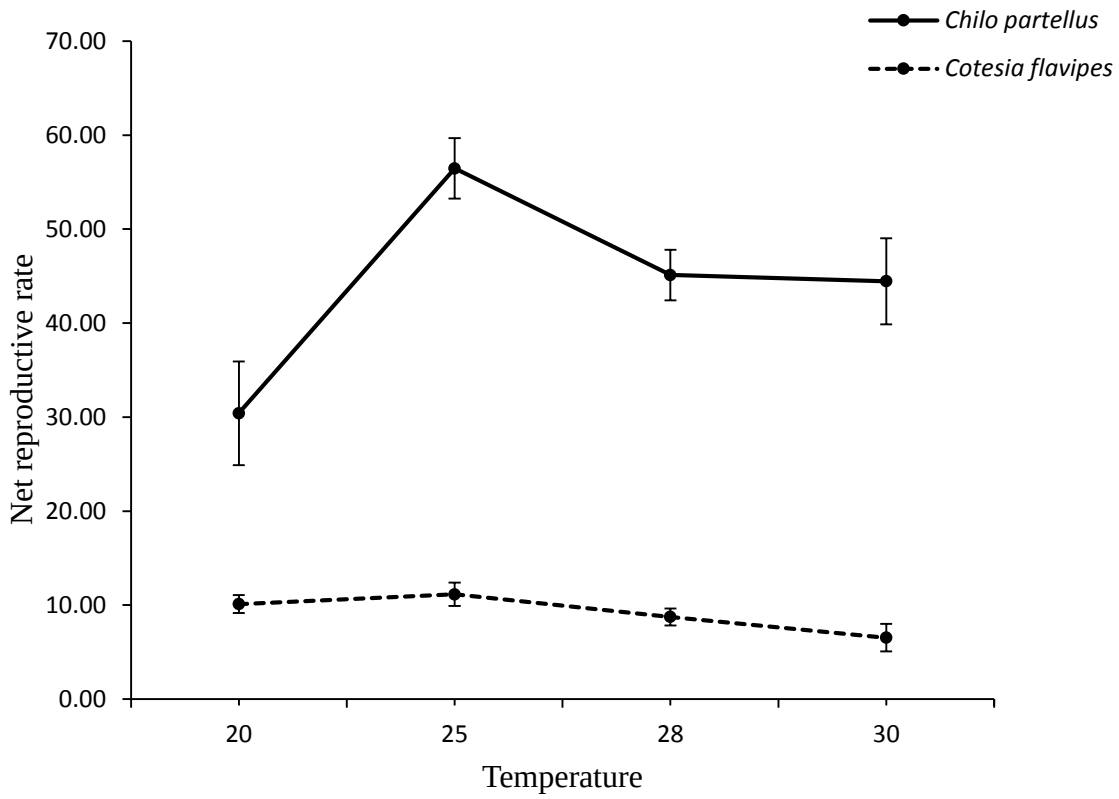

Figure 10: Net Reproductive Rate (Ro) of *Chilo partellus* and its larval parasitoid *Cotesia flavipes* at four constant temperatures.

Intrinsic rate of increase of *C. partellus* increased significantly with increase in temperature. The lowest intrinsic rate was 0.04 at 20^0C and the highest was 0.11 at 30^0C (Fig. 11). *Cotesia flavipes* showed increase in intrinsic rate of increase between 20°C (r_m=0.07) and 28°C (r_m=0.11) then declined steadily with further increase in temperature to 0.10 at 30°C. At 30°C the larval parasitoid *C. flavipes* had lower intrinsic rate of increase than its host *C. partellus*. Intrinsic rate of increase for *C. flavipes* and *C. partellus* at 30°C were 0.10 and 0.11 respectively.

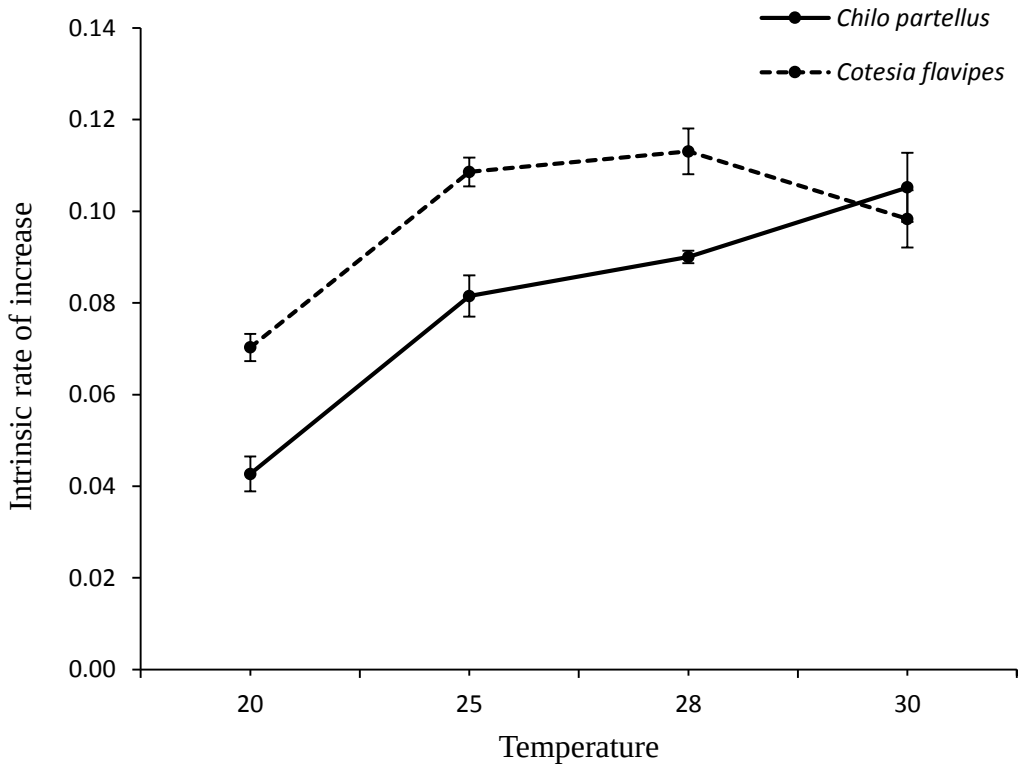

Figure 11: Intrinsic Rate of Increase (r_m) of *Chilo partellus* and its larval parasitoid *Cotesia flavipes* at four constant temperatures.

Finite rate of increase increased markedly with increase in temperature to an optimum then decreased steadily with further increase in temperature (Fig.12). There was a significant increase in the finite rate of increase of *C. flavipes* between 20ºC (1.07) and 28ºC (1.12) and then decreased to 1.10 at 30ºC. *Chilo partellus* had a similar trend to its larval parasitoid *C. flavipes* with a continuous increase in the finite rate from 1.04 (20^0C) to 1.11 at 30ºC.The highest and lowest finite rates of increase for *C. flavipes* were 1.07 at 20ºC and 1.12 at 28ºC respectively. Its host *C. partellus* had the lowest finite rate of increase (1.04) at 20ºC and the highest (1.11) at 30ºC.

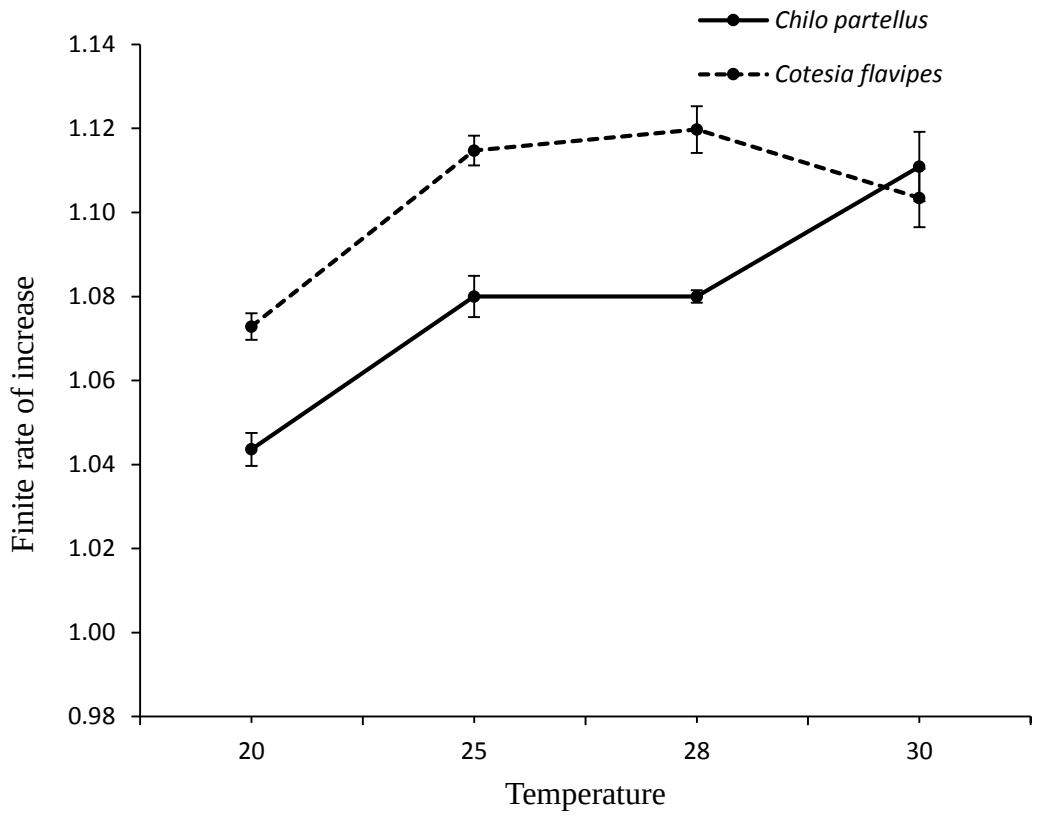

Figure 12: Finite Rate of Increase (λ) of *Chilo partellus* and its larval parasitoid *Cotesia flavipes* at four constant temperatures.

CHAPTER FIVE

DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

5.1. Discussion

This study provides evidence of significant influence of temperature on larval development time of *B. fusca*, *S. calamistis* and *C. partellus*. Some other studies have reported on influence of temperature on the development, reproduction and survival of other crop pests (Bale *et al*., 2002; Karuppaiah and Sujayanad, 2012). A change in development rate is the most rapid response to changing temperatures. Studies show that temperature influences development rate due to its effect on metabolic rates as it induces physiological changes (Davidowitz and Nijhout, 2004). Increase in temperature increases metabolism which in turn increases the development rate. In this study, larval development rates were found be inversely related to temperature, findings that corroborate results of Mbapila *et al*. (2002) on *C. partellus*.

Reduction in larval development time with increase in temperature has also been described in other crop pests. Rwomushana *et al.* (2008) working on Fruit fly *Bactrocera invadens* reported a decrease in larval development time with increase in temperature This reduction in development time is attributed to increased metabolic activity and feeding (Davidowitz and Nijhout 2004). Even though development was possible in all temperature regimes tested for *B. fusca*, significant variation of larval development duration was observed. Mean larval development of 78.3 days recorded at 20^0C for *B. fusca* is slightly shorter than 90.12 days reported at 20^0C by Khadioli *et al*. (2014b). In the field, *B. fusca* larvae take 30 to 45 days to complete development (Overholt *et al*., 2001). This difference is attributed to fluctuations in temperature and other environmental

factors. In this study, *B. fusca* larvae were reared at constant temperatures. Constant low temperature causes a decrease in growth rate resulting in longer development times. This may describe the longer development times noted in this study and other laboratory studies on *B. fusca* (Khadioli *et al*., 2014b) as compared to the larval development time in the field (Overholt *et al*., 2001). Apart from low temperature causing this slower growth, Use of artificial diet may also be causing prolonged development. Faster development on natural diet than in artificial diet has been reported in other stem borers; *Sesamia calamistis* (Shanower *et al*., 1993) and *Chilo orichalcociliellus* (Mpabila *et al*., 2002).

Sesamia calamistis larval development times in this study corroborate those reported by Shanower *et al*. (1993) and Khadioli *et al*. (2014b).Development of *S. calamistis* larvae was observed at all the temperature regimes tested in this study. Khadioli *et al.* (2014b) reported that *S. calamistis* larvae did not develop at temperatures below 15^0C and above 35^0C. This also corroborates findings by Usua (1968) and Shanower *et al.* (1993) who reported that *S. calamistis* larvae did not survive at temperatures above 34^0C.These extreme temperatures were not tested in this study.

Larval duration of *C. partellus* decreased with increasing temperature. These results corroborate findings by Mpabila *et al*. (2002) and Tamiru *et al.* (2012). Results of this study indicate that a 10^0C increase in temperature can half the development time. This implies that areas with higher temperatures can have twice the number of generations of *C. partellus* as the cooler areas in a year. Pupal development of *B. fusca*, *S. calamistis* and *C. partellus* followed the same trend as their respective larvae. There was a decrease in pupal development time with increase in temperature. The crucial role played by temperature on development of stem borers is underscored by the significant variation in

larval and pupal development times at the tested temperature regimes. Exposure to lower temperature leads to slower development rates and consequently longer development times. On the other hand, higher temperatures increase the rate of development resulting in shorter development times.

Although larval survival for *S. calamistis* was lower than that of *B. fusca* at three of the four temperature regimes tested, the range between the lowest and the highest survival was greater in *B. fusca* than in *S. calamistis*. Survival is one of the major factors that determine insect distribution and abundance. Ong'amo *et al*. (2006) reported *B. fusca* being dominant in highland tropics, moist transitional zones and moist mid altitudes of Kenyan agro ecological zones. *Sesamia calamistis* on the other hand has a very wide distribution with typically low densities (Overholt *et al*., 2001, Ong'amo *et al*., 2006). According to this study, the lower survival of *S. calamistis* at each of the temperature regime tested as compared to *B. fusca* may be one of the factors causing the wide distribution but low densities of *S. calamistis* along the agro ecological zones of Kenya.

Pupal survival was higher than larval survival at all the temperature regimes tested. This higher survival by pupae can be attributed to the inactivity and the comparative anatomy of the pupae. The pupae are in an inactive state with minimal movements thus can avoid heat stress at both high and low temperatures.

There was a decrease in longevity with increase in temperature for the model stem borer adults. Longevity of *B. fusca* decreased from 9.1 days recorded at 20^0C to 4.2 days recorded at 30^0C. Khadioli *et al*. (2014b) reported *B fusca* female longevity ranging from 10.47 days (20^0C) to 4.71 days (30^0C) while male longevity for the same temperature

range ranged from 9.92 days and 4.43 days. *Sesamia calamistis* had longevity ranging from 8.6 days recorded at 20^0C to 7.4 days at 30^0C. Khadioli *et al.* (2014b) reported female longevity of *S. calamistis* ranging from 8.89 days to 6.73 days within the same temperature range. Male longevity of *S. calamistis* ranged from 8.35 days to 7.40 days in the same study. In this study, adult stem borers were not separated according to sex after eclosion. This may explain the slight variation in longevity with those observed by Khadioli *et al*. (2014b). Longevity of *C. partellus* decreased with increase in temperature ranging from 10.2 days (20^0C) to 7.3 days (30^0C) which supports findings by Mbapila *et al*. (2002), Tamiru *et al*. (2012) and Khadioli *et al*. (2014a).

There was a positive relationship between temperature and development rate of the larval parasitoids. Total development time and egg to cocoon formation development time reduced with increase in temperature for both *C. sesamiae* and *C. flavipes*. For *C. flavipes*, egg to cocoon development time reduced to nearly a third with increase in temperature from 21.4 days recorded at 20^0C to 8.8 days at 30^0C. Jiang *et al*. (2004) reported decrease in development time of *C. flavipes* with increase in temperature. Development time from egg to cocoon formation ranged from 14.08 days (22^0C) to 11.82 days (30^0C) for Larval stage 4 (L4) of host. This is similar to the range of development time from egg to cocoon formation of 21.4 days (20^0C) to 8.8 days (30^0C) observed in this study. A higher total development time was observed at 30^0C than at 28^0C for both *C. sesamiae* Kitale and *C. sesamiae* Mombasa. This suggests that the optimum temperature for development of *C. sesamiae* is 28^0C. At temperatures above 28^0C, development is impeded for *C. sesamiae* which corroborate findings of Jiang *et al*. (2004) and Jiang *et al*. (2008).

There was a positive relationship between survival rate of *C. flavipes* and temperature. On the other hand, survival of *C. sesamiae* generally decreased with increase in temperature. This study suggests that low temperature could be an impediment to the establishment of *C. flavipes* due to lower survival rate coupled with lower fecundity.

Longevity of both *C. sesamiae* and *C. flavipes* was inversely related to temperature. Decrease in longevity with increase in temperature has been reported in some other parasitoids (Hance *et al.,* 2007, Appiah *et al*., 2013.) Adult longevity of braconid parasitoids *Fopius arisanus* and *Diachasmimorpha longicaudata* was shortest at 35^0C and longest at 15^0C, and females lived longer than males at all temperatures tested. The decreased longevity at high temperatures for *C. sesamiae* and *C. flavipes* implies that the parasitoid will have less time for host searching as compared to lower temperatures. In this regard, parasitism levels may be low at areas with high temperatures since searching adult parasitoids have less time to locate hosts and parasitize them. Comparing the longevity at low and high temperatures tested, for both *C. sesamiae* and *C. flavipes*, adult parasitoids at lower temperatures have about 2 more days to live than adults of the same parasitoid in higher temperature areas.

There was no significant effect of temperature on the fecundity of *C. sesamiae* and *C. flavipes*. This is attributed to the rearing temperatures that the mated females were exposed to. All mated females were reared at 25^0C before being exposed to their respective parasitoids. After exposure the parasitized stem borer larvae were then subjected to different temperature regimes. Thus the minor variations in fecundity in this study are due to individual differences among the females. Temperature significantly influenced the number of emerged parasitoid adults per host larva. More parasitoid adults

per host larva were produced at lower temperatures than higher temperatures tested. Saeki and Crowley (2012) reported that Cut worm parasitoid *Copidosoma bakeri* brood size significantly increased when higher temperature was applied in early host development.

The progeny sex ratio was significantly affected by temperature with the highest sex ratio at 30^0C for *C. sesamiae* Kitale and *C. flavipes*. The highest sex ratio for *C. sesamiae* Mombasa was at 20^0C. These findings corroborate study by Jiang *et al*. (2004) on effect of temperature on sex ratio. Studies by Mbapila and Overholt, (2001); Ngisong *et al.* (1995) however did not show any significant effect of temperature on progeny sex ratio. Lower sex ratios (with fewer females) were recorded at 25^0C and 28^0C as compared to 20^0C and 30^0C for *C. sesamiae*. Since all the parasitoid females were reared at the same temperature (25^0C), the variation in sex ratios at the different temperature regimes can be attributed to the differential mortality of the male and female parasitoid juveniles inside their respective hosts at each given temperature regime. Male biased sex ratios results in lower population growth. Lower population growth of the parasitoid translates to less control on the host population. This study suggests that temperature is likely to affect the efficiency of stem borer biocontrol by larval parasitoids in areas with temperatures between 25^0C and 28^0C.

Synchrony between the life table parameters of both the host and their respective parasitoids is paramount to an effective biological control. Temperature among other factors is likely to cause host-parasitoid asynchrony due to its differential effect on development, reproduction and survival (Hance *et al*., 2007). Differential development, reproduction and survival results in host and parasitoid populations having different rates

of population growth. In this study, generation time, net reproductive rate, intrinsic rate of increase and finite rate of increase were used to assess stem borer-parasitoid interactions at different temperature regimes.

Generation time decreased with increase in temperature for both the stem borers and parasitoids at the tested temperature regimes. Generation time of both *B. fusca* and *C. sesamiae* Kitale decreased with increase in temperature. However, this trend was not the same for all the temperature regimes tested as a longer generation time was recorded at 30^0C than 28^0C for both *B. fusca* and *C. sesamiae* Kitale. The increase in generation time between 28^0C and 30^0C for both *B. fusca* and *C. sesamiae* Kitale as compared to the lower temperatures tested suggests that the optimum development temperature for both *B. fusca* and *C. sesamiae* Kitale is between 20^0C and 28^0C. At temperatures above 28^0C, both *B. fusca* and its larval parasitoid *C. sesamiae* Kitale experience physiological stress thus take longer to develop although the temperatures are high.

Increased temperature can speed up the growth cycle of crop pests leading to a faster increase in pest populations (Cairns *et al*., 2012). Generation time of *S. calamistis* ranged between 88.6 days at 20^0C and 51.9 days at 30^0C. Similarly, generation time of *C. sesamiae* Mombasa decreased from 29.9 days at 20^0C to 17.0 days at 30^0C. So a 10^0C temperature increase resulted in the reduction of generation time to nearly half of the time taken at 20^0C.Generation time of *C. partellus* ranged from 78.1 days at 20^0C to 36.0 days recorded at 30^0C. Generation time of *C. flavipes* ranged from 32.6 days at 20^0C to 18.8 days at 30^0C. These results imply that populations of stem borers and their respective parasitoids in warmer areas will have twice the number of generations in a year as the same populations in the cooler areas. This corroborates estimation by Bale *et al.* (2002)

that a 2^0C temperature increase has the potential to increase the number of generations per year.

The net reproductive rate of the stem borers was higher than that of their respective host at each temperature regime tested. The only exception was the *S. calamistis* at 30^0C which had a lower net reproductive rate than its larval parasitoid *C. sesamiae* Mombasa. The net reproductive rate increased between 20^0C and 25^0C then declined with further increase for the stem borers and their respective parasitoids. Net reproductive rate was lowest at 30^0C for both *B. fusca* and *C. sesamiae* Kitale. The net reproductive rate for *B. fusca* ranged between 26.5 at 25^0C and 6.9 at 30^0C. This is almost a fivefold decrease with just 5^0C increase in temperature. At 30^0C, the net reproductive rate of *S. calamistis* was lower than that of its larval parasitoid *C. sesamiae* Mombasa. This implies that at this temperature, the parasitoid is producing more offspring than its host. The net reproductive rate of *C. partellus* ranged from 56.5 at 25^0C to 44.4 at 30^0C. Khadioli *et al.* (2014a) reported a highest net reproductive rate for *C. partellus* as 56.72 at 25^0C. This is not different from the highest net reproductive rate of 56.45 observed in this study for the same pest. Between 25^0C and 30^0C, *C. partellus* had net reproductive rate that is five to six times that of *C. flavipes*.

Stem borer and parasitoid comparisons of Intrinsic rate of increase had similar trends to those of their respective finite rate of increase. The intrinsic rate of increase for the stem borers and their respective parasitoids increased from 20^0C to 25^0C then decreased with further increase in temperature. At all the temperature regimes tested, the parasitoids had higher intrinsic rate of increase than their hosts. The only exception was *C. flavipes* which had lower intrinsic rate of increase than its host *C. flavipes* at 30^0C. Results of this

study confirm those reported by Khadioli *et al*. (2014a) in which intrinsic rate of increase of *C. partellus* ranged from 0.02 (18^0C) to 0.10 (30^0C) At temperatures above 28^0C, *C. partellus* population is growing faster than that of its larval parasitoid *C. flavipes*. This suggests that biological control of *C. partellus* at warmer areas with temperature between 28^0C and 30^0C may be negatively affected as the host population is growing faster than that of its larval parasitoid. A slight increase in temperature will result in a less efficient biocontrol. On the other hand, at temperatures above 28^0C, *S. calamistis* has lower population growth than that of its larval parasitoid *C. sesamiae* Mombasa. This implies a more efficient biocontrol at warmer areas.

5.2. Conclusions

Temperature change due to climate change will affect biological control of lepidopteran stem borers

I. Temperature affected the development and survival of *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus* larvae. Larval development of stem borers was slow at lower temperatures tested and was faster at higher temperature tested. Increase in temperature will result in more generations of stem borers per growing season due to increased development rate.

II. Temperature influenced the development, survival and longevity of *Cotesia flavipes* and *Cotesia sesamiae*. Development, survival and longevity of both *C. flavipes* and *C. sesamiae* increased with increase in temperature. Decreased adult longevity of the larval parasitoids at higher temperatures is one of the factors causing lower levels of parasitism in warmer areas. This is due to a decreased host searching time.

III. Changes in temperature due to climate change are likely to disrupt the host parasitoid synchrony between the stem borers and their associated larval parasitoids as reflected in the variations in their respective life table parameters. The host parasitoid synchrony most likely to be affected is that between *Chilo partellus* and *Cotesia flavipes*. *Chilo partellus* completed development at lower regimes tested. This implies that it will establish in cooler highland areas previously thought to be unfavorable to it. Lower temperature could be an impediment to the establishment of *C. flavipes* due to lower survival rates coupled with lower fecundity.

5.3. Recommendations

1. There is need to undertake similar studies under field conditions. In the field, temperatures are high during the day and low at night. Studies on effect of temperature on the development, survival as well as host-parasitoid synchrony of lepidopteran stem borers and their associated larval parasitoids should be carried out on variable temperatures. The findings of this study will complement the current study on constant temperature.
2. Studies on the level of larval parasitism of stem borers especially in warmer agro ecological zones should be carried out. This will identify the areas in need of augmentation of the larval parasitoid population.
3. There is also need for similar studies on the egg and pupal parasitoids with a view to identify potential candidates for augmentation in biological control in the face of temperature change.

REFERENCES

Andrewartha, H.G. and **Birch, L.C.** (1954). *The distribution and abundance of animals*. University of Chicago Press, Chicago, USA. P. 118.

Appiah, E. F., S. Ekesi, D. Salifu, K. Afreh-Nuamah, D. Obeng-Ofori, F. Khamis, and **S. Mohamed.** (2013). "Effect of Temperature on Immature Development and Longevity of Two Introduced Opiine Parasitoids on Bactrocera Invadens." *Journal of Applied Entomology* **137**: 571–79.

Bale, J S., Gregory J. M., Ian D. H., Caroline A., Martijn B., Valerie K. B., and **Jennifer B.**. (2002). "Herbivory in Global Climate Change Research: Direct Effects of Rising Temperature on Insect Herbivores." *Global Change Biology* **8**: 1–16..

Bosque-Perez, N.A., and **Schulthess, F**. (1998). Maize: West and Central Africa, pp. 11-24. In: Polaszek (Ed) African Cereal Stem Borers: Economic Importance, Taxonomy, Natural Enemies and Control. CAB International, Wallingford, Oxon, UK.

Branca, A., LeRu, B.P., Vavre, F., Silvain, J-F., and **Dupas, S.** (2011). Intraspecific specialization of the generalist parasitoid *Cotesia sesamiae* revealed by polyDNAvirus polymorphism and associated with different Wolbachia infection. *Molecular Ecology*, **20**: 959–971.

CAB, (1977). *Chilo partellus* (Swinhoe) Distribution Maps of Pests No. 184 (revised) Commonwealth Agricultural Bureaux, Commonwealth Institute of Entomology, London.

Cairns, J.E. Sonder, K., Zaidi, P.H. Verhulst, N., Mahuku, G., Babu, R., Nair, S.K., Das, B., Govaerts, B., Vinayan, M.T., Rashid, Z., Noor, J., Devi, P., San Vicente, F., and **Prasanna, B.M.** (2012). Maize production in changing climate: impacts, adaptation and mitigation strategies. Pp 1-58 in Sparks, D. (Ed) *Advances in Agronomy*, Vol 114, Elsevier Inc. Academic Press.

Calatayud, P.-A., Le Rü, B., Schulthess, F. and **Silvain, J.-F.** (2006). Research on the lepidopteran graminaceous stems borers and their antagonists: achievement and perspectives. *Annales de la Société Entomologique de France* **42**: 259–262.

Cardwell, K. F., Schulthess, F., Ndema, R. and **Ngoko, Z**. (1997) A systems approach to assess crop health and maize yield losses due to pests and diseases in Cameroon. *Agriculture, Ecosystems and environmen*t **65**: 33-47.

Davidowitz, G. and **Nijhout, H. F**. (2004). "The Physiological Basis of Reaction Norms: The Interaction among Growth Rate, the Duration of Growth and Body Size." *Integrative and Comparative Biology* **44** : 443–49.

Dupas, S., Gitau, C.W., Branca, A., Le Rü, B.P. and **Silvain**, **J-F**. (2008). Evolution of a polydna virus gene in relation to parasitoid-Host species immune resistance. *Journal of Heredity* **99**: 491-499.

Godfray H.C.J. (1994) Parasitoids: Behavioral and Evolutionary Ecology. Princeton University Press, Princeton, USA.

Hance, T., Van Baaren J., Vernon, P. and **Boivin, G**. (2007). Impact of extreme temperatures on parasitoids in a climate change perspective. *Annual Reviews of Entomology* **52**:107–126.

Harris, K.M. (1962). Lepidopterous stem borers of cereals in Nigeria. *Bulletin of Entomological Research* **53**: 139-171.

Harris, K.M., and **Nwanze, K**. (1992). *Busseola fusca* Fuller. The African Maize Stem Borer: A handbook of information. Information Bulletin 33, International Crops Research Institute for the Semi-arid Tropics, Patancheru, India.

Jiang, N., Goufa Z., Overholt, W. A., and **Schulthess, F**.. (2008). "Host-Parasitoid Community Model and Its Potential Application in Biological Control of Cereal Stemborers in Kenya." *Population Ecology* **50**: 405–16.

Jiang, N., Sétamou, M., Ngi-Song, A. J. and **Omwega, C**. (2004). "Performance of *Cotesia flavipes* (Hymenoptera: Braconidae) in Parasitizing *Chilo partellus* (Lepidoptera: Crambidae) as Affected by Temperature and Host Stage." *Biological Control* **31**: 155–64.

Karuppaiah, V., and **Sujayanad, G. K**. (2012). "Impact of Climate Change on Population Dynamics of Insect Pests." *World Journal of Agricultural Sciences* **8** 240–46.

Kfir, R., (1992). Seasonal abundance of the stem borer *Chilo partellus* (Lepidoptera: Pyralidae) and its parasites on summer grain crops. *Journal of Economic Entomology* **85**: 518–529.

Kfir, R., Overholt, W. A., Khan, Z.R. and **Polaszek A**. (2002). Biology and management of economically important lepidopteran cereal stem borers in Africa. *Annual reviews of Entomology* **47**: 701-731.

Khadioli, N., Tonnang, E.H., Muchugu, E., Ong'amo, G., Achia, T., Kipchirchir, I., Kroschel, J. and **LeRu, B.** (2014a). Effect of temperature on the phenology of *Chilo partellus* (Swinhoe) (Lepidoptera, Crambidae); simulation and visualization of the potential future distribution of *C. partellus* in Africa under warmer temperatures through the development of life-table parameters. *Bulletin of Entomological Research*, **104**: 809–822.

Khadioli, N., Tonnang, E.H., Ong'amo, G., Achia, T., Kipchirchir, I., Kroschel, J. and **LeRu, B**. (2014b). Effect of temperature on the life history parameters of noctuid lepidopteran stem borers, *Busseola fusca* and *Sesamia calamistis*. *Annals of Applied Biology*. **165:** 373-386.

Kipkoech, A.K., Mithofer, D., Yabann, W. K., Maritim, H.K. and **Schulthess, F**. (2008). Assessing yield and efficiency implications of relying on parasitoids for control of cereal stemborers: The case of small-scale maize farmers in Kenya. *Crop Protection* **27**: 1318– 1326.

Levitus, S., Antonov, J.I., Wang, J., Delworth, T.L., Dixon, K.W. and **Broccoli, A.J**. (2001). Anthropogenic warming of earth's climate system. *Science* **292**: 267–270.

Mailafiya, D. M., Le Ru, B.P., Kairu, E. W., Calatayud P. and **Dupas, S**. (2009). Geographic distribution, host range and perennation of *Cotesia sesamiae* and *Cotesia flavipes* Cameron in cultivated and natural habitats in Kenya. *Biological Control* **54**: 1–8

Mbapila, J.C. and **Overholt, W.A.** (2001). Comparative development, longevity and population growth of exotic and native parasitoids of lepidopteran cereal stemborers in Kenya. *Bulletin of entomological Research* **91:**347-353.

Mbapila, J.C., Overholt, W.A. and **Kayumbo, H.Y**. (2002). Comparative Development and Population Growth of an Exotic Stemborer, *Chilo partellus* (Swinhoe), and an Ecologically Similar Congener, *C. orichalcociliellus* (Strand) (Lepidoptera: Crambidae). *International Journal of Tropical Insect Science*, **22:**21–27.

Mochiah, M.B., Ngi-song A.J., Overholt, W.A. and **Botchery, M**. (2001). Host suitability of four cereal stem borers (Lepidoptera; Crambidae, Noctuidae) for different geographic populations of *Cotesia sesamiae* (Cameron) (Hymenoptera; Braconidae) in Kenya. *Biological Control* **21:** 285-292.

Mochiah, M.B., Ngi-song A.J., Overholt, W.A. and **Stouthamer, R**. (2002). Wolbachia infection in *Cotesia sesamiae* causes cytoplasmic incompatibility: implications for biological control. *Biological Control* **25**: 74-80.

Ngi-Song, A.J. and **Overholt, A.W**. (1997). Host Location and Acceptance by *Cotesia flavipes* Cameron and *C.sesamiae* (Cameron) (Hymenoptera: Braconidae), Parasitoids of African Gramineous Stemborers: Role of Frass and Other Host Cues *Biological Control* **9:** 136–142.

Ngi-song, A.J., Overholt, W.A. and **Stouthamer, R**. (1998). Suitability of *Busseola fusca* and *Sesamia calamistis* (Lepidoptera: Noctuidae) for the Development of Two Populations of *Cotesia sesamiae* (Hymenoptera: Braconidae) in Kenya. *Biological Control* **12**: 208-214.

Ngi-Song, A.J., Overholt, W.A., and **Ayertey, J.N**. (1995). Host suitability of African gramineous stem borers for the development of *Cotesia flavipes* and *Cotesia sesamiae* (Hymenoptera: Braconidae). *Environmental Entomology.* **24**:, 978–984.

Nye, I.W.B. (1960). The insect pests of graminaceous crops in East Africa. Colonial Research Study 31. Her majesty's stationary Office, London.

Obonyo, M., Schulthess, F., Gerald, J.,Wanyama, O., Le Ru, B. and **Calatayud, P**. (2008). Location, acceptance and suitability of lepidopteran stem borers feeding on a cultivated and wild host-plant to the endoparasitoid *Cotesia flavipes* Cameron (Hymenoptera: Braconidae). *Biological Control* **45**: 36‑47.

Ochieng, R.S., Onyango, F.O. and **Bungu, M.D.O**. (1985). Improvement of techniques for mass-culture of *Chilo partellus* (Swinhoe). International Journal of Tropical Insect Science. **6**: 425-428.

Ofamata, V.C., Overholt, W.A., Van Huis, A., Egwuatu, R.I. and **Ngi-Song, A.J**. (2003). Niche overlap and interspecific association between *Chilo partellus* and *Chilo orichalcociliellus* on the Kenya Coast. *Entomologia Experimentalis et applicata* **93**: 141-148.

Ong'amo, G.O., Le Ru, B. P., Dupas, S., Moyal, P., Calatayud, P. and **Silvain, J**. (2006). Distribution, pest status and agro-climatic preferences of lepidopteran stem borers of maize in Kenya. *Annales de la Société Entomologique de France* **42**: 171-177.

Overholt, W. A., Ogeda, K. and **Lammers, P**. (1994a). Distribution and sampling of *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) in maize and sorghum in Kenya. *Bulletin of Entomological Research* **84**: 367–378.

Overholt, W.A., Maes, K.V.N. and **Goebel, F.R**. (2001). Field Guide to the Stem Borer Larvae of Maize, Sorghum and Sugarcane in Eastern and Southern Africa. Icipe Science Press, Nairobi, Kenya. 8-24.

Overholt, W.A., Ngi-Song, A.J., Kimani, S.K., Mbapila, J., Lammers, P. and **Kioko, E**. (1994b.). Ecological considerations of the introduction of *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) for biological control of *Chilo partellus. Bio control News and information.* **15**: 19-24.

Overholt, W.A., Ngi-Song, A.J., Omwega, C.O., Kimani-Njogu, S.W., Mbapila, J., Sallam, M.N., and **Ofomata, V**. (1997). A review of the introduction and establishment of *Cotesia flavipes* Cameron in East Africa for biological control of cereal stem borers. *Insect Science and Applications* **17**: 79–88.

Polaszek, A. (1998). African Cereal Stem Borers: Economic Importance, Taxonomy, Natural Enemies and Control. Wallingford, UK: CABI. 530.

Rwomushana, I., Ekesi, S., Ogol, O. and **Gordon, I**. (2008). Effect of temperature on development and survival of immature stages of *Bactrocera invadens* (Diptera: Tephritidae) *Journal of applied entomology* **132:** 832-839.

Saeki, Y., and **Crowley, P**. (2012). Temperature effects during development on a polyembryonic parasitoid and its host. *Journal of Thermal Biology* **37**: 602-607.

Seshu Reddy, S.V., (1983). Study of the stem borer complex of sorghum in Kenya.

Shanower, T. G., Schulthess, F., and **Bosque-Perez, N**. (1993) Development and fecundity of Sesamia calamistis (Lepidoptera: Noctuidae) and Eldana saccharina (Lepidoptera: Pyralidae). *Bulletin of Entomological Research*, **83:**237-243.

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

Smith Jr, J. W., Wiedenmann, R. N. and **Overholt, W. A**. (1993). *Parasites of Lepidopteran Stemborers of Tropical gramineous Plants.* ICIPE Science Press, Nairobi, Kenya. P 37-44.

Songa, J.M., Overholt, W.A., Okello, R.O. and **Mueke, J. M**. (2002). Control of lepidopteran stem borers in maize by indigenous parasitoids in semi-arid areas of eastern Kenya. *Biological Agriculture and Horticulture* **20**: 77-90.

Songa, J.M., Zhou, G. and **Overholt, W.A**. (2001). Relationships of stem borer damage and plant physical conditions to maize yield in a semi-arid zone of eastern Kenya. *Insect Science and its application* **21**: 243-249.

Tamiru, A., Getu, E., Jembere, B. and **Bruce, T**. (2012) Effect of temperature and relative humidity on the development and fecundity of Chilo partellus (Swinhoe) (Lepidoptera: Crambidae). *Bulletin of entomological Research*. **102**:9-15.

Tezze, A. A. and Botto, E.N. (2004). Effect of cold storage on the quality of *Trichogramma nerudai* (Hymenoptera: Trichogrammatidae). *Biological Control*. **30:** 11-16.

Usua, E. J. (1968) Temperature and relative humidity effects on the development of the immature stages of the Maize stem borers, Busseola fusca and Sesamia calamistis. *Journal of Economical entomology* **61**: 1091-1093.

Van Leerdam, M.B., Smith, J.W. and **Fuchs, T.W**. (1985). Frass mediated, host finding behavoiur of *Cotesia flavipes*, a Braconid parasite of *Diatraea saccharalis* (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America* **78**: 647-650.

Van Rensburg, J.B. (2007). First report of field resistance by the stem borer, *Busseola fusca* (Fuller) to Bt-transgenic maize *South African Journal of Plant and Soil* **24**: 147-151.

Van Rensburg, J.B., Walters, M.C and **Giliomee, J.H**. (1985). Geographical variation in the seasonal moth flight activity of the maize stalk borer, *Busseola fusca* (Fuller), in South Africa. *South. African Journal of Plant and Soil* **2**: 124–26.

Warui, C.M. and **Kuria, J.N**. (1983). Population incidence and the control of maize stalk borers *Chilo partellus* Swinhoe, *Chilo orichalcociliellus* Strand and *Sesamia calamistis* Hampson in Coast Province, Kenya. *Insect Science and its application* **4**: 11-18.

Zhou, G., Overholt, W.A. and **Mochiah, M.B**. (2001). Changes in the distribution of Lepidopteran Maize Stem borers in Kenya from the 1950s to 1990s. *Insect Science and its applications* **21**: 395-402.