

**AN INTERACTION MODEL BETWEEN *Cotesia flavipes* AND *Cotesia sesamiae*,
PARASITOIDS OF THE GRAMINEOUS STEM-BORERS AT THE KENYA COAST.**

By

SIMON MURIITHI KARUKU

A Dissertation Submitted in Partial Fulfilment of the Requirements for the Degree of
Master of Science in Statistics of Kenyatta University.

June, 2002

Karuku, Simon
*An interaction model
between cotesia*

KENYATTA UNIVERSITY LIBRARY



2004/269908

DECLARATION

This is my original work and has not been presented for a degree award in any other University, in part or whole.

Sign.



.....
SIMON MURIITHI KARUKU

13/06/02

We certify that **Simon Muriithi Karuku** conducted the work herein under our supervision.

Sign.

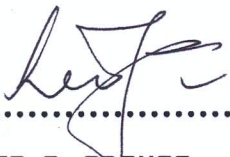


.....
DR. WILLIAM A. OVERHOLT

International Centre of Insect Physiology and Ecology (ICIPE)

Plant Health Division

Sign.



.....
DR. LEO O. ODONGO

Kenyatta University

Department of Mathematics

DEDICATION

DEDICATED TO MY PARENTS

ACKNOWLEDGEMENTS

I gratefully acknowledge my indebtedness to the Vice-Chancellor of Kenyatta University, Professor George Eshiwani, for granting me the opportunity to study under the University's Staff Development Programme.

Much gratitude is extended to my supervisors, Drs. William Overholt (Plant Health Division-ICPIPE), Leo Odongo (Mathematics Department-Kenyatta University) and Guofa Zhou (Biological Sciences Department - State University of New York at Buffalo), for their professional guidance, useful suggestions, academic advice and critical evaluation of this project. I am most appreciative of their generous supply of the substance from which I've drawn heavily. Indeed, no word of gratitude can truly be enough. In no way, however, are they culpable for the final product- that is my burden.

This research was supported in part by the International Centre of Insect Physiology and Ecology (ICPIPE) through Dr. Adedapo Odulaja, formerly the Head, Biostatistics Unit (ICPIPE), under the auspices of the Dissertation Research Internship Programme (DRIP) to whom I am most grateful. I am therefore thankful to the Director, Research and Partnership of the ICPIPE, Professor Onesmo Ole Moi-Yoi for the DRIP scholarship. I wish to express my sincere appreciation to Ms. Margaret Wabiri, Senior Research Assistant (ICPIPE) for her encouragement and useful suggestions. I would like to thank Mr. Gerphas Okuku of ICPIPE/WAU project for his assistance in conducting experiments.

My heartfelt thanks are due to Dr. Gachang'i Njenga, the Chair, Department of Mathematics (K.U.) for his immense support throughout the course, besides being my dedicated lecturer. I am equally indebted to my other academic lecturers in the Department: Drs. Charles Wafula, James Kahiri and Romanus

Odhiambo, Mr. Augustine Ruto and the late Mr. George Githu, who have built in me a strong foundation.

I am grateful to my colleagues in the Department of Mathematics (K.U.) - Kithikii Kasungo and Benjamin Muema, who provided a critical audience against which my thoughts and presentations have been tested. They have both been of good company to me. Their critiques were most helpful to me. I have profited greatly from helpful discussions with my colleague at the ICIPE-Mr. Martin Thuo (BCED), which provided me with a lot of motivation. In spite of all this indispensable assistance, I alone am responsible for errors of facts or interpretation in this study.

Finally, very special thanks go to my parents, Mr. Gilbert Karuku and Mrs. Rose Karuku for being very dear parents to me and for their love and inspirations, which have immensely contributed to the success of my academic endeavours. And the keen interest of my sister Eunice Wamaitha in the progression of my academic career is of special mention. Their prayers to God must have inspired all the people mentioned above to avail their assistance when I was in need.

I regret that for reasons of academic etiquette, my great debt to various people who rendered their help throughout the preparation of this report cannot be acknowledged individually. However, my appreciation to them for their kindness to me is no less.

THANK YOU ALL!

ABSTRACT

One of the greatest challenges facing the people of sub-Saharan Africa is the production of sufficient food to feed a rapidly increasing population in the face of dwindling finances. As the population grows at 3% and food production at 2% per annum, an annual shortage of 250 million tons of food is expected by year 2020. The greatest obstacle to increasing the production of maize and sorghum, the staple food in many African communities south of the Sahara, is damage by phytophagous insects. Larval feeding in the plant whorl and later through stem tunneling causes plant damage. Infested plants have poor growth and reduced yield and are more susceptible to secondary infection and wind damage. Estimates of yield losses due to stem-borers are in the neighbourhood of 20-40% of the potential yield. To realize the potential of the Gramineae family in ensuring food security in the world, the stem-borers have to be effectively controlled. Various methods have been tried in a bid to control these pests. In biological control, one of the approaches is to find an exotic natural enemy that will successfully fit into the community of existent natural enemies. Hampered by a lack of economic and convenient tools, however, advances in biological control have been largely overshadowed by the rush to exploit insecticides and the ready availability and comparative simplicity of cultural methods. But that is changing. Effects on non-target organisms, resistance development and environmental pollution have incapacitated insecticides and other chemical-based methods.

In this study, a simple one host-two parasitoids interaction model with a non-linear trend is developed to predict and understand the reasons for the ultimate impact of the exotic parasitoid *Cotesia flavipes* (Cameron) (Hymenoptera Braconidae) on stem-borer population dynamics in the coastal area of Kenya. Results indicate that the ultimate extent of suppression of the stem-borers is largely determined by three attributes of the parasitoids namely; the net reproductive rate, the degree of aggregation and the searching efficiency. The model predicts coexistence of all the species considered with *C. flavipes* dominating the interactive system. Implications of the results for introduction scheme of parasitoids to control pest are discussed. We argue that a model of intermediate complexity may offer the best prospects of predictive biological control in situations where it is not practicable to obtain the information needed to build and parameterize a large tactical simulation model. The conclusions we reach are of relevance to classical biological control practices, and in particular to those programs in which more than one parasitoid species has been introduced to combat a particular pest of a perennial standing crop system.

TABLE OF CONTENTS

Title	Page
Title page	i
Declaration	ii
Dedication	iii
Acknowledgements	iv
Abstract	vi
Table of Contents	vii
List of Figures and Tables	ix
Prologue	xi
CHAPTER ONE: General Introduction-Fundamental Concepts	
1.0: Biological Control	1
1.1: Types of Biological Control	4
1.2: Pests Most Suitable for Biological Control	5
1.3: Integrated Control	5
1.4: Natural Enemies	7
1.5: Factors Important to Successful Parasitism	8
1.6: The Basic Theory of Competition	9
CHAPTER TWO: Some Basic Mathematical Models in Population Ecology	
2.0: Introduction.	12
2.1: The Geometric Model	12
2.2: The Malthusian Model.	13
2.3: The Logistic Model.	14
2.4: The Ricker Model.	18
2.5: The Lotka-Volterra Competition Model	19
CHAPTER THREE: The Model	
3.0: Introduction	24

3.1: The Life Cycle of the Host	27
3.2.1: The Biology of <i>C. flavipes</i>	28
3.2.2: The Biology of <i>C. sesamiae</i>	29
3.3: Description of the Model	30
CHAPTER FOUR: An Empirical Study	
4.0: Introduction	35
4.1: Materials and Methods	35
4.1.1: Estimation of Interspecific Competition Coefficients	35
4.1.2: Curve Fitting	36
4.1.3: Sensitivity Analysis	36
4.2: Results	36
4.2.1: Estimates for the Interspecific Competition Coefficients	36
4.2.2: Model-fitting	37
4.2.3: Sensitivity Analysis	40
CHAPTER FIVE: Discussion	46
CHAPTER SIX: Conclusions and Areas for Further Research	48
REFERENCES	51
APPENDIX	56

LIST OF FIGURES AND TABLES

Figure		Page
Fig.1.0.1	Diagrammatic Representation of Successful Biological Control	2
Fig.2.3.1	Diagrammatic Representation of the Logistic Model	15
Fig.2.5.1	Zero Growth Isocline for Species A Generated by the L-V competition equations	21
Fig.2.5.2	Graphical Representation of the Relative Abundance of Species A	22
Fig.2.5.3	Zero Growth Isocline for Species B Generated by the L-V competition equations	23
Fig.2.5.4	Graphical Representation of the Relative Abundance of Species B	23
Fig.3.2.1	A General Life Cycle of the Parasitoid Species <i>C. flavipes</i> and <i>C. sesamiae</i>	29
Fig.3.3.1	Diagrammatic Illustration of the Three-Species System Discussed in the Model	32
Fig.4.1	The season-to-season changes of the larvae of the stem-borers and the two parasitoids	38
Fig.4.2	Numerical Simulations for the Model when $m=0.536$ and $n=0.552$	40
Fig.4.3	Numerical Simulations for the Model when $r_f = 0.18828$ & $r_s = 0.12804$	40
Fig.4.4	Numerical Simulations for the Model when $\beta_{fs}=1.48644$ & $\beta_{sf}=1.44996$	41
Fig.4.5	Numerical Simulations for the Model when $R_{of}=R_{os} = 7.69$	42
Fig.4.6	Numerical Simulations for the Model when $R_{of}=R_{os} = 20.96$	42
Fig.4.7	Numerical Simulations for the Model when $R_{of}=R_{os} = 2.96$	43
Fig.4.8	Numerical Simulations for the Model using parameters at 22°C	44
Fig.4.9	Numerical Simulations for the Model using parameters at 28°C	44
Fig.4.10	Numerical Simulations for the Model using parameters at 31°C	45

Table 3.1	Observed Densities of <i>Ch. Partellus</i> , <i>C. flavipes</i> and <i>C. sesamiae</i> at various sites on the Kenyan Coast	26
Table 4.1	Parameter values obtained from the laboratory experiments conducted to estimate the interspecific competition coefficients.	37
Table 4.1	Parameters and their values used in computing the interspecific competition coefficients	37

"A mathematical model is neither an hypothesis nor a theory. Unlike the scientific hypothesis, a model is not verifiable directly by experiment. For all models are both true and false. ... leave out a lot and are in that sense false, incomplete, inadequate. The validation of a model is not that it is 'true' but that it generates good testable hypotheses relevant to important problems."

R. Levins, 1966

Am. Sc., 54 p.426

CHAPTER ONE

GENERAL INTRODUCTION-FUNDAMENTAL CONCEPTS

1.0: Biological control

Biological control is a form of population management. It is the purposeful use of an organism(s) to reduce a plant or animal population that is inimical to man (Samways, 1981).

DeBach (1964) defines biological control as "the action of parasites, predators and pathogens in maintaining another organism's density at a lower average than would occur in their absence"

This involves natural enemies that act to suppress or maintain pest or potential pest species below economically injurious levels. The organisms being suppressed are noxious in that they consume desirable plants or plant products, attack livestock or affect man's health. Biological control is thus the deliberate pitting of beneficial organisms (agents) against harmful ones (targets); i.e., the deployment of natural enemies against specific animal pests or weeds (Samways, 1981). The term control is generally applied where pests are maintained at a level below that at which crop or other damage is too severe; that is, below the economic threshold.

An undesirable organism may be eliminated locally or, more usually, its numbers are suppressed to a level where it is no longer a nuisance nor causes economic damage. Complete eradication is ambitious and seldom achieved. Besides, a natural enemy that completely eliminates its prey is then without food or host and so perishes in turn. In biological control it is more desirable to reduce the pest population to a level that is no longer of economic or health concern, yet leaves sufficient pests to allow survival of the control organism. This organism maintains its own population and prevents the pests from returning to damaging levels (see Fig. 1.0.1).

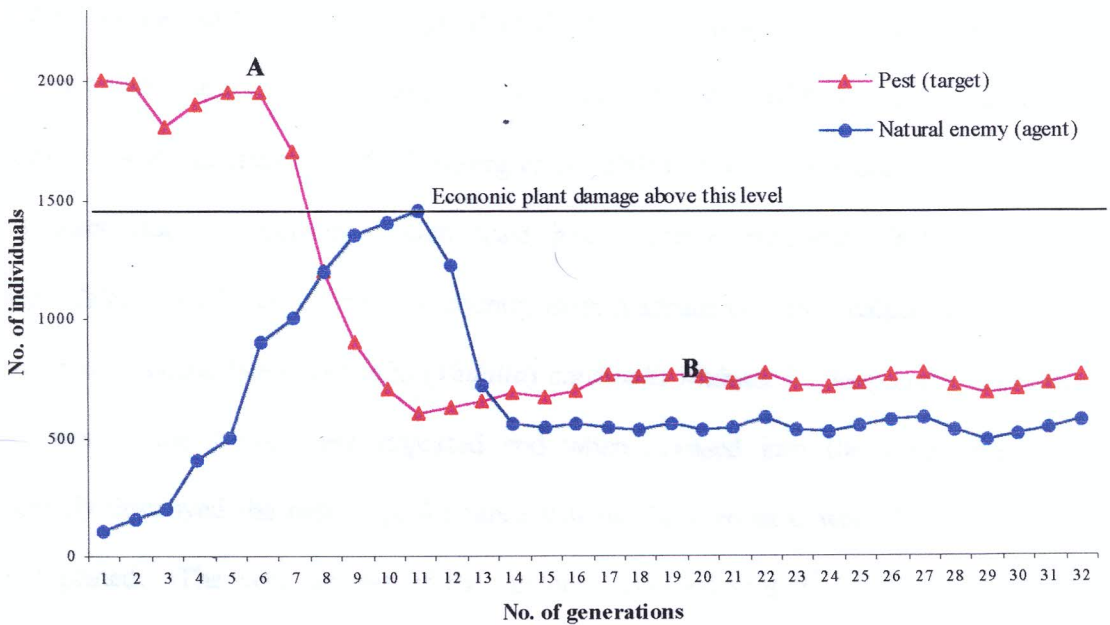


Fig.1.0.1: Successful biological control: The increase in the population of the natural enemy causes a decrease in the pest from damaging level (A) to a non-damaging one (B). With now fewer pests to sustain it, the natural enemy population declines. Both populations then continue at a low equilibrium level (modified from Samways, 1981)

Owing to the undesirable environmental effects of the most potent insecticides, the idea of combating a pest with the aid of its natural enemies is attractive. Theoretically it should also be cheaper. Unfortunately, it is very difficult to achieve in practice although there have been some great successes. The control of the prickly pear cactus in Australia by means of the moth *Cactoblastic cactorum* is a classic example. It is, however, easier to control a plant than an insect pest because the former is static and the control can be brought to it. The biological control of insect pests has occasionally been achieved, but it is a far more sophisticated matter than even the use of the right insecticide technique and offers less guarantee of success.

The only effective controls on insects, that is to say the only organism that kill enough of them fast enough, are microorganisms and other insects. Microorganisms cannot readily be made to control a particular outbreak since their own multiplication depends on environmental

conditions, especially climatic ones, which cannot be guaranteed. Limited success has been obtained with bacterial preparations against lepidopteran caterpillars and beetle larvae.

The best controls are thus other insects. The classic case occurred towards the end of the 19th century in California (Ehler, 1990; Eilenberg *et al.*, 2001). Citrus plantations were being ruined by a plant bug, the cottony-cushion scale insect, *Icerya purchasi* Maskell (Homoptera: Margarodidae), which had entered the country from Australia or New Zealand where its natural predator is a vedalia beetle (*Rodolia (Vedalia) cardinalis* Mulsant [Coleoptera: Coccinellidae]). Specimens of the beetle were imported and when released into the Californian orchards completely destroyed the pest, a performance that has been equaled whenever the process has been repeated. The very success of the venture raised extravagant hopes for the future of biological control, which have not usually been realized, although the principle is likely to be developed.

DeBach (1964) gives an example of recent control, which was not only a complete success but demonstrates how cheap biological control, can be. Citrus crops are very important to the economy of Greece and surrounding countries. Many coccids (scale insects) attack them, but in 1962 the principal one was *Chrysomphalus dictyospermi*, which produced leaf-drop, dead twigs and fruit, encrusted with scale. Several species of likely parasites were transported by air from the breeding houses in the University of California. One of them, a small chalcid, *Aphytis melinus* (Hymenoptera: Chalcididae), survived well under local conditions and in a couple of years had eliminated the scale at a cost of a few hundred dollars. That figure includes the cost of transporting the parasites to Greece and colonizing them there but not, of maintaining the breeding establishment. By any standards the cost compares well with that of chemical control, which in this case had not been particularly successful.

Perhaps the best-known method of biological control is that used to combat exotic pests. Exotic pests frequently invade regions without their adapted natural enemy complex and, in the absence of effective local natural enemies, they can reach very high population levels. Their control involves the introduction and establishment of effective natural enemies imported from the pest's area of origin. This method is frequently called *classical biological control* in recognition of its relatively early first use in the 1800s (Crawley, 1992).

1.1: Approaches to Biological Control

In a bid to harmonize the terminology in biological control across different research disciplines, Eilenberg *et al.* (2001) provide a unified framework for studying this rapidly growing area. They outline and define four strategies of biological control as discussed below in brief:

(i) Classical biological control

This is the intentional introduction of an exotic, usually co-evolved, biological control agent for permanent establishment and long-term pest control. In its original form, it is the use of exotic biological control agents imported from its native home into the target area against exotic pests that have arrived without their natural enemies. In the absence of their natural enemies, the exotic pests multiply rapidly and spread to become a major pest. Thus, classical biological control attempts to introduce the natural enemies also into the new area so that they will reestablish equilibrium with the pest and keep it under control. This is often referred to as an old association because the natural enemy and pest were in the same place or ecosystem. The term 'neo-classical' (or 'new association') biological control has been used when an exotic natural enemy is introduced against a native pest.

(ii) Inoculation biological control

This is the intentional release of a living organism as a biological control agent with the expectation that it will multiply and control the pest for an extended period, but not permanently.

The number of predators released is insufficient to control the pest insects, and success depends on the ability of the released organisms to multiply and reduce the target population. This type of release or application to control pest insects is strongly dependent on population regulation and density dependent processes. Sufficient pest numbers (or other means for growth of the biological control agent) must be maintained following the initial release to support a second or third generation of the released agent, and attention must be focused on ensuring that conditions enable this multiplication to take place.

(iii) **Inundation biological control**

This is the use of living organisms to control pests when, exclusively, the released organisms themselves achieve control. Inundatively released biological control agents must normally contact and kill a sufficiently high proportion of the pest population or by other means reduce the damage level to give economic control before dispersing or being inactivated. The success depends solely on the released population and not their progeny; thus attention is paid to storage, formulation and application. In practice, if there is limited multiplication of the released organism, residual effects (some inoculative effects) often follow inundation biological control.

(iv) **Conservation biological control**

Conservation means premeditated actions for protecting and maintaining natural enemies. It is the modification of the environment or existing practices to protect and enhance specific natural enemies or other organisms to reduce the effect of pests. This approach attempts to increase natural enemy populations or their beneficial effects for control of native or exotic pests. In this strategy, natural enemies are not released. It is rather a combination of protecting biological control agents and providing resources so that they can be more effective. It includes limited and selective use of pesticides but also active processes such as providing refuges adjacent to crops or within crops, facilitating transfer of natural enemies between crops or even directly provisioning food or shelter for natural enemies.

1.2: Pests most suitable for Biological Control

Not all pests can be controlled by biological control technique. The pests most suitable are exotic pests that have been introduced into a country without their natural enemies. The goal in biological control is to find out what the effective natural enemies are, where they can be found, and to try to import them from their native area into the affected areas to control the pests.

Biological control is most suited for single, dominant, exotic pests that are not closely related to indigenous beneficial species. It is not appropriate for a complex of pests, or pests with many related members, which are of economic importance because it may attack them as well.

1.3: Integrated Control

Van den Bosch *et al.* (1971) define integrated control as follows:

Integrated control is a pest population management system that utilises all suitable techniques either to reduce pest populations and maintain them at levels below those causing economic injury, or to so manipulate the populations that they are prevented from causing such injury. Integrated control achieves this deal by harmonising techniques in an organised way, by making the techniques compatible, and blending them into a multifaceted, flexible system. In other words, it is a holistic approach aimed at minimising pest impact while simultaneously maintaining the integrity of the ecosystem.

Though there is a general agreement that the development of an integrated control program requires the exercise of judgement and the selective acquisition of much ecological information, opinions vary considerably regarding the extent to which mathematical and statistical techniques are needed to exploit this information. At opposite ends of the spectrum of opinion, we see positions that, respectively, may be called "quantitative" and the "qualitative" view. To so designate them involves an oversimplification, since each position necessarily contains a combination of both approaches, nevertheless, the attitudes they represent are sufficiently

different that the future of integrated control will certainly be influenced accordingly to which predominates.

The *quantitative* view holds that, in general, the ecosystem in which integrated control is needed are susceptible to detailed analysis to an extent that the relations between their main components can be understood and the interactions of these components predicted. That is to say: by a series of formal steps a mathematical model can eventually be prepared that simulates the quantitative interactions of the main entities of the ecosystem, and such a model can be used to predict the result of changing the action of certain of these entities and so make possible pest management by conscious orderly manipulation based on a prior knowledge of the outcome. To some ecologists such an approach constitutes an essential part of *system analysis* which is therefore seen not only as "the use of scientific method with conscious regard for the complexity of the object of study" but also as an application distinguished by the use of advanced mathematical and statistical techniques and by the use of computers" (Dale, 1970). In its latter, more restricted sense, and as it applies to ecological problems, systems analysis comprises the four successive phases that characterize problem solving.

1. The lexical phase, in which a choice is made (by an ecologist rather than a mathematician) of the entities that compose the system.
2. The parsing phase, in which the relationships between selected entities are defined.
3. The modeling phase, in which an attempt is made to specify by means of a model, the mechanism by which changes in the system take place.
4. The analysis phase, which involves solution of the model, in some sense, and validation of the model outputs by comparing them to the real system outputs (Huffaker, Messenger & DeBach, 1971).

Having a descriptive model described in a computer program, one may, at will change the various components of that system to determine the optimum way in which the pest density may be regulated or maintained at any level set by the simulator. The desired level might be a pest

population below the economic level. The relative cost of alternative programs for achieving this level could be compared. In another situation, it might be useful to determine just how close to the desired population level we might reach by altering a single factor as others are held constant.

1.4: Natural Enemies

A natural enemy is an organism (an animal or plant) that causes the premature death of another organism. In nature all populations of organisms have restraints preventing their unlimited increase. These restraints may be divided into two groups. First there are those that exert their effect irrespective of the density of the population on which they act (*density independent* factors). These factors affect the population no matter what the population level. Examples are weather and climate. Second, there are those whose influence varies according to the density of the population (*density dependent* factors). When the density dependent process is positive, its effect is proportionately strongest with a high population and relatively weakest with a low one. In other words, the percentage mortality is highest when the prey population is high and lowest when prey individuals are few and widely scattered. The result is that the population is regulated within certain limits. As biological control is a form of induced population regulation, it is of value to understand these density-dependent regulatory processes in natural populations.

Parasitoids and predators are an important positive regulatory pressure upon many insect prey populations. Parasitoids are insects that lay their eggs on, in, or near the bodies of other insects (Godfray & Shimada, 1999). The eggs hatch and the parasitoid larvae kill the host as they feed on it. 'Some parasitoids consume their host immediately (*idiobionts*) while others allow their host to feed and increase in size (*koinobionts*); some parasitoids feed alone on the host while others develop in large broods (*solitary* versus *gregarious*); some species feed internally in the

host (*endoparasitoids*), others externally (*ectoparasitoids*)' (Godfray and Shimada, 1999). They have only a single age-class (the adult female) that searches for hosts. These natural enemies can contribute towards maintaining their hosts at a characteristically low level (see Samways, 1981).

The interactions between parasitoid species are classified as either *exploitation* or *interference* competition. In the simpler case of exploitation competition, the parasitoid species are independent of each other in their use of the host species; hence the covariance between their distributions in the host population is zero. This assumes that exploitation competition does not lead to the exclusion from a host of one parasitoid species due to the presence of another. In contrast, in the case of interference competition, interactions between the two parasitoid species may be antagonistic or synergistic. These interactions cause the presence of one species to influence the probability that the other is present; there is thus a non-zero covariance term, which alters the statistical distribution of each parasitoid species. Where interactions between the parasitoid species are antagonistic, the covariance term is negative; where interactions are synergistic, the covariance is positive.

1.5: Factors important to successful parasitism

Godfray & Shimada (1999) noted that excellent biological control implies superior parasitoid properties relative to the situation. They identified four main characteristics that are pertinent to the efficiency of a parasitoid. These are,

- (1) its adaptability to the varying physical conditions of the environment,
- (2) its searching capacity, including its general mobility,
- (3) its power of increase relative to that of its prey, and
- (4) Other intrinsic properties, such as synchronization with host, its host specificity, degree of discrimination, ability to survive host-free periods, and special behavioural traits that alter its performance as related to density or dispersion of its host and its own population.

1.6: The Basic Theory of Competition

Owing to the complexity of insect behaviour and physiology, numerous factors that modify the size of their populations exist. These factors include climate, food and competition with other animals of the same or of different species.

When two or more animals are seeking the same resource, which is in short supply, then competition is said to occur. Varley et al. (1973) defined competition as a 'manifestation of the struggle for existence in which two or more organisms of the same or of different species exert a disadvantageous influence upon each other because their more or less active demands exceed the immediate supply of their common resources'. This implies that populations existing within the same (narrow) ecological niche cause competition; that is, once the population has grown to a size at which one individual cannot obtain resources without affecting another, competition will occur.

Competition is divided into intra-specific (within-species) competition, which is the competition between individuals of the same species, and inter-specific (between-species) competition, which is the competition between individuals of different species. Intra-specific competition increases when a population grows until it strains or surpasses its carrying capacity. If in a population, mortality from competition increases as the population density increases, then we say that competition acts in a density-dependent manner. In this case, stabilization of a population is feasible.

Two competitive outcomes are possible: coexistence or displacement. The problem of interest, therefore, is the prediction of the possible outcome and the determination of the variables and conditions that produce either of the two outcomes.

In either intra- or inter-specific competition, two extreme forms of competition do exist: 'contest' and 'scramble' competition. In the former, each successful competitor gets all it requires for survival or reproduction while the unsuccessful one gets insufficient or none at all.

The competitors seeking the resource harm one another in the process even if the resource is not in short supply. In the latter, the resource is shared amongst all the competitors, each competitor trying to acquire as much of the resource as possible. Thus a number of organisms utilise common resources that are in short supply. For species with scramble competition, the effect of population growth may be an increased mortality, or decreased growth by individuals, or both. The principle of *competitive exclusion* states that complete overlap between niches is impractical. Thus the 'victor' will eventually eliminate the 'loser'.

Varley et al. (1973) outline three factors to consider when assessing the effect of competition, viz;

- (i) a measure of the changes in the supply of resources,
- (ii) a measure of the number of individuals competing in the population, and
- (iii) an assessment of the disadvantageous influences that may show either as a reduction in the number or proportion which survive, or as a reduction in growth rate, adult weight or reproductive capacity.

Parasitoid population ecologists have been concerned with the contentious issue of multiple introductions of parasitoids as a biological control strategy. At opposite ends of the spectrum, we see two antagonistic approaches. On the one hand, it is argued on *a priori* grounds that the most effective parasitoid species will always cause a greater depression of the host equilibrium on its own than in competition with other species (e.g., Turnbull & Chant, 1961; Turnbull, 1967; and Watt, 1965). On the other hand, Huffaker (1971) and van den Bosch (1968) take a more pragmatic stance, arguing that the identification of the "most effective" parasitoid species is impractical (see Ehler, 1990).

In the next chapter, we discuss some basic mathematical models that are frequently utilized in population ecology.

CHAPTER TWO

SOME BASIC MATHEMATICAL MODELS IN POPULATION ECOLOGY

2.0: Introduction.

'In formulating a stochastic model to describe a real phenomenon it used to be that one compromised between choosing a model that is a realistic replica of the actual situation and one whose mathematical analysis is tractable. That is, there did not seem to be any payoff in choosing a model that faithfully conformed to the phenomenon under study if it were not possible to mathematically analyse that model. Similar considerations have led to the concentration on asymptotic or steady-state results as opposed to the more useful ones on transient time. However, the relatively recent advent of fast and inexpensive computational power has opened up another approach-namely, to try to model the phenomenon as faithfully as possible and then to rely on simulation study to analyse it' (Ross, 1990). With the ubiquitous availability of computers, and, statistical program packages such as SAS or BMDP that contain easy-to-handle routines for solving non-linear regression problem, the numerical solution of large ecological models became feasible. In this chapter, we discuss some basic mathematical models that describe population growth. We begin with the most elementary idea in ecology: the growth in the number of individual organisms making up a single population. We then incorporate density-dependence in birth and death rates. Later, we introduce a second population of a competing species and model the growth of the two competing populations.

2.1: The Geometric model

This is the simplest population growth model. For many organisms, time does not really behave as a continuous variable (Gotelli, 1998). Consider a unicellular organism that reproduces by the process of binary fission, and whose population has non-overlapping generations (e.g. amoeba). Let N_t be its population density at time t . Further, let N_0 be its initial population density and

suppose that no limit affects its population growth. Then its rate of increase per unit time is given by

$$R = \frac{N_t}{N_{t-1}}, \quad t = 1, 2, \dots \quad (2.1.1)$$

and hence its density at time t is given by

$$N_t = N_0 R^t, \quad t = 1, 2, \dots \quad (2.1.2)$$

which is an expanding geometric series. This model (2.1.2) is much too simple to be realistic for many natural populations. It leads to populations that continue to grow indefinitely. Obviously, population growth is always, sooner or later, checked.

2.2: The Malthusian Model.

The Reverend Thomas R. Malthus (1766-1834), while giving the first qualitative formulation of population growth, observed that increase of population follows a geometric progression in contrast to its mean of subsistence that tends to grow in arithmetic progression (see Biswas, 1988). Suppose that population growth is a continuous process. Then from simple differential equations, we can derive a mathematical model of population change. Let N_t be the population density at any time t , then the population's instantaneous growth rate is given by

$$\frac{dN_t}{dt} = rN_t \quad (2.2.1),$$

where r (=instantaneous birthrate – instantaneous deathrate) is the intrinsic rate of natural increase in the given ecosystem if the population size does not exert pressure on the environment. This is a potential rate of increase under conditions of unlimited resources and is related to R in (2.1.2) by $r = \log_e R$. Equation (2.2.1) says that the rate of change of the population is proportional to the existing population, under condition of unlimited resources. The integral form of (2.2.1) is

$$\int \frac{dN_t}{dt} dt = \int rN_t dt$$

$$\Rightarrow \int \frac{dN_t}{N_t} = \int r dt$$

$\Rightarrow \ln N_t = rt + C$, C being the constant of integration.

If the initial size of the population is N_0 (at time $t=0$),

$$C = \ln N_0 \Rightarrow \ln N_t - \ln N_0 = rt \quad (2.2.2)$$

$$\Rightarrow N_t = N_0 e^{rt} \quad (2.2.3)$$

Curves based on these equations are known as the exponential population growth curves.

Malthus did not take into account of the fact that in any given environment the growth of the population may stop due to the density of the population that the environment can sustain (Biswas, 1988).

2.3: The Logistic Model.

If in equation (2.2.1) $r > 0$, we have growth. Here the population grows and continues to expand to infinity, that is $\lim_{t \rightarrow \infty} N_t = +\infty$. On the other hand, if $r < 0$, we have decay. Here the population will shrink and tend to zero; that is, we are facing extinction. Evidently, the first case, $r > 0$ is inadequate and the model is inappropriate. The premise has to do with environmental limitations. The complication is that the population growth is eventually limited by some factor, usually one from among the many factors. When a population is far from its limits of growth, it can grow exponentially. However, when nearing its limits the population size fluctuates, even chaotically. To remedy this flaw in the Malthusian model, Pierre F. Verhulst (1804-1849) proposed the logistic model in 1838 (Gotelli, 1998). He postulated that the rate of the population growth was jointly proportional to the existing population (Biswas, 1988). That is the actual rate of increase per individual as opposed to the intrinsic rate (r , which is a constant) is reduced as the

population (N_t) rises to a stable upper limit 'K', which is a limiting size for the population. 'K' is also called the 'carrying capacity' and it depicts the maximum population size that can be supported by the resources in the environment.

To derive the differential equation for this model, consider equation (2.2.1). If the population is very small we would expect the effect of intra-specific competition to be very low as well, and the growth rate $\frac{dN_t}{dt} \left(\frac{1}{N_t} \right)$ would be at the maximum, ' r ' (Fig.2.3.1). On the other hand, when N_t is very high, intra-specific competition would stop the population from increasing any further, so the growth rate would be zero. Assuming the simplest situation in which ' r ' decreases at a constant rate as N_t , and the amount of competition increases, we can represent this situation graphically as in Fig.2.3.1 below:

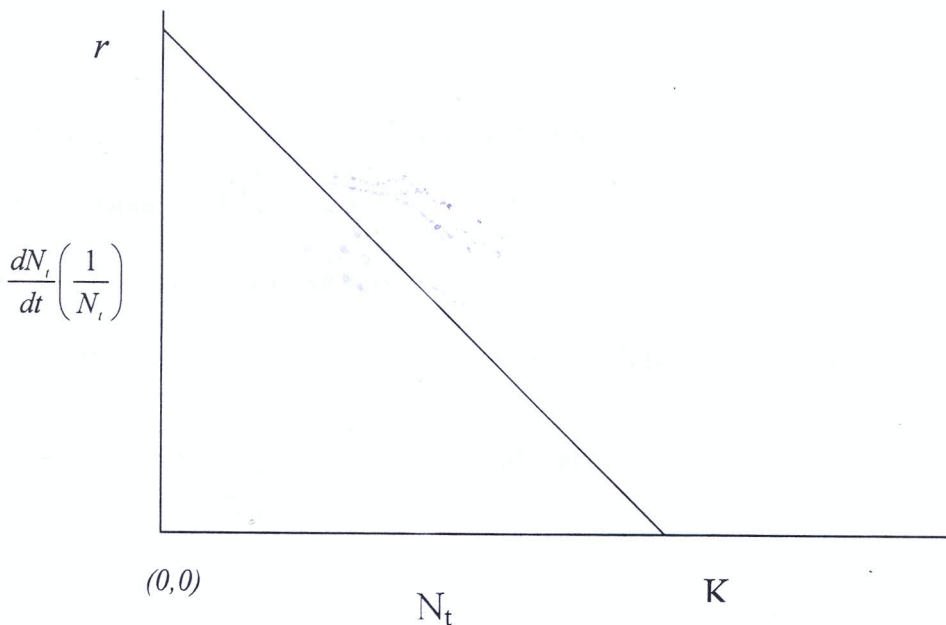


Fig.2.3.1: Diagrammatic representation of the logistic model.

The population where r is zero is labelled with a K

Now using the general equation of a straight line,

$$y = mx + c$$

we obtain the equation for the above graph as

$$\frac{1}{N_t} \frac{dN_t}{dt} = -\left(\frac{rN_t}{K}\right) + r \quad (2.3.1)$$

$$\text{Rearranging, this gives the rate of increase as } \frac{dN_t}{dt} = rN_t(1 - N_t/K), \quad (2.3.2)$$

which is the logistic model.

The feedback term $(1 - N_t/K)$ reflects the fact that every individual subtracts equally from the carrying capacity 'K'. It is the addition of this feedback term in (2.3.2) that makes the logistic curve depart from the Malthusian curve. The term N_t/K measures the retarding force due to the environmental resistance. In the initial stage when N_t is small, this force is negligible and equation (2.3.2) reduces to the Malthusian equation. On the other hand, as N_t approaches 'K', this force increases and its value approaches unity. We observe that $N_t = K \Rightarrow \frac{dN_t}{dt} = 0$

That is, as the population increases, the rate of increase (r^*), (where $r^* = r\left(1 - \frac{N_t}{K}\right)$) is progressively reduced and it approaches zero (birthrate = deathrate) when the population has reached the value of 'K'.

To solve equation (2.3.2), we recognise a non-linear equation that is separable. The constant solutions are $N_t=0$ and $N_t=K$. The non-constant solutions may be obtained by separating the

$$\begin{aligned} \text{variables } \frac{dN_t}{N_t\left(1 - \frac{N_t}{K}\right)} = rdt \quad \text{and integrating} \quad \int \frac{dN_t}{N_t\left(1 - \frac{N_t}{K}\right)} &= \int rdt \\ \Rightarrow \int \frac{dN_t}{N_t} + \int \frac{dN_t}{(K - N_t)} &= \int rdt. \end{aligned}$$

If the initial size of the population is N_0 (assuming N_0 is not equal to both 0 or K), we get

$$N_t = \frac{K}{1 + he^{-rt}}, \text{ where } h = \frac{K - N_0}{N_0} \quad (2.3.3)$$

This is the fundamental equation of the logistic growth, which can be taken as the generalisation of the Malthusian model (Biswas, 1988). From equation (2.3.3), it is clear that as $t \rightarrow \infty$, N approaches the asymptotic value or carrying capacity, K .

Differentiating (2.3.2), we get $\frac{d^2N_t}{dt^2} = r \frac{dN_t}{dt} \left(1 - \frac{2N_t}{K}\right)$.

Substituting for dN_t/dt from (2.3.2), we get $\frac{d^2N_t}{dt^2} = r^2 N_t \left(1 - \frac{N_t}{K}\right) \left(1 - \frac{2N_t}{K}\right)$. (2.3.4)

Now, $d^2N_t/dt^2 = 0$ has three roots, first at $N_t = 0$, the second at $N_t = K/2$ and the third at $N_t = K$.

At the extreme values, $N_t = 0$ and $N_t = K$, the rate of increase is zero. The logistic curve is flat at these points. At the intermediate value, the population increases steeply. The constant h is

related to the point (t') of inflection of the curve on the time axis by $t' = \frac{\ell n h}{r}$. The predicted

population size at this time (N_t') is always half of the value of K , ($N_t' = K/2$) (Varley *et al.*,

1973). One flaw of the logistic model is that it does not tell us when a population is facing extinction since it never implies that. Even starting with a small population, it will always tend to 'K'. The three major assumptions for this model are

- (i) All individuals are equivalent,
- (ii) The parameters r and K are constants, and
- (iii) There is no time lag in the response of the actual rate of increase per individual to changes in population density.

Assumption (i) implies that age and sex differences are ignored. Assumption (ii) implies that the environment is constant. Assumption (iii) is a common assumption in differential equation models of a population.

2.4: The Ricker Model.

In 1954, W.E. Ricker developed a simple way of showing the effects of density-dependent mortalities on fishes, which he also applied to insects (Varley et al., 1973).

$$\text{The model, written as } N_{t+1} = \alpha N_t \exp(-\beta N_t) \quad (2.4.1)$$

assumes a negative exponential density dependent relationship. The parameter α is the finite rate of population change; that is, the average number of births per individual per generation. On the other hand, β gives the strength of density dependence. In its original form, N_t is supposed to represent the number of members of a given population in generation t divided by the carrying capacity of the environment (as earlier defined, carrying capacity is the largest number of members that can coexist under optimal nutritional conditions in the environment). Two things determine the shape of the Ricker's reproduction curves: α and β .

Dividing (2.4.1) by N_t and taking the natural (Naperian) logarithms, we obtain

$$\ln(N_{t+1}/N_t) = \ln\alpha - \beta N_t \quad (2.4.2)$$

Thus $\ln(N_{t+1}/N_t)$ can be regressed against N_t to evaluate $\ln\alpha$ (and hence α) and β , and to find out how accurately this model describes the dynamics of insect populations.

We now consider a system in which two insect populations or population units, designated as 'A' and 'B' with parameters having these suffixes, are both feeding exclusively on the same food.

2.5: The Lotka-Volterra Competition Model

Interesting mathematical models that we have not so far considered are those that incorporate interactions between species. The earliest inter-specific competition model in ecology was proposed in the 1920s and 1930s by the American biophysicist Alfred J. Lotka (1880-1949) and, independently, by the Italian mathematician Vito Volterra (1860-1940) (Gotelli, 1998). The Lotka-Volterra model (simply called L-V model) is an extension of the logistic model to cover two competing species, and is based on two equations of population growth; one for each of the two competing species.

The feedback term $(1-N_i/K)$ in equation (2.3.2) represents intra-specific competition. We need to generalize it, so that it includes inter-specific competition as well. How do we do this? Let the rate of increase for the two competing species A and B, be governed by equation (2.3.2). Let each have its own intrinsic rate of increase (r_A or r_B) and its own carrying capacity (K_A or K_B). If these two species are interacting, that is, affecting the population growth of each other, another term must be introduced into equation (2.3.2). Let α be a competition coefficient—a number giving the degree to which an individual of species B affects through competition the growth or equilibrium level of species A's population, relative to the effect of an individual of species A. If $\alpha=1$, then individuals of the two species are interchangeable—each has an equal effect in depressing the growth of species A. On the other hand, suppose $\alpha=2$. Each individual of species B that is added to the environment depresses the growth of N_A by the same amount as adding two individuals of species A (Gotelli, 1998). Thus α expresses the impact on population growth of species A of an individual of species B, relative to the impact of an individual of species A. Similarly, let β be a competition coefficient, measuring the extent to which species A presses upon the resources used by species B. That is, β is

the per capita effect of species A on the population growth of species B. Then, the carrying capacities are reduced according to

$$K'_A = \frac{K_A}{1 + \alpha(N_B/N_A)} \quad \text{and} \quad K'_B = \frac{K_B}{1 + \beta(N_A/N_B)} \quad (2.5.1)$$

Substituting these in equation (2.3.2), we obtain the celebrated L-V equations as

$$\frac{dN_A}{dt} = r_A N_A \left(1 - \frac{N_A}{K'_A} \right) \quad (2.5.2)$$

$$\frac{dN_B}{dt} = r_B N_B \left(1 - \frac{N_B}{K'_B} \right)$$

Though these equations are too simple to be realistic for many natural populations, they are much quoted since they assist us to picture the way in which competition may act (Varley et al., 1973).

Depending on the relations of α and β to K_A and K_B , the L-V equations lead to different results of competition. To predict the outcome of competition over time, we determine population sizes for species A and B for which population growth of both species will be zero. That is, we determine the equilibria. Thus by setting both L-V equations equal to zero, we produce expressions that define the permissible ratios of species A and species B at equilibrium.

Now at equilibrium point $\frac{dN_A}{dt} = 0$ and $\frac{dN_B}{dt} = 0$

Let us first determine the population sizes for which the population growth of species A is equal to

zero:
$$\frac{dN_A}{dt} = 0 = r_A N_A \left(1 - \frac{N_A}{K'_A} \right) \quad (2.5.3)$$

This expression is equal to zero if any of the three factors r_A , N_A or $(1 - N_A/K'_A)$ is equal to zero. If $r_A=0$, then the maximum population growth rate for species A would be zero. But this is a trivial case of a population with no growth potential. Another trivial case is if $N_A=0$ since the implication is that we have a population with no individuals of species A. Since we are interested with situations

in which species A exists (to see what happens when it competes with species B). we are left with one and only one non-trivial case- when $(1 - N_A/K'_A) = 0$

$$\Rightarrow 0 = 1 - \frac{(N_A + \alpha N_B)}{K_A}$$

$$\text{Solving this, we find } \hat{N}_A = K_A - \alpha N_B \text{ and } \hat{N}_B = (K_A - N_A)/\alpha \quad (2.5.4)$$

Plotting N_A against N_B , we obtain a straight line with N_A -intercept= K_A ; N_B -intercept= K_A/α and the slope= $-\alpha$. Thus the graph looks like this:

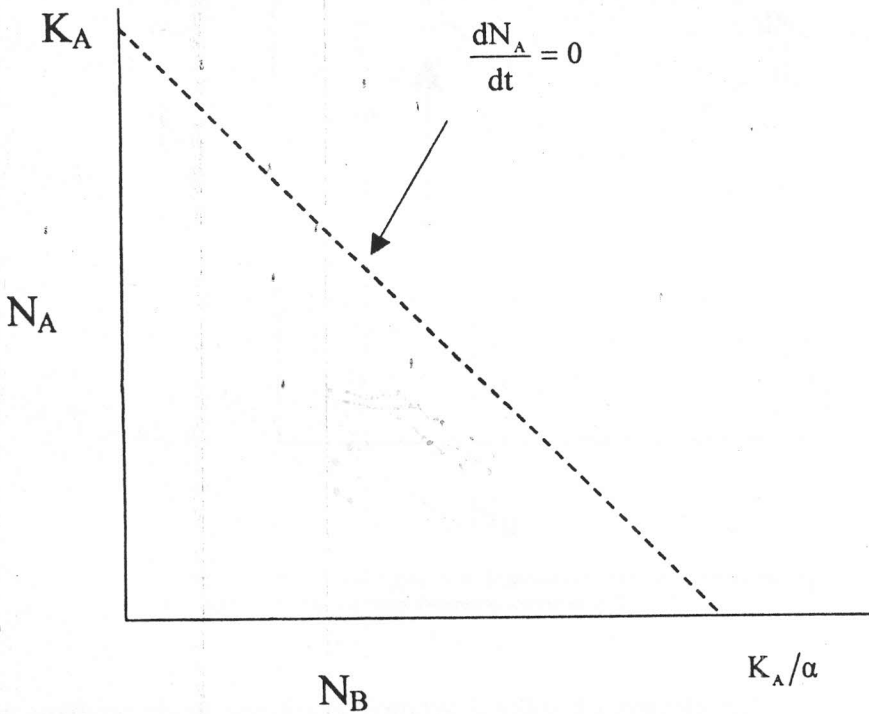


Fig.2.5.1: The N_A - isocline generated by the L-V competition equations.

The line, called an isocline (zero growth isocline) for species A, represents all combinations of N_A and N_B for which $dN_A/dt=0$.

If N_A and N_B correspond to a point below this line, then we have fewer individuals of the two species than the numbers required to cause dN_A/dt to be zero (i.e., $dN_A/dt>0$). Thus there would be plenty of resources for species A, and the population of species A would increase in size. On the

other hand, if the density pairs fall above the isocline, then we have more individuals of the two species than would cause growth to be zero. Thus N_A would fall due to the presence of so many individuals (leading to depletion of resources). Graphical representation of these areas of increases or decreases looks like this:

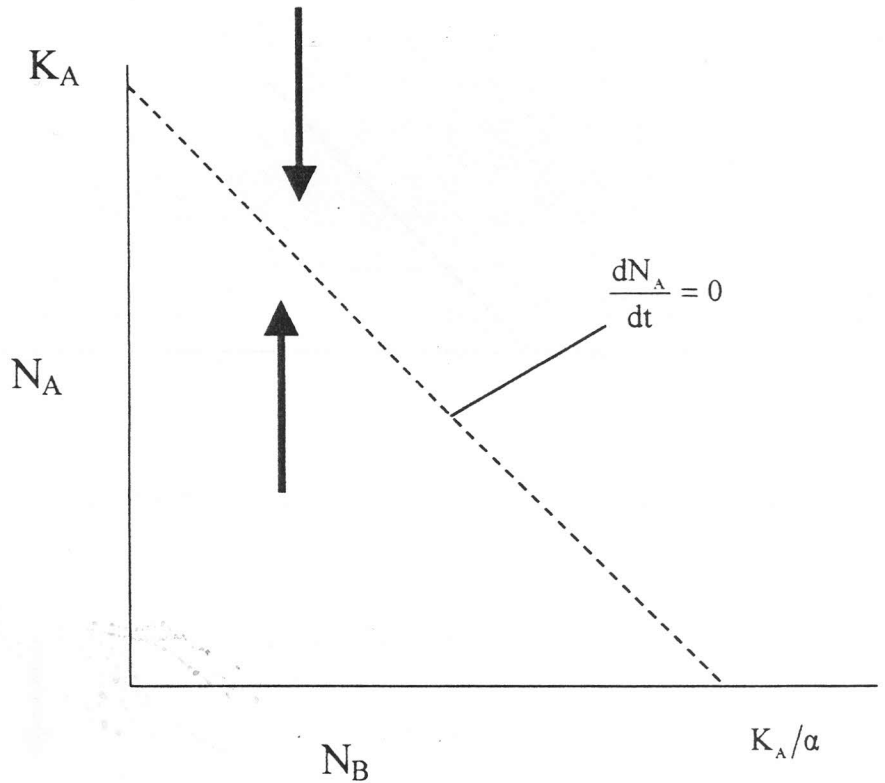


Fig.2.5.2: Relative abundance of species A. An upward arrow represents increase in N_A , while a downward arrow represents decrease in N_A .

We cannot infer anything about species B from the isocline for species A.

Analogously by imitating the above argument, but with all the A's and B's reversed, we can determine the population sizes for which species B population growth is zero. The equilibrium population density in this case is $\hat{N}_B = K_B - \beta N_A$ (2.5.5)

The zero growth isocline and the graphical representation of the areas of increase or decrease for species B are as shown in Figures 2.5.3 and 2.5.4 respectively:

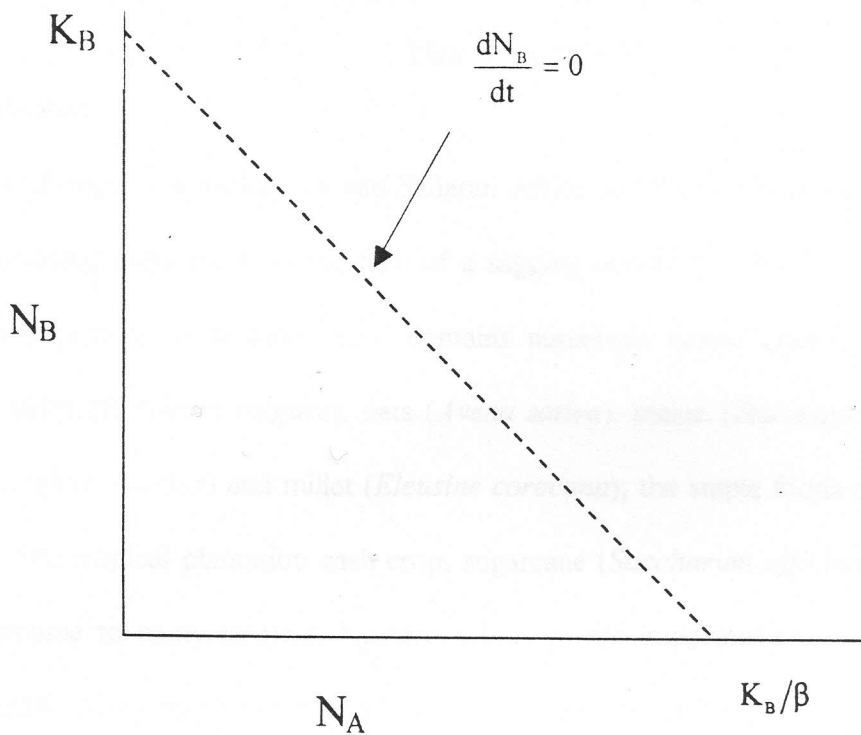


Fig.2.5.3: Isocline for species B. Below the isocline there are few individuals of species A and species B, and hence plenty of resources.

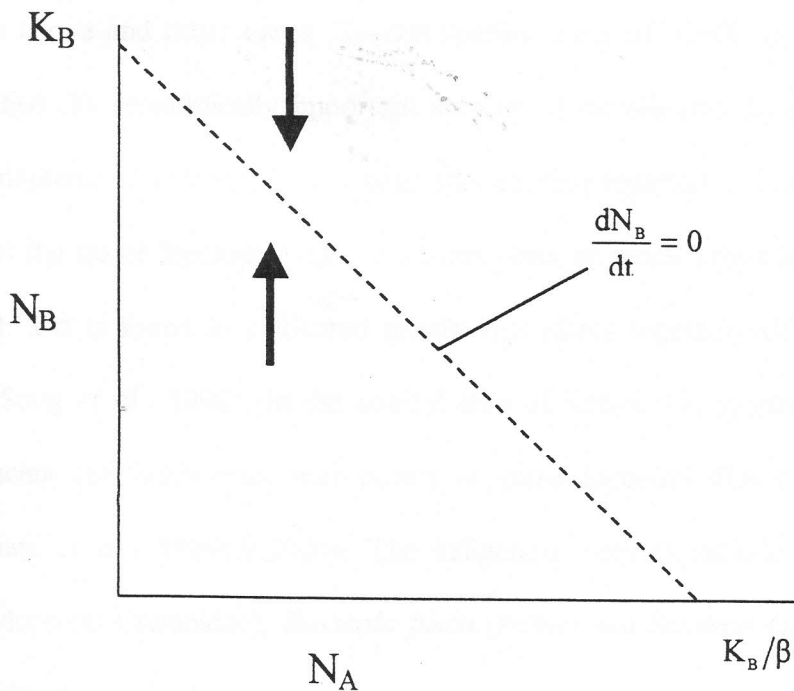


Fig.2.5.4: Relative abundance of species B. An upward arrow represents growth of species B while a downward arrow represents decrease in N_B .

CHAPTER THREE

THE MODEL

3.0: Introduction

The major challenge now facing the sub-Saharan Africa and Kenya in particular is that of feeding the ever-increasing population, in the face of a sagging economy. The Gramineae is the family of plants most important to humans, as it contains numerous cereal grasses like wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), oats (*Avena sativa*), maize (*Zea mays*), rice (*Oryza sativa*), sorghum (*Sorghum bicolor*) and millet (*Eleusine coracana*), the staple foods of most of the world's population. The tropical plantation cash crop, sugarcane (*Saccharum officinarum*) is important for providing income to many farmers. Numerous grasses are important sources of fibres as well as livestock feeds. Many insect pests attack them but lepidopteran stem-borers are ubiquitous and the most damaging (Mohyuddin and Greathead, 1970; Bosque-Perez & Schulthess, 1998; Seshu Reddy, 1998). Stem-borers are the immature stages of certain moths, which feed internally within the stems of the above and other crops. Several species, most of which are indigenous occur. Maes (1997) identified 20 economically important species of stem-borers in Africa. *Chilo partellus* Swinhoe (Lepidoptera: Crambidae) is an exotic species, first reported in Africa from Asia in the 1930s. It is one of the major lepidopterous stem-borer pests of cereal crops in Kenya (Overholt *et al.*, 1994a, 1997), and is found in cultivated gramineous plants together with indigenous stem-borer species (Ngi-Song *et al.*, 1996). In the coastal area of Kenya, *Ch. partellus* is the most abundant and is displacing the indigenous stem-borers at some locations (Overholt *et al.*, 1994a; Kfir, 1997; Ofomata *et al.*, 1999a,b,2000). The indigenous species include *Chilo orichalcociliellus* Strand (Lepidoptera: Crambidae), *Busseola fusca* (Fuller) and *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae).

The indigenous natural enemies of *Ch. partellus*, including the most common, gregarious, larval endoparasitoid, *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae) are unable to maintain the pest population density below economically injurious levels (Overholt *et al.*, 1994b; Omwega and Overholt, 1997). For instance, Overholt *et al.* (1994b) showed that *C. sesamiae* accounted for as low as 0.5-3% mortality of late instar *Ch. partellus* larvae in the coastal zone of Kenya. In 1991, *Cotesia flavipes* Cameron (Hymenoptera: Braconidae), a gregarious larval endoparasitoid of stem-borers in Asia, was introduced into Kenya for biological control of *Ch. partellus*. It was selected as the best candidate for introduction because of its history of success outside of Africa and its importance as a parasitoid of stem-borers in its aboriginal home (Overholt *et al.*, 1994b). A colony of *C. flavipes* was initiated at the International Centre of Insect Physiology and Ecology (ICIPE) in Nairobi, Kenya, using parasitoids collected from *Ch. partellus* at Rawalpindi, Pakistan, by the International Institute of Biological Control (IIBC) (Overholt *et al.*, 1994c). A *C. sesamiae* colony was also initiated in 1991 with parasitoids collected from *Ch. partellus* in the coastal zone of Kenya (Ngi-Song *et al.*, 1995). Laboratory studies at the ICIPE revealed that *C. flavipes* and *C. sesamiae* could successfully parasitise not only the target stem-borer, but also *Ch. orichalcociliellus* and *S. calamistis* (Ngi-Song *et al.*, 1995) (Table 2). Both *C. flavipes* and *C. sesamiae* are ecologically similar, attacking medium- and large-sized stem-borer larvae (Smith *et al.*, 1993). Laboratory and field studies, carried out to investigate the intrinsic and extrinsic competition between these two parasitoid species suggested that the former was superior to the latter when *Ch. partellus* was the host (Mbapila, 1994; Ngi-Song *et al.*, 1995; Overholt *et al.*, 1997 and Sallam *et al.*, 1999).

In the long rains season of 1993 (March-July), *C. flavipes* was released at three sites in the Coast Province of Kenya (Mtwapa, Kaloleni and Kikoneni) over a period of 6-8 weeks (Overholt *et al.*, 1994c). Recoveries since 1994 have demonstrated that the parasitoid is firmly established (Overholt, 1998) in various regions of the coastal Kenya (Overholt *et al.*, 1997 & Overholt, 1998) (see Table

3.1). Recently, some evidence has been established suggesting that this exotic braconid wasp might become an important mortality factor of stem-borers at the coast. For instance, in the long rains season of 1999, Zhou *et al.* (2001) reported that *C. flavipes* accounted for a 52.94% and a 33.07% decrease of *Ch. partellus* density in the north and south coast, respectively. They also reported a 37.1% and an 18.08% reduction of the total stem-borer complex in the north and south coast, respectively, courtesy of this parasitoid during the same season. Elsewhere in southwestern Kenya, comparative studies suggested that the parasitoid was causing greater mortality to stem-borers than in the coastal area (Overholt *et al.*, 1997). A better understanding of the dynamics of the interactive system will be expected if it is described and analyzed by a mathematical model. In this study, therefore, a simple model of the one host-two parasitoids interaction including the parasitoids' intra- and inter-specific competition is presented. The model, essentially a modification of the classical Lotka-Volterra competition model, is developed with special reference to the system of the stem-borer and the two parasitoids, *C. flavipes* and *C. sesamiae*. The relevant variables are the population numbers of individual species populations on a particular season (generation). Data for the model come from various sites in the coastal area, Kenya and are shown in Table 3.1.

Time (t)	Season (long rain/short rain)	Density of <i>C. sesamiae</i> (No. of parasitoids per 100 plants)	Density of <i>C. flavipes</i> (No. of parasitoids per 100 plants)	Density of <i>Ch. partellus</i> (No. of larvae per 100 plants)
0	1992lr	7.95	0	83
1	1992sr	1.29	0	88.3
2	1993lr	0.58	0.63	96.6
3	1993sr	1.84	0.11	115.4
4	1994lr	2.47	0.79	126
5	1994sr	4.23	1.12	144
6	1995lr	2.09	0.16	135
7	1995sr	9.97	0.17	140.5
8	1996lr	2.94	2.35	143
9	1996sr*	13	3.19	161.8
10	1997lr	4.05	4.03	170.2
11	1997sr	16	6.21	183.1
12	1998lr	4.93	15.27	142
13	1998sr	9.8	12.52	104
14	1999lr	7.89	15.65	112

$$1996sr^* = (1995sr + 1997sr) / 2$$

Table 3.1: Densities of the two parasitoids and the stem-borers at various sites on the Kenyan coast.

The model attempts to address some specific questions relating to the impact of the parasitoids on the stem-borers and that of the exotic parasitoid species on the indigenous one. These questions are:

- (i) what is the likelihood that *C. flavipes* will have a significant impact on stem-borers in the future?
- (ii) can the levels of parasitism observed explain the decline in stem-borer density?
- (iii) what will be the ultimate impact of *C. flavipes* on *C. sesamiae*?
- (iv) what are the reasons behind (iii) above?

The life cycles of the stem-borer and the parasitoids are outlined below, and then the model described, which addresses the above and, possibly, other questions relating to their interactions with special focus on the competition between the parasitoids.

3.1: The Life Cycle of the Host

The biology, management and population dynamics of *Chilo partellus* in East Africa has been intensively studied (in the absence of any significant natural enemies). We outline a simplified description of its life cycle as given in Ofofata (1998) and the references therein.

The adult moths are nocturnal and live for approximately one week. Oviposition begins on the night of emergence and continues for two nights. Ovipositing a mean of 434 eggs, the eggs are deposited in masses on the undersurface of leaf blades. The egg developmental period is 4 to 5 days at 26-28°C. Eggs hatch early in the morning and on hatching, larvae crawl to the tips of the leaves where they either suspend themselves on fine silken threads and are blown away to infest neighbouring plants or crawl towards the leaf whorls or sheaths depending on the stage of the plant. Young larvae feed actively on tender leaves, but bore into the stems as they increase in size. On a natural diet, the larval stage lasts for 16 to 41 days at 24-33°C. When larvae are fully-grown, they start preparing for pupation by cutting exit holes in the stem to enable the emerging moths to escape. The pupal stage

lasts 4 to 8 days. The life cycle may be continuous where favourable conditions for host plant growth exist throughout the year. However, the cycle is usually interrupted by a cold or dry season, during which host plants are not available or are unsuitable for growth and development of the stem-borers. The mature larvae then enter diapause inside old stems or stubbles and pupate on return of favourable conditions. Diapausing larvae of *Ch. partellus* lose their cuticular pigments, cease to feed and become resistant to desiccation. Diapause is broken with the onset of favourable conditions. There is large variation in the duration of the larval stage and the period spent in facultative larval diapause. Consequently, overlapping generations occur.

3.2.1: The Biology of *C. flavipes*

Cotesia (= *Apanteles*) *flavipes* is a gregarious braconid wasp that develops within the larvae of the African gramineous stem-borers. An adult parasitoid has a short lifespan of about 3 days. Gifford and Mann (1967) reported that the adult females lived 4-5 days while adult males lived 4-7 days at 28.3°C. Potting *et al.* (1997) reported that the average lifespan of fed female wasps in a humid environment (70-80% RH) at 22°C was 6.1 days, whereas fed parasitoids in a dry environment (35-40% RH) at 31°C lived an average of only 8 hours. They, therefore, inferred that temperature, humidity and food availability had significant effect on the longevity of the female wasps. The adults mate and the females lay eggs, in most cases, immediately after emerging from their cocoons. Soon after mating, eggs are deposited into medium- and large-sized larvae of caterpillars. To locate the host microhabitat, female *C. flavipes* use olfactory stimuli that are emitted by the infested stem but, also, by the undamaged leaves of the infested plant (Potting *et al.*, 1995). Depositing approximately 35-45 eggs in a single oviposition, in each of the first 3 encountered hosts (Potting *et al.*, 1997), a female lays about 150 eggs during her life. Kajita and Drake (1969) reported that the mean number of eggs at 25°C in *Chilo suppressalis* larvae is 36.5. Around 40% of the wasps are

killed inside the stem (Potting *et al.*, 1997). The duration of immature stages takes about 18 days at 25°C and the sex ratio is typically female biased (60-70%)(Gifford & Mann, 1967; Ngi-Song *et al.*, 1995). Gifford & Mann (1967) reported that at an average temperature of 28°C, *C. flavipes* attains larval maturity in about 11 days. The pupal stage has a mortality rate of 11% and lasts for approximately 6.2 days at 25°C, while at 30°C, the stage has a mortality rate of 22% and lasts for approximately 5.6 days (Kajita & Drake, 1969). *Cotesia* larvae emerge after about 15-20 days and spin their cocoons on or near the host, which dies when the wasps emerge. The life cycle, from egg to adult, is approximately 22-30 days, depending on the temperature.

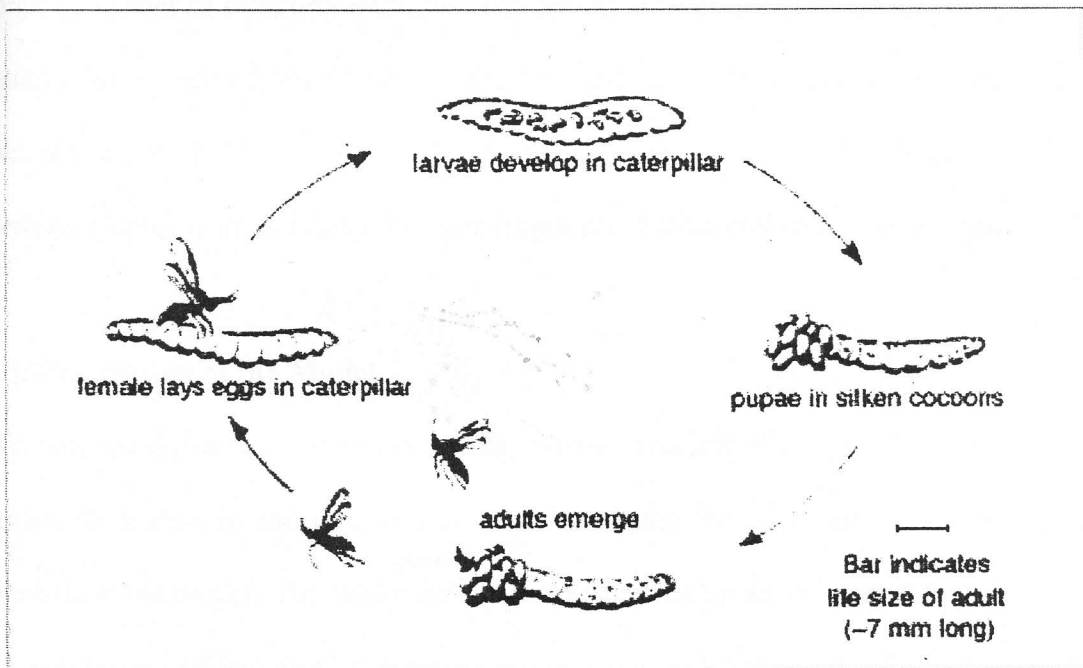


Fig. 3.2.1: A general life cycle of the parasitoid species *C. flavipes* and *C. sesamiae*

3.2.2: The Biology of *C. sesamiae*

We outline the life history of *Cotesia* (= *Apanteles*) *sesamiae* as described by Ullyett (1935).

Cotesia sesamiae is a gregarious braconid larval endoparasitoid that develops within the larvae of the African gramineous stem-borers. An adult parasitoid has a short lifespan of 3-4 days, when food is readily available. Without food, adult longevity is about 1 day. Commonly from 60-100 cocoons are produced from a single host. The white cocoons are spun within the lumen of the maize stalk and are loosely held together with strands of fine silk, the whole mass often surrounding the now sluggish host but attached to the walls of the burrow. Both males and females are produced from each mass of cocoons and mating takes place very shortly after emergence. An adult *C. sesamiae* chooses for oviposition a host that is approximately in the middle of its life. Location of the host is largely a matter of olfactory stimulus. The period from oviposition to the emergence of fully-grown parasite larva varies from 14 days in the warmest part of the summer to 21 days during the cooler weather of late summer and early autumn. In a humid environment (80% RH) at 26°C the pupal period occupies from 5-7 days. Dry conditions are detrimental to the pupal stage.

3.3: Description of the Model

We now establish a competition model, whose structure (Fig. 3.3.1) is based on changes from season to season in the densities of stem-borer and the two parasitoids. Firstly we list all the symbols in the model. The values for the parameters are given in brackets.

- ϕ average no. of female *C. flavipes* emerging from each parasitised *Ch. partellus* (23±2).
- σ average no. of female *C. sesamiae* progeny emerging per *Ch. partellus* attacked (19±3).
- ϵ_f average no. of eggs laid per *C. flavipes* adult (30±3).
- ϵ_s average no. of eggs laid per *C. sesamiae* parasitoid (24±3).
- a_f searching efficiency per *C. flavipes* (0.0060).
- a_s searching efficiency per *C. sesamiae* (0.0032).

m, n parameters of the negative binomial distribution, which measure inversely the degree of aggregation or contagion of, respectively, *C. flavipes* and *C. sesamiae* within the host population (0.67, 0.69).

λ finite rate of increase per adult *Ch. partellus* = average no. of offspring produced by an unparasitised stem-borer (30 ± 10).

N_t densities (population size) of *Ch. partellus* in season t .

F_t densities of adult *C. flavipes* in season t .

S_t densities of adult *C. sesamiae* in season t .

r_f intrinsic rate of increase of *C. flavipes* on *Ch. partellus* at 25°C (0.1569).

r_s intrinsic rate of increase of *C. sesamiae* on *Ch. partellus* at 25°C (0.1067).

R_{of} net reproductive rate of *C. flavipes* = maximum no. of *C. flavipes* adults in season $t+1$ per *C. flavipes* adult in season t on *Ch. partellus* at 25°C (20.96).

R_{os} net reproductive rate of *C. sesamiae* on *Ch. partellus* at 25°C (7.69).

κ_f *C. flavipes* carrying capacity = the equilibrium *C. flavipes* population density from the logistic equation [2.3.2] (77 ± 21).

κ_s *C. sesamiae* carrying capacity (72 ± 15).

α_{ff} *C. flavipes* intraspecific competition coefficient (0.0089).

α_{ss} *C. sesamiae* intraspecific competition coefficient (0.0097).

β_{fs} the per capita effect of *C. flavipes* on the population growth of *C. sesamiae* (1.2387).

β_{sf} the per capita effect of *C. sesamiae* on the population growth of *C. flavipes* (1.2083).

g_f the relative index of the efficiency of utilizing *C. flavipes* as a potential control agent in the presence of *C. sesamiae*.

g_s efficacy of *C. sesamiae* as a control agent in the presence of *C. flavipes*.

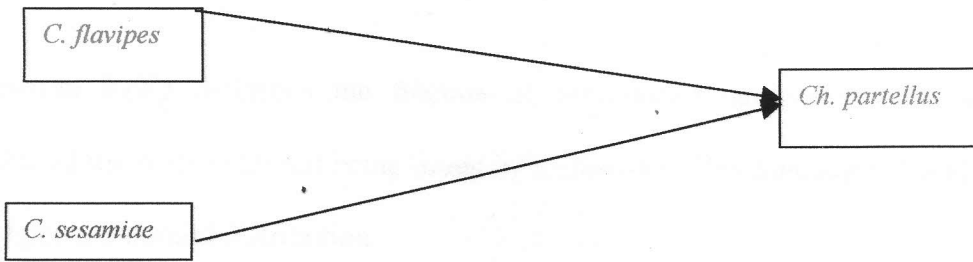


Fig 3.3.1: diagrammatic illustration of the three-species system discussed in our model—the two parasitoid species *C. flavipes* and *C. sesamiae* attacking *Ch. partellus*.

The equations

The model is defined by three equations. The first one:

$$N_{t+1} = \lambda N_t h_f(F_t) h_s(S_t) \quad (3.2.1)$$

describes the changes from season t to season $t+1$ of stem-borer density, based on the loss due to parasitism. Equation (3.2.1) states that the density of *Ch. partellus* in season $t+1$ equals the product of the density in season t , the host finite rate of increase and the instantaneous risk of parasitism.

Though there exists a number of ways that the risk of parasitism might be modeled (e.g. see Hassell and May, 1985), we have deliberately chosen a very simple form, which was described by May (1978). The reasons for our choice are

- (i) there is no evidence of density dependence between stem-borers of successive seasons (G. Zhou, personal communication),
- (ii) the host-parasitoid encounters are not random but aggregated (Smith and Wiedenmann, 1977) and
- (iii) some of the approaches are mathematically intractable and hence difficult to solve numerically.

The function $h_f(F)$ describes the fraction of stem-borers surviving parasitism. That is, the probability of the stem-borer not being found by *C. flavipes*. This function is based on the zero term of the negative binomial distribution

The function $h_f(F_t)$ describes the fraction of stem-borers surviving parasitism. That is, the probability of the stem-borer not being found by *C. flavipes*. This function is based on the zero term of the negative binomial distribution

$$h_f(F_t) = \left(1 + \frac{a_f F_t}{m}\right)^{-m} \quad (3.2.2)$$

A thorough treatment of the negative binomial can be found in Bliss & Fisher (1953) and in Richter & Söndgerath (1990). The corresponding function for the fraction of stem-borers that escape

parasitism by *C. sesamiae* is

$$h_s(S_t) = \left(1 + \frac{a_s S_t}{n}\right)^{-n} \quad (3.2.3)$$

The next, precisely symmetrical derivations

$$\begin{aligned} F_{t+1} &= \phi N_t [1 - h_f(F_t)] g_f(F_t, S_t) \\ S_{t+1} &= \sigma N_t [1 - h_s(S_t)] g_s(F_t, S_t) \end{aligned} \quad (3.2.4)$$

respectively describe the change in the *C. flavipes* and *C. sesamiae* densities from season t to season $t+1$, modified by the effect of intra- and inter-specific competition. The functions $g_f(F_t, S_t)$ and $g_s(F_t, S_t)$ are analogues of the familiar L-V differential equation model for two species competition (May, 1974) modified by adopting the Richards model (Richards, 1959). They are respectively

given by:

$$\begin{aligned} g_f(F_t, S_t) &= \exp\left\{r_f \left[1 - \left(\frac{\alpha_{ff} F_t + \beta_{fs} S_t}{K_f}\right)^v\right]\right\} \\ g_s(F_t, S_t) &= \exp\left\{r_s \left[1 - \left(\frac{\alpha_{ss} S_t + \beta_{sf} F_t}{K_s}\right)^v\right]\right\} \end{aligned} \quad (3.2.5)$$

The intra-specific competition coefficients, α_{ff} and α_{ss} , were, respectively, estimated from the relationships $\phi = \varepsilon_f \exp(-\alpha_{ff} \varepsilon_f)$ and $\sigma = \varepsilon_s \exp(-\alpha_{ss} \varepsilon_s)$.

The parameters a_f and a_s were estimated by Rogers' (1972) random parasitoid equation

$$N_{par} = N[1 - \exp\{-T_r a P / (1 + abN)\}],$$

using data collected in the coastal area of Kenya by Sallam (1998), where N_{par} = total number of stem-borers attacked, N = initial number of stem-borers available, P = parasitoid density, T_t = total time available and b = handling time. The parameters r_f and r_s were calculated from the expression

$$\sum_x \exp\{-r_m x\} \ell_x m_x = 1$$

while R_{of} and R_{os} were calculated from the formula $R_o = \sum_x \ell_x m_x$ due to Birch (1948), by Mbapila and Overholt (2001), by exposing the fourth instar larvae of *Ch. partellus* to cultures of *C. flavipes* from southern Pakistan and *C. sesamiae* from the Coast Province of Kenya. Here, x is the age of individuals in days, ℓ_x the number of individuals alive at age x as a proportion and m_x the number of female progeny produced per female in the age interval x .

The interspecific competition coefficients, β_{fs} and β_{sf} , were respectively estimated by

$$\beta_{fs} = \frac{\sum_{i=1}^3 (p_{fi}/p_i)(p_{si}/p_i)b_{fi}}{\sum_{i=1}^3 (p_{fi}/p_i)^2 b_{fi}} \quad \text{and} \quad \beta_{sf} = \frac{\sum_{i=1}^3 (p_{fi}/p_i)(p_{si}/p_i)b_{si}}{\sum_{i=1}^3 (p_{si}/p_i)^2 b_{si}}, \quad \text{where,}$$

p_{fi} and p_{si} are the frequencies of stem-borer species i in the diets of *C. flavipes* and *C. sesamiae*, respectively, p_i = standing frequency of stem-borer species i in the environment, b_{fi} and b_{si} are, respectively, the mean weight of *C. flavipes* and *C. sesamiae* cocoon emerging from the fourth instar larvae of stem-borer species i ; and summations are taken over the three stem-borer species; *Chilo orichalcociliellus*, *Chilo partellus* and *Sesamia calamistis*. This expression is due to Schoener (1974).

CHAPTER FOUR

AN EMPIRICAL STUDY

4.0: Introduction

The primary purpose of the model is to examine effects of competition on the equilibrium levels and the dynamical stability of the interactive system. With regards to the two parasitoid species, *Cotesia flavipes* and *C. sesamiae*, we wish to identify a range of conditions over which coexistence (or displacement) can occur. Laboratory experiments were conducted to estimate the values for the interspecific competition coefficients. The model was fitted to the data of Table 3.1 and repeatedly varied by computer simulation. Parameter sensitivity studies were made with standard parameter set for the parasitoids, which included an initial reasonable estimate for the uncertain parameter. The conditions of coexistence or displacement for the three species and the effects of the parasitoids on the stem-borer equilibrium levels were explored.

4.1: Materials and Methods

4.1.1: Estimation of interspecific competition coefficients

Insects: Mated females of the two parasitoid species, *C. flavipes* and *C. sesamiae*, and the fourth-instar larvae of 2 stem-borer species, *Ch. partellus* and *S. calamistis* were used for the experiments.

Parasitism: Using soft forceps, twenty-five fourth-instar larvae of the two stem-borer species were singly exposed to individual mated female parasitoids of a particular species in a sleeve cage. Parasitism was detected by observing the encounter between the female parasitoid and the host. Care was taken to allow only one oviposition per host. After completing oviposition, the female parasitoid left the host. All parasitised larvae were placed individually in glass vials containing an artificial diet and then held in incubators at 25°C for emergence of parasitoid progeny. All cocoons

that formed from parasitised hosts were removed from the artificial diet and kept separately in vials plugged with cotton wool. The dates of cocoon formation and their weights upto the day they began to darken were recorded.

4.1.2: Curve Fitting

Using the data of Table 3.1, a series of model runs was conducted. Various variations of the initial population densities for the three species were made. For simulation purposes, we selected $\nu = 0.5$.

4.1.3: Sensitivity Analysis

In the parameter sensitivity runs, each parameter was varied in five equal increments in a range covering the region of interest (usually from 10 to 20%). All other parameters were held constant. The sensitivity assessments were all made by comparing the time graphs for the species population densities. The comparative runs with five different parameter values provided an indication of the sensitivity of the simulation results to the uncertainties in the parameter under study.

Computer simulations using parameters in other agroclimatic zones (different from the zone of our immediate interest) were considered with an aim of understanding the performance of the parasitoids in these zones. We also considered more fundamental changes in the model's assumptions or those which, given the available data, are less likely but nevertheless instructive.

4.2: RESULTS

4.2.1: Estimates for the interspecific competition coefficients

For convenience, and without loss of generality, the three stem-borer species, *Ch. orichalcociliellus*, *Ch. partellus* and *S. calamistis* were labeled as species 1,2 and 3, respectively. Table 4.1 below lists the parameters and their values.

Parameter	Value
b_{f1}	18.5000*
b_{f2}	44.0909
b_{f3}	47.9167
b_{s1}	16.0800*
b_{s2}	31.5000
b_{s3}	48.8000

Table 4.1: Results from the competition experiment.

*Owing to unavailability of *Ch. orichalcociliellus* species at the time of the experiment,

$$b_{f1} \text{ and } b_{s1} \text{ were estimated by } \frac{b_{f1}}{92 + b_{f1}} = 16.74\% = \frac{b_{s1}}{80 + b_{s1}} \text{ (see Okech and Overholt, 1996).}$$

The other parameters, used for computing the interspecific competition coefficients are given in

Table 4.2 below:

Parameter	Value†	Parameter	Value #
p_{f1}	0.3507	p_1	0.0600
p_{f2}	0.4140		
p_{f3}	0.2353		
p_{s1}	0.2799	p_2	0.8800
p_{s2}	0.3519		
p_{s3}	0.3682	p_3	0.0600

Table 4.2: Parameters and their values used in computing the interspecific competition coefficients. {† Source: Ngi-Song et al. (1995); # Source: Overholt et al. (1994a)}

4.2.2: Model fitting

The model predicts coexistence of the three species, with *C. flavipes* dominating the interactive system (Figure 4.1).

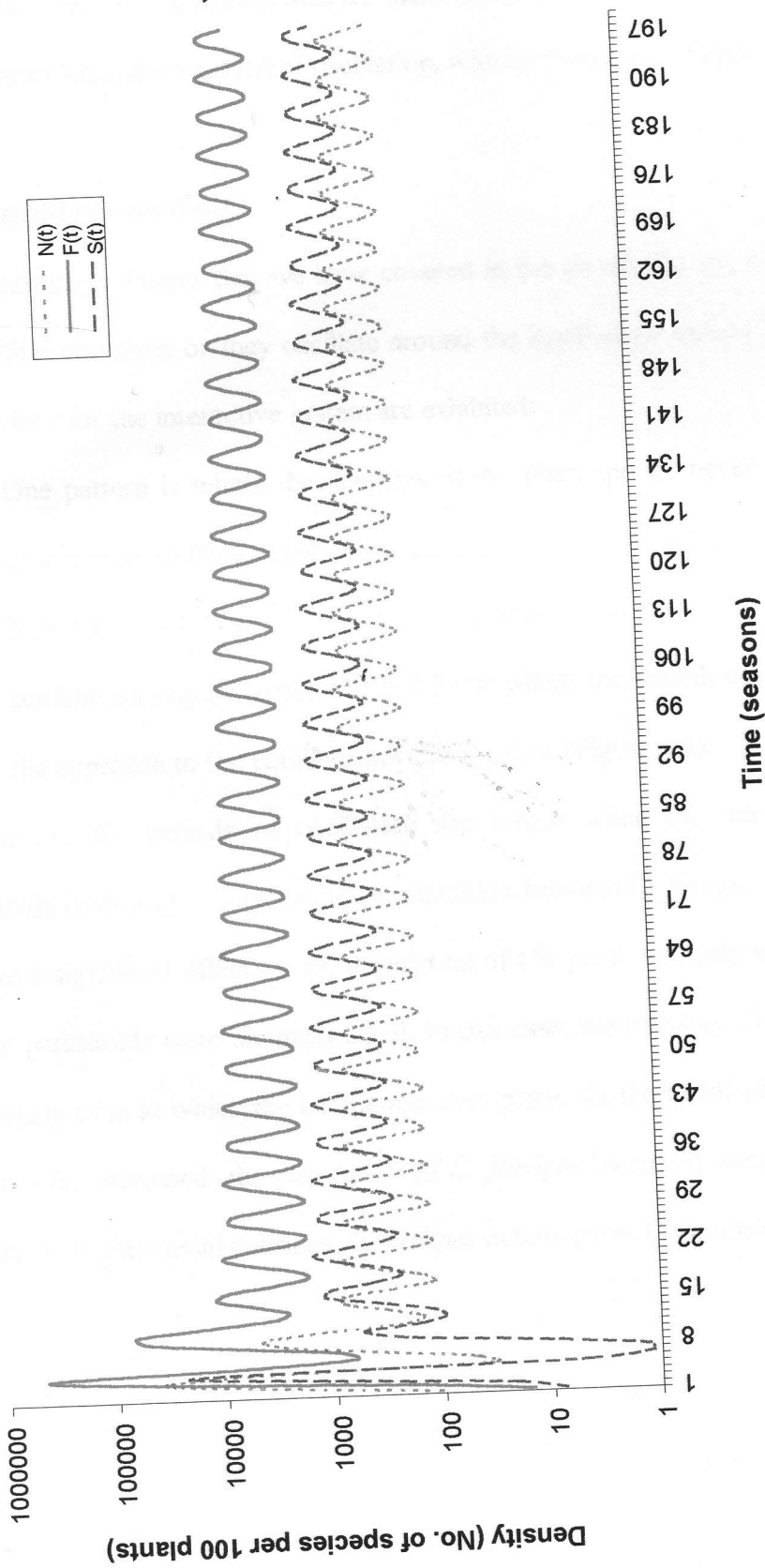


Figure 4.1: The season-to-season changes of the larvae of the stem-borers and the two parasitoids.

It also offers a clear prediction that *C. flavipes* will lead to a greater depression of stem-borer population densities. The densities for the three species continue to oscillate around the equilibrium, the two parasitoid species maintaining *Ch. partellus* below their cycles. Each of the three species has a short period of oscillation, with no indication of approaching the equilibrium.

4.2.3: Sensitivity Analysis

Within parameter ranges that we have covered in the simulation, the three species rapidly approach the equilibrium values or they oscillate around the equilibrium values. In other words, two patterns of behaviour for the interactive system are exhibited:

- (i) One pattern is where the densities of the three species never approach the equilibrium but continue to oscillate around the equilibrium (e.g., Figure 4.1).
- (ii) The other pattern is where population densities of the three species rapidly approach their equilibrium (e.g., Figures 4.2 & 4.3) or where the system continues for a long time even if the approach to the equilibrium values is slow (Figure 4.4).

In case (i), the periods of oscillation are longer when the interspecific competition for the parasitoids is stronger. Interspecific competition between *C. flavipes* and *C. sesamiae* was observed to have a significant effect on the population of *Ch. partellus*, only when the net reproductive rates for the parasitoids were assumed equal. In this case, the intensity of competition was dependent on the density ratio at which the interaction took place. As the initial adult density ratio of *C. flavipes*: *C. sesamiae* increased, the population of *C. flavipes* increased over *C. sesamiae* in the interactive system. At higher initial densities, *C. flavipes* outcompetes *C. sesamiae* and dominates the system.

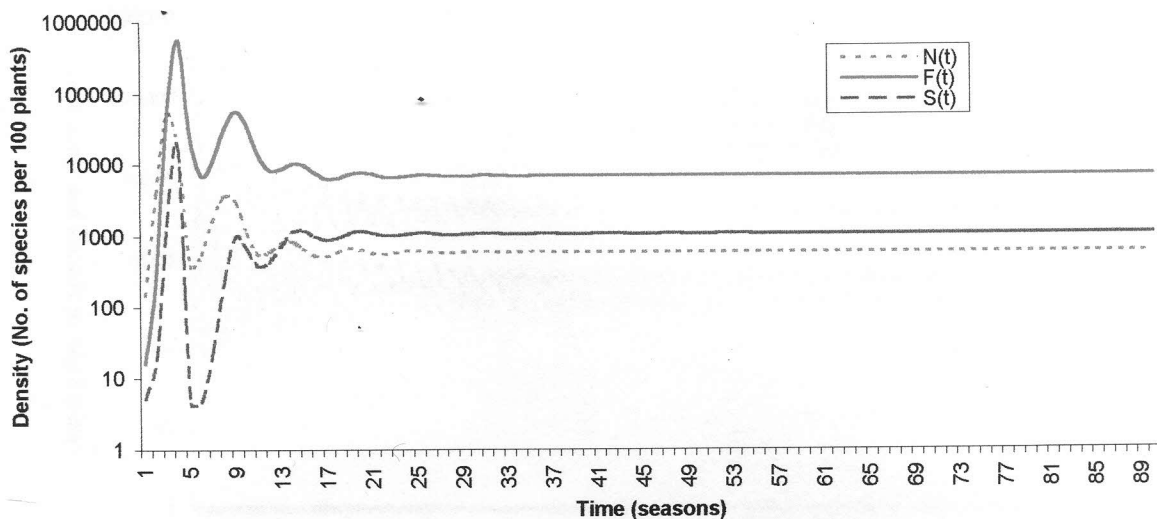


Figure 4.2: Numerical simulations for the model when $m=0.536$ and $n=0.552$; all the other parameters are as given in section 3.3.

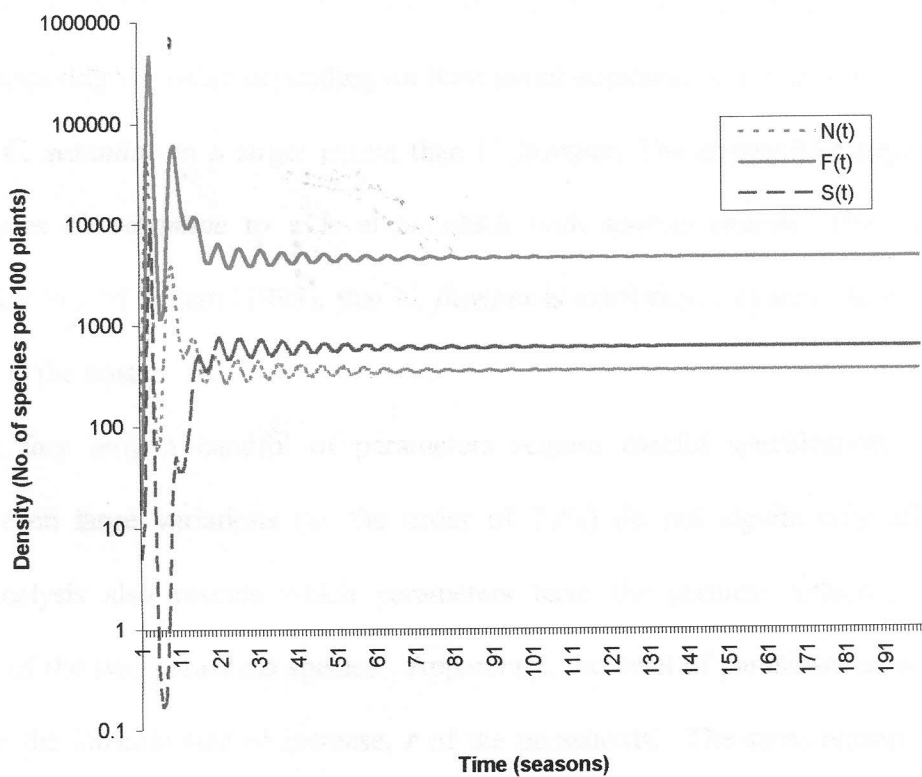


Fig.4.3: Numerical simulations for the model when $r_r=0.18828$ & $r_s=0.12804$; all the other parameters are as given in section 3.3.

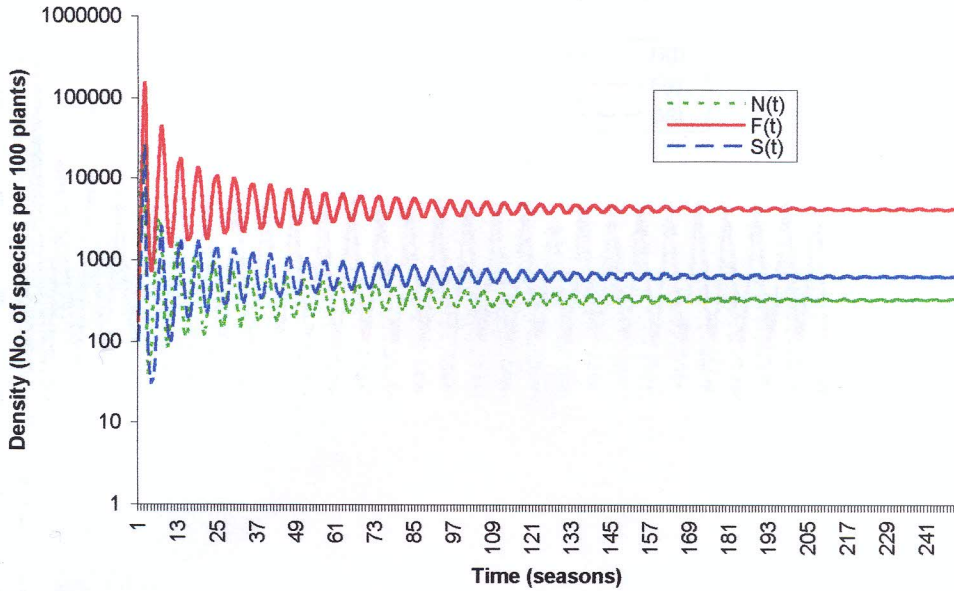


Fig.4.4: Numerical simulations for the model when $\beta_b=1.48644$ & $\beta_{sf}=1.44996$, all the other parameters are as given in section 3.3.

This suggests that at the lowest density ratio, there exists an unstable equilibrium point, with one species outcompeting the other depending on their initial numbers. Both species suffer interspecific competition, *C. sesamiae* to a larger extent than *C. flavipes*. The competitive aggressiveness of *C. flavipes* reduces *C. sesamiae* to a level at which both species coexist. This observation is in agreement with that of Sallam (1998), that *C. flavipes* is extrinsically superior to *C. sesamiae* when *Ch. partellus* is the host.

It turns out that only a handful of parameters require careful specification. For remaining parameters, even large variations (of the order of 20%) do not significantly affect the results. Sensitivity analysis also reveals which parameters have the greatest influence on the relative effectiveness of the two parasitoid species. Apparently, the level of parasitism achieved is primarily influenced by the intrinsic rate of increase, r of the parasitoids. The same reason tends to explain why *C. flavipes* dominates the interactive system (see Figures 4.5, 4.6 & 4.7). When the parameters R_{of} and R_{os} are assumed to be equal, the two parasitoid species coexist sympatrically.

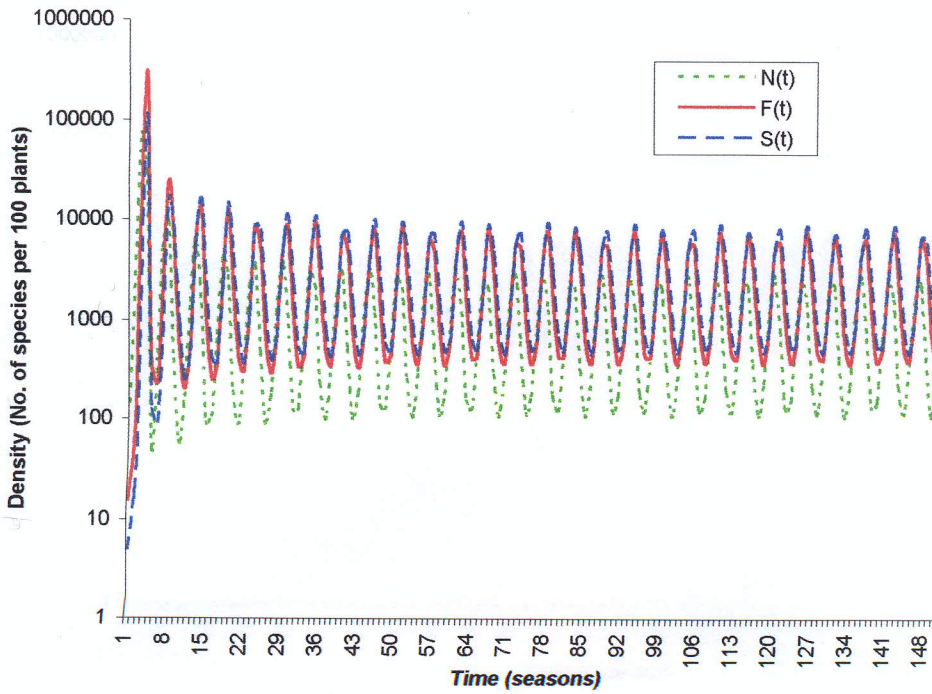


Fig.4.5: Numerical simulations for the model when $R_{of}=R_{os}=7.69$, all the other parameters are as given in section 3.3.

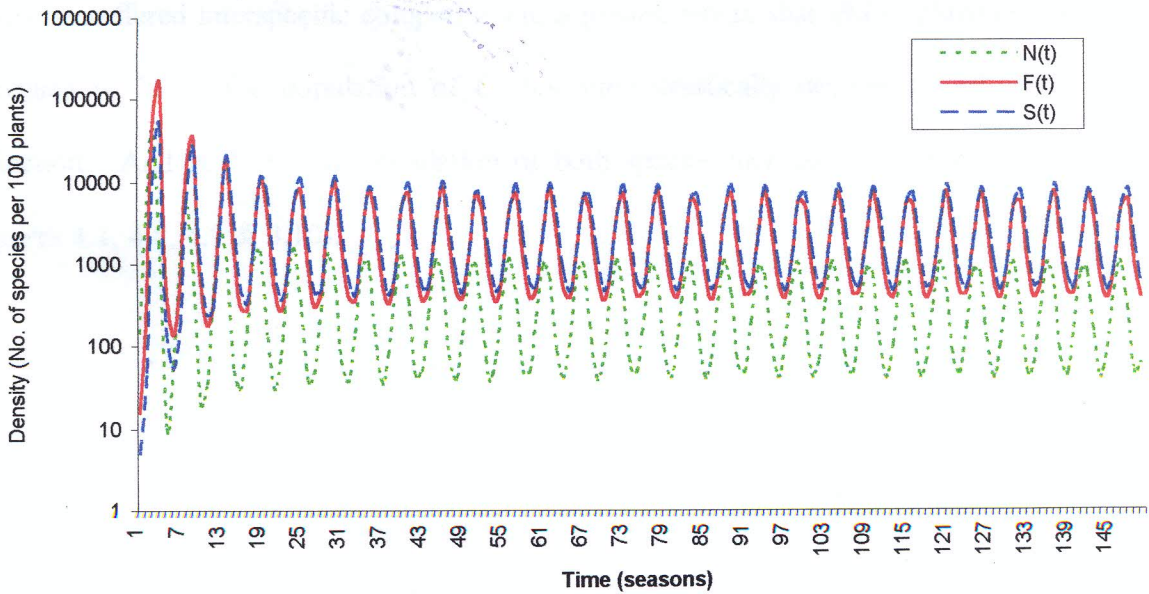


Fig.4.6: Numerical simulations for the model when $R_{of}=R_{os}=20.96$, all the other parameters are as given in section 3.3.

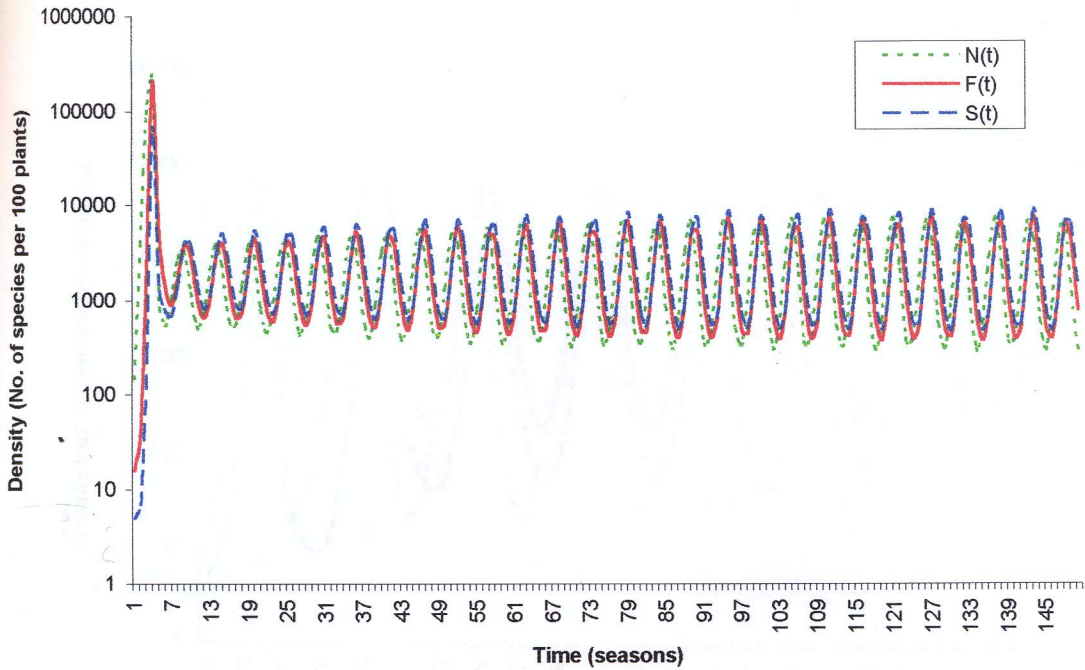


Fig.4.7: Numerical simulations for the model when $R_{of}=R_{os}=2.96$, all the other parameters are as given in section 3.3.

Temperature variation had an effect on competition between the two parasitoids. At 25°C , *C. sesamiae* suffered interspecific competition to a greater extent than did *C. flavipes*. As temperature increased to 28°C , the population of *C. sesamiae* drastically decreased and almost approaches extinction. And at 31°C , the population of both species increased - thus both species coexisted (Figures 4.1, 4.8, 4.9 & 4.10).

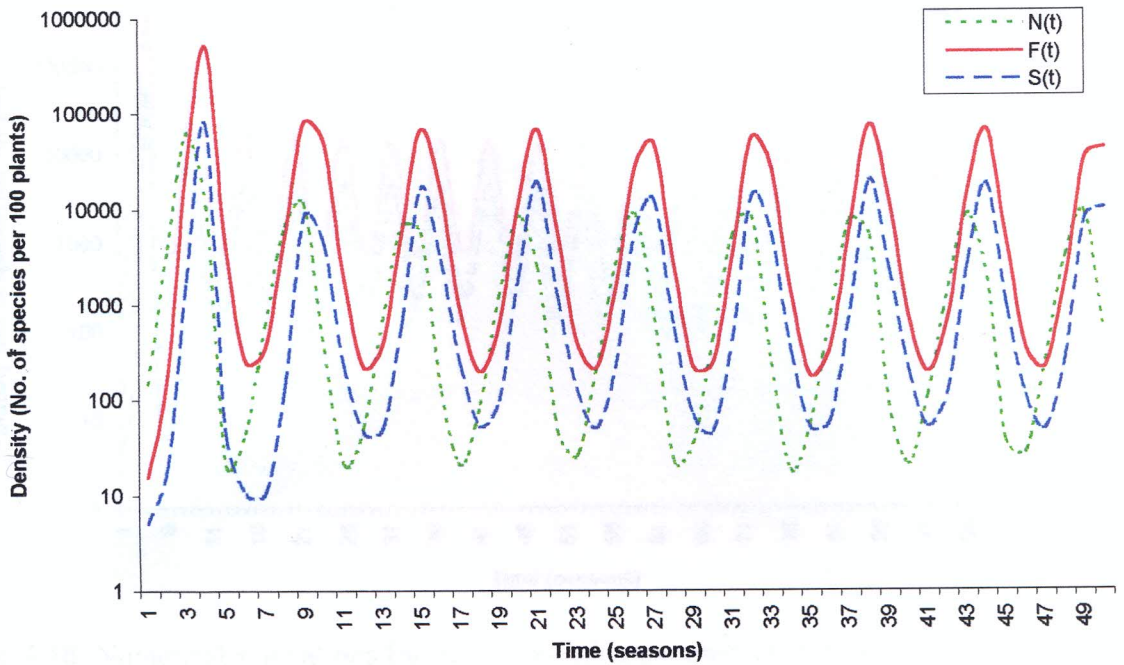


Figure 4.8: Numerical simulations for the model using parameters at 22°C.

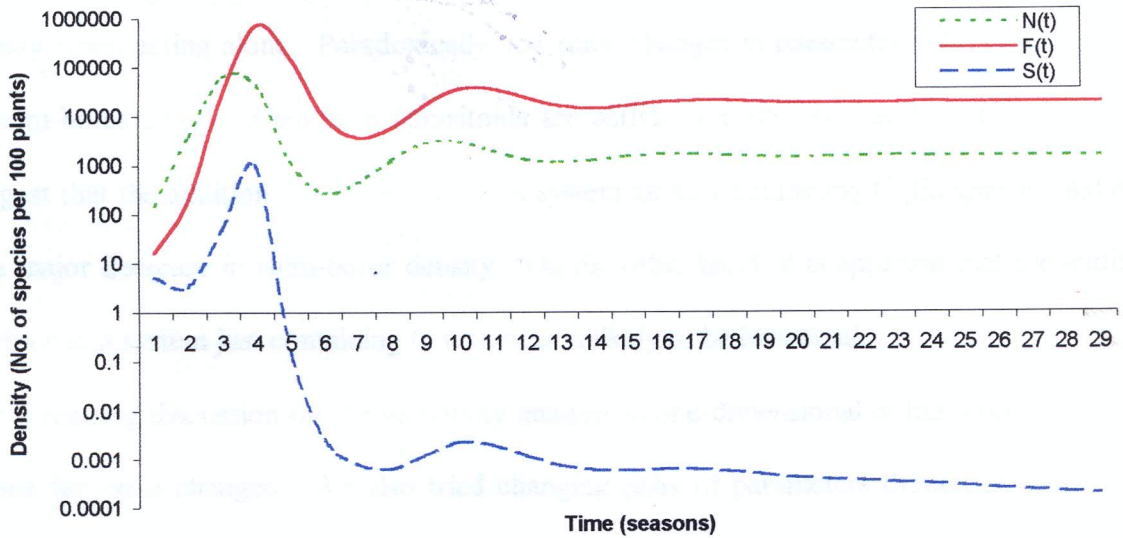


Figure 4.9: Numerical simulations for the model using parameters at 28°C.

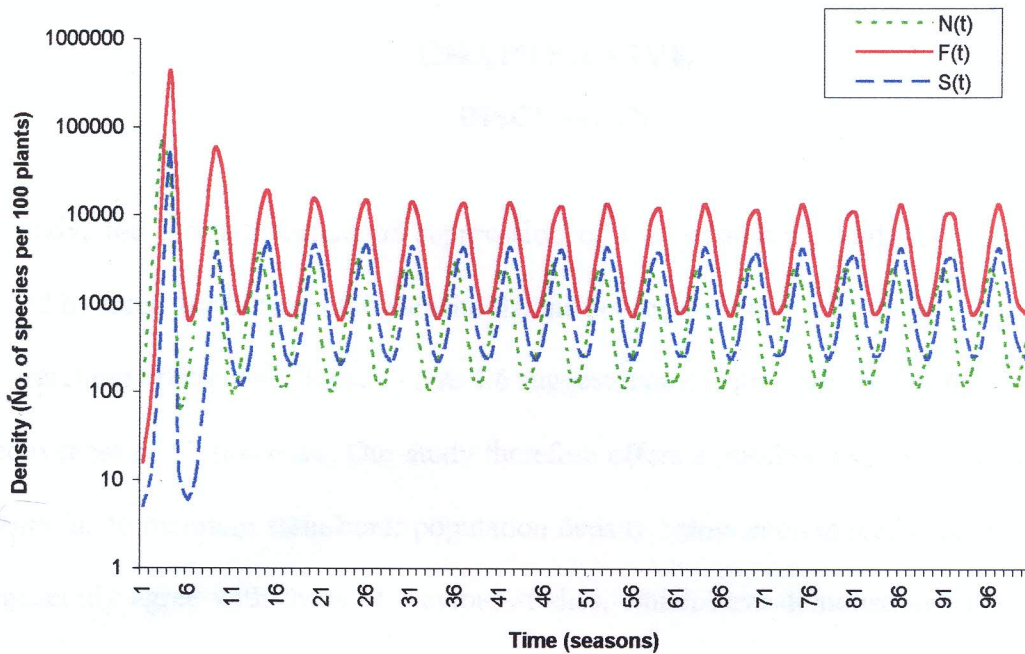


Figure 4.10: Numerical simulations for the model using parameters at 31°C.

When the degree of aggregation is decreased, or when the searching efficiency for *C. flavipes* is more pronounced, there is an improvement in the ability of the parasitoid to reduce stem-borer density when acting alone. Paradoxically, the same changes in parameter values lead to an increase in stem-borer density when both parasitoids are active. On the one hand, therefore, this seems to suggest that the addition of *C. sesamiae* to a system already containing *C. flavipes* is unlikely to lead to a major decrease in stem-borer density. On the other hand, it is apparent that the addition of *C. flavipes* to a system just containing *C. sesamiae* is likely to be beneficial.

The foregoing discussion on the sensitivity analysis is one-dimensional in that only one parameter at a time has been changed. We also tried changing pairs of parameters though in no case were our conclusions about the superiority of *C. flavipes* challenged. With twenty-two parameters, there is always the possibility that our conclusions are not robust for relatively small changes in large combination of parameters. What our analysis does indicate is that this is rather unlikely.

CHAPTER FIVE

DISCUSSION

In this study, the ultimate extent of suppression of *Ch. partellus* population density is largely determined by three attributes of the parasitoids: the net reproductive rate, the degree of aggregation and the searching efficiency. Figures 4.5 & 4.6 suggest that it is primarily a low R_{os} value that limits the effectiveness of *C. sesamiae*. Our study therefore offers a possible explanation for the inability of *C. sesamiae* to maintain stem-borer population density below economically injurious levels. Our results generally agree with those of previous studies, which have demonstrated that *C. flavipes* is extrinsically superior to *C. sesamiae* when *Ch. partellus* is the host (Overholt et al., 1997; Sallam, 1998). We found no evidence to suggest that competition within and between the parasitoid species is the most important in regulating the densities of stem-borers.

One question that we need to ask ourselves is 'what are the implications of this study for a natural enemy introduction program?' When introduction programs of natural enemies to control pest insects are projected, the following two cases can be assumed to occur and the targets of program will be different for the two cases.

- (i) One case is where population densities of the pest and the natural enemies rapidly approach their equilibrium values or where the system continues for a long time even if the approach to the equilibrium values is slow. In this case, our concern is on the equilibrium density of the pest insect and the target must be to retain the density to a low level.
- (ii) The other case is where the densities of the interacting species never approach the equilibrium but continue to oscillate around the equilibrium. In this case, the target will be to minimize the maximum density of the pest insect.

As examined in the previous sections, the intrinsic rate of increase makes a great effect on the equilibrium level of the host density. If case (i) exists in a certain host-parasitoid system, an efficient parasitoid to control the pest should have the intrinsic rate of increase such that the equilibrium density of the host is minimized.

The feeding behaviour and the physiological processes of the parasitoids are complex ones. As such, it is not easy to simplify it satisfactorily to incorporate into a simple mathematical model of this nature. Although *Chilo partellus* is assumed to be the only host for the parasitoids in this study, the proportion of the other stem-borer species, *C. orichalcociliellus*, and *S. calamistis* will inevitably influence the manner in which the densities of the three species considered in our model evolve. In fact, the trend in the proportion of the stem-borers in the coastal area of Kenya has been changing since 1994 (W. Overholt, personal communication). We deliberately made the above assumption to study the qualitative effect on the host-parasitoid system. The other limitation to the range of applicability of the model is the fact that most of our parameters are based on the maize (*Zea mays*) plant. Different parameters are, however, expected if other gramineous plants are utilized for the experiments. This would in turn change the manner in which the interactive system evolves over time.

CHAPTER SIX

CONCLUSIONS AND SUGGESTIONS FOR FURTHER RESEARCH

For purposes of illustration we have exhibited the behaviour of models in which the relationship among population growth, competition and resources is specified in detail. However, we believe that these models are applicable to a variety of situations and in particular to situations of competition between parasitic organisms. The fundamental restriction is that the biota considered must be those in which the rate of population growth is proportional to the amount of resource consumed. For higher organisms with complex life cycles and elaborate behaviour patterns, these models could not possibly mirror the complicated interactions that may occur. But this objection applies to all of the simplistic models (Hassel & May, 1985) upon which most competitive theory is based. Inevitably, the more precisely a model is defined, the more limited is its range of applicability. Typical constraint on time compelled this study to proceed rapidly. But despite the limitations of this basic model with reference to particular systems, we feel that the model possesses considerable utility. It is conceptually useful for the development of a general theory of resource-limited growth and competition. It is this function to which we have applied the model in this present discussion. Furthermore, the model has been designed for empirical testing, even though the whole idea of model validation is a thorny issue (for further discussion along these lines, see Rykiel, 1996).

The assumptions upon which the model is based and hypotheses generated from its consideration are empirically testable. The values of its parameters and functions can be estimated and through a process of modifying, fitting and testing this basic model, numerical simulations of resource-limited growth and competition may be generated for particular species. With this approach, the reality of this basic model, the robustness and generality of the conclusions drawn from it may be determined

empirically. The present study shows the usefulness of similar competition models in predicting the outcome of a classical biological control programme. Though the study was conducted with limited parameters, further studies in the field with other interacting parameters would help in developing a model, which would enable the pest management personnel to take corrective action well in advance.

It seems likely that the results of this study stimulate future studies. Theoretically, it is an open problem whether or not the stem-borer population density has the same qualitative effects as given in this report when other factors such as plant species, aggregative response and time lag of the parasitoid (Watt, 1959) are introduced. An implicit assumption of this model is that the parameters obtained by using another gramineous plant (like sorghum) will not be significantly different from the ones we obtained by using the maize (*Zea mays*) plant. Intuitively, we feel that there is a need to incorporate all the resource states for the interactive system in the model to make it more realistic. Plants provide important cues to the searching parasitoids. A study carried out by Ngi-Song *et al.* (1996) revealed that *C. flavipes* preferred volatiles from maize over those from sorghum, while maize and nappier grass were equally attractive. In contrast, *C. sesamiae* showed a preference for sorghum and nappier grass over maize.

The assumptions of a single host for the two parasitoids was made only to facilitate the analytical treatment of the model within the time frame of the study- and we take no credit for this. A more elaborate model would need to be constructed to explore the consequences of considering the other stem-borer species in the parasitoids' habitat (i.e., *Ch. orichalcociliellus* and *S. calamistis*). We believe that these stem-borer species would have an important effect on the outcome of competition. Besides, the evidence on which some of the parameter estimates in section 3.3 were made is rather weak. The consequences of the limitations of these models through the use of numerical simulations

ought to be examined. Finally, we have assumed time-invariant parameters. It is likely that most of the parameters in the model will change seasonally leading to changes over the year in population densities. The sensitivity analysis suggests that seasonal changes will not affect predictions about the relative effectiveness of the two parasitoids, though a more detailed simulation approach is required to produce accurate predictions of population levels during the year.

Nevertheless, we believe that the qualitative conclusions based on the model presented here will persist even when they are made more realistic by the inclusion of such complicating factors.

REFERENCES

- BIRCH, L. C. (1948). The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology* **17**, 15-26.
- BISWAS, S. (1988). Stochastic processes in demography and its applications. Wiley Eastern Limited, India.
- BLISS, C.I. & FISHER, R.A. (1953). Fitting the binomial distribution to biological data and a note on the efficient fitting of the negative binomial. *Biometrics* **9**, 176-200.
- BOSQUE-PEREZ, N.A. & SCHULTHESS, F. (1998). Maize: West and Central Africa. In *African cereal stem borers: economic importance, taxonomy, natural enemies and control* (A. Polaszek, ed.) CABI, Wallingford, Oxon, UK. pp.11-24.
- DALE, M. B. (1970). System analysis and ecology. *Ecology* **51**, 2-16.
- DEBACH, P. (1964). Successes, trends and future possibilities. In *Biological Control of Insect Pests and Weeds* (P.DeBach, ed.) Chapman and Hall, London. pp. 673-713.
- DEBACH, P. (1974). Biological control by natural enemies. Cambridge University Press, New York.
- DEBACH, P. & ROSEN, D. (1991). Biological control by natural enemies. 2nd ed. Cambridge University Press, New York.
- EHLER, L.E. (1990). Introduction strategies in biological control of insects. In *Critical Issues in Biological Control* (M. Mackauer, L.E. Ehler, & J. Roland, eds.) Intercept, Andover, pp. 111-134.
- EILENBERG, J., HAJEK, A. & LOMER, C. (2001). Suggestions for unifying the terminology in biological control. *Biocontrol* **46**, 387-400.
- FRIEDLANDER, C.P. (1976) The biology of insects. Hutchison & Co. (Publishers) Ltd. London.
- GODFRAY, H.C.J. & SHIMADA, M. (1999). Parasitoids: a model system to answer questions in behavioral, evolutionary and population ecology. *Researches on Population Ecology* **41**, 3-10.
- GOTELI, N.J. (1998). A Primer of ecology. 2nd ed. Sinauer Associates Inc. USA.
- HASSELL, M.P. & MAY, R.M. (1985). From individual behaviour to population dynamics. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (R.M. Sibly & R.H. Smith, eds.). Blackwell Scientific Publications. Oxford. pp. 3-32.
- HUFFAKER, C.B. (1971). Biological Control. Plenum, New York.

- HUFFAKER, C. B., MESSENGER, P. S. & DEBACH, P. (1971). The natural enemy component in natural control and the theory of biological control. In *Biological Control* (C.B. Huffaker, ed.), Plenum, New York. pp.16-67.
- INGRAM, W. R. (1958). The lepidopterous stalk borers associated with gramineae in Uganda. *Bulletin of Entomological Research* **49**, 367-383.
- KAJITA, H. & DRAKE, E. F. (1969). Biology of *Apanteles chilonis* and *A. flavipes* (Hymenoptera: Braconidae), parasites of *Chilo suppressalis*. *Mushi* **42**, 163-179.
- KFIR, R. (1997). Natural control of the cereal stemborers *Busseola fusca* and *Chilo partellus* in South Africa. *Insect Science and Its Applications* **17**, 61-68.
- MAES, K. (1997). The taxonomy of the lepidopteran cereal stemborers of Africa. *Insect Science and Its Applications* **17**, 9-12.
- MAY, R.M. (1974). Biological populations with nonoverlapping generations: stable points, stable cycles and chaos. *Science* **186**, 645-647.
- MAY, R.M. (1978). Host-parasitoid systems in patchy environments; a phenomenological model. *Journal of Animal Ecology* **47**, 833-844.
- MBAPILA, J.C. & 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.
- MOHYUDDIN, A.I. & GREATHEAD, D.J. (1970). An annotated list of the parasites of graminaceous stemborers in East Africa, with a discussion of their potential in biological control. *Entomophaga* **15**, 241-274.
- NEWSON, L. D., SMITH, R. F. & WHITCOMB, W. H. (1976). Selective pesticides and selective use of pesticides. In *Theory and practice of biological control* (C. B. Huffaker & P. S. Messenger, eds.). Academic Press Inc., London.
- NGI-SONG, A.J., OVERHOLT, W.A., & AYERTEY, J.A. (1995). Suitability of African gramineous stemborers for the development of *Cotesia flavipes* and *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae). *Environmental Entomology* **24**, 978-984.
- NGI-SONG, A.J., OVERHOLT, W.A., NJAGI, P.G.N., DICKE, M., AYERTEY, J.A. & LWANDE, W. (1996). Volatile infochemicals used in host and host habitat location by *Cotesia flavipes* Cameron and *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae), larval parasitoids of stemborers on Gramineae. *Journal of Chemical Ecology* **22**, 307-323.

- OFOMATA, V.C. (1998). Ecological interactions between *Chilo orichalcociliellus* Strand and *Chilo partellus* Swinhoe (Lepidoptera: Pyralidae) on the Kenya Coast. Ph.D. Thesis. Nnamdi Azikiwe University, Awka, Anambra State, Nigeria.
- OFOMATA, V.C., OVERHOLT, W.A., VAN HUIS, A., EGWUATU, R.I. & NGI-SONG, A.J. (1999a). Niche overlap and interspecific association between *Chilo partellus* and *Chilo orichalcociliellus* on the Kenya coast. *Entomologia Experimentalis et Applicata* **93**, 141-148.
- OFOMATA, V.C., OVERHOLT, W.A., & EGWUATU, R.I. (1999b). Diapause termination of *Chilo partellus* (Swinhoe) and *Chilo orichalcociliellus* (Strand) (Lepidoptera: Pyralidae). *Insect Science and Its Applications* **19**, 187-191.
- OFOMATA, V.C., OVERHOLT, W.A., LUX, S.A., VAN HUIS, A. & EGWUATU, R.I. (2000). Comparative studies on the fecundity, egg survival, larval feeding and development of *Chilo partellus* (Swinhoe) and *Chilo orichalcociliellus* Strand (Lepidoptera: Crambidae) on five grasses. *Annals of the Entomological Society of America* **93**, 492-499.
- OKECH, S.H.O. & OVERHOLT, W.A. (1996). Comparative biology of *Cotesia chilonis* (Hymenoptera: Braconidae) on selected African Gramineous stemborers. *Biocontrol Science and Technology* **6**, 595-602.
- OMWEGA, C.O. & OVERHOLT, W.A. (1997). Progeny production and sex ratios of field populations of the parasitoids *Cotesia flavipes* and *Cotesia sesamiae* reared from gramineous stemborers in coastal Kenya. *Insect Science and Its Applications* **17**, 137-142.
- OVERHOLT, W. A. (1998). Biological Control. In *African Cereal Stem borers: economic importance, taxonomy, natural enemies and control* (A. Polaszek, ed.) CABI, Wallingford, Oxon, UK. pp 349-362.
- OVERHOLT, W.A., NGI-SONG, A.J., KIMANI, S.W., MBAPILA, J.P., LAMMERS, P. M., & KIOKO, E. (1994a). Ecological considerations of the introduction of *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) for biological control of *Chilo partellus* (Swinhoe)(Lepidoptera: Pyralidae), in Africa. *Biocontrol News and Information* **15**, 19N-24N.
- OVERHOLT, W. A. OGEDAH, K. & LAMMERS, P. M. (1994b). Distribution and sampling of *Chilo partellus* (Swinhoe)(Lepidoptera: Pyralidae) in maize and sorghum at the Kenya coast. *Bulletin of Entomological Research* **84**, 367-378.
- OVERHOLT, W. A., OCHIENG, J. O., LAMMERS, P. & OGEDAH, K. (1994c). Rearing and field release methods for *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) a parasitoid of tropical gramineous stem borers. *Insect Science and Its Applications* **15**, 253-259.

- OVERHOLT, W.A., NGI-SONG, A.J., OMWEGA, C.O., KIMANI-NJOGU, S.W., MBAPILA, J.P., SALLAM, M.N. & OFOMATA, V.C. (1997). A review of the introduction and establishment of *Cotesia flavipes* Cameron in East Africa for biological control of cereal stemborers. *Insect Science and its Application* **17**, 79-88.
- POTTING, R. P. J., VET, L. E. M. & DICKE, M. (1995). Host microhabitat location by the stem borer parasitoid *Cotesia flavipes*: the role of herbivore volatiles and locally and systematically induced plant volatiles. *Journal of Chemical Ecology* **21**, 525-539.
- POTTING, R. P. J., OVERHOLT, W. A., DANSO, F. O. & TAKASU, K. (1997). Foraging behaviour and life history of the stem borer parasitoid *Cotesia flavipes* (Hymenoptera: Braconidae). *Journal of Insect Behaviour* **10**, 13-29.
- RICHARDS, F. J. (1959). A flexible growth function for empirical use. *Journal of Experimental Botany* **10**, 290-300.
- RICHTER, O. & SÖNDGERATH, D. (1990). Parameter Estimation in Ecology: the link between data and models. VCH Publishers USA.
- ROGERS, D. J. (1972). Random search and insect population models. *Journal of Animal Ecology* **41**, 369-383.
- ROSS, S.M. (1990). A course in Simulation. Macmillan Publishing Company. New York. USA.
- RYKIEL, E. J., Jr. (1996). Testing ecological models: the meaning of validation. *Ecological Modeling* **90**, 229-244.
- SALLAM, M. N. (1998). "Comparative evaluation of certain aspects of the biology of *Cotesia flavipes* and *Cotesia sesamiae* (Hymenoptera: Braconidae) for the management of *Chilo partellus* (Lepidoptera: Pyralidae) in Kenya." Ph.D. dissertation, Kenyatta University, Nairobi, Kenya.
- SALLAM, M. N., OVERHOLT, W. A. & KAIRU, E. (1999). Comparative evaluation of *Cotesia flavipes* and *C. sesamiae* (Hymenoptera: Braconidae) for the management of *Chilo partellus* (Lepidoptera: Pyralidae) in Kenya. *Bulletin of Entomological Research* **89**, 185-191.
- SAMWAYS, M.J. (1981). Biological control of pests and weeds. Camelot Press Ltd. Southampton, Great Britain.
- SESHU REDDY, K.V. (1998). Maize and sorghum: East Africa. In *African Cereal Stem borers: economic importance, taxonomy, natural enemies and control* (A. Polaszek, ed.) CABI, Wallingford, Oxon, UK. pp 25-27.

- SCHOENER, T. W. (1974). Some methods for calculating competition coefficients from resource-utilization spectra. *The American Naturalist* **108**, 332-340.
- SMITH, J. W., Jr., WIEDENMANN, R.N. & OVERHOLT, W.A. (1993). *Parasites of Lepidopteran Stem-borers of Tropical Gramineous Plants*. ICIPE Science Press, Nairobi. 89pp.
- SMITH, J. W., Jr., & WIEDENMANN, R.N. (1997). Foraging strategies of stem-borer parasites and their applications to biological control. *Insect Science and Its Applications* **17**, 37-49.
- SMITH, R.F., & REYNOLDS, H.T. (1996). Effects of manipulation of cotton agro-ecosystems on insect pest populations. In *The Careless Technology* (M.J. Farvar & J.P. Milton, eds.). Natural History Press, Garden City, New York.
- TURNBULL, A. L. (1967). Population dynamics of exotic insects. *Bulletin of Entomological Society of America* **13**, 333-337.
- TURNBULL, A. L. & CHANT, D. A. (1961). The practice and theory of biological control of insects in Canada. *Canadian Journal of Zoology* **39**, 697-753.
- ULLYETT, G.C., (1935). Notes on *Apanteles sesamiae* Cameron, a parasite of the maize stalk borer (*Busseola fusca* Fuller) in South Africa. *Bulletin of Entomological Research* **26**, 253-262.
- VAN DEN BOSCH, R. (1968). Comments on population dynamics of exotic insects. *Bulletin of Entomological Society of America* **14**, 112-115.
- VAN DEN BOSCH, R., LEIGH, T. F., FALCON, L. A., STERN, V. M., GONZALES, D. & HAGEN, K. S. (1971). The developing program of integrated control of cotton pests in California. In *Biological Control* (C. B. Huffaker, ed.). Plenum, New York. pp. 377-394.
- VAN DEN BOSCH, R., MESSENGER, P.S., & GUTIERREZ, A.P. (1982). An introduction to biological control. Plenum Press, New York.
- VARLEY, G.C., GRADWELL, G.R. & HASSELL, M.P. (1973). *Insect population ecology*. Blackwell Scientific Publications, Oxford.
- WATT, K. E. F. (1959). A mathematical model for the effect of densities of attacked and attacking species on the number attacked. *Canadian Entomologist* **91**, 129-144.
- ZHOU, G., BAUMGÄRTNER, J. & OVERHOLT, W.A. (2001). Impact assessment of an exotic parasitoid on stem-borer (Lepidoptera) population dynamics in Kenya. *Ecological Applications* **11**, 1554-1562.

APPENDIX

Temperature	<i>C. flavipes</i>		<i>C. sesamiae</i>	
	R_{of}	r_f	R_{os}	r_s
22	13.4	0.1011	8.35	0.0839
25	21.0	0.1569	7.69	0.1067
28	13.8	0.1508	1.32	0.1142
31	10.2	0.1433	5.84	0.1094

Appendix 1: Net reproductive rate and the intrinsic rate of increase of *C. flavipes* and *C. sesamiae* on *Ch. partellus* at four constant temperatures.

(Source: Mbapila & Overholt, 2001).

KENYATTA UNIVERSITY LIBRARY