

**A COMPETITION MODEL FOR *Chilo partellus* (SWINHOLE)
AND *Chilo orichalcociliellus* (STRAND) ON THE KENYAN
COAST**

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By

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*A competition model for
chilo partellus (SWINHOLE)*

*A dissertation submitted for the partial fulfillment of the degree of
Master of*

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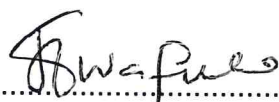
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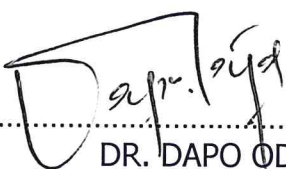
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ABSTRACT

Stem-borers are among the most damaging pests of cereal crops worldwide (Nye, 1960 Reddy, 1991). In Africa, *Chilo partellus* (Swinhoe) and *Chilo orichalcociliellus* (Strand) species are among the most injurious noctuids and pyralids (Seshu, 1991 Overhalt *et al*, 1994a). With the exception of *C. Partellus*, which is an Asian Species, the rest are thought to be indigenous to Africa.

Population dynamics of *C. Partellus* and *C. orichalcociliellus* have been investigated in some African countries including South Africa (Kfir, 1994), Madagascar (Delebol, 1975a) and Kenya (Warui and Kuria, 1983, Overhalt *et al*, 1994). Investigations by Overhalt *et al* (1994a) on the distribution and sampling of *C. Partellus* on maize and sorghum on the Kenyan Coast from 1990 to 1993 indicated that it was the most abundant stem-borer species in all field, accounting for more than 80% of the total. *C. orichalcociliellus* and *S. calamists* accounted for less than 10%. A decrease in the absolute numbers of *C. orichalcociliellus* on the Kenyan coast has been observed since the invasion of *C. Partellus* in the early 1960s.

In this dissertation, we have developed a competition model for the two species; *C. orichalcociliellus* and *C. Partellus* on maize, sorghum, wild sorghum and Napier grass at the Kenyan Coast. We have done this by modifying the model of

inter-specific competition, established by Sun *et al* (1991). Finally we used data from Ofomata 1998 to estimate the various parameters and incorporated them in our model. Computer simulations were then carried out to obtain the average population density for each species in a period of 4,000 days. We have been able to show that at no one point does the population density of either of the species attain the zero mark. This has led to the conclusion that the two species may co-exist for a very long period of time but at different densities.

We have also suggested further areas of study including examining the consequences of periodic variations in the intrinsic growth rate of each of the species and/or the carrying capacities of each of the grasses in our model.

DEDICATION

I dedicate this work to my mother **Mrs. MARY OTIENO** for the sacrifices she made towards my education and the sacrifices she continues to make towards my siblings' education and to my supervisor, **Dr. DAPO ODULAJA** for his exceptional support during my research.

Acknowledgement

It is impossible to successfully complete work of such magnitude on one's own. Indeed, any author who is tempted to claim all the credit for his or her work would be guilty of intellectual dishonesty. The truth is that this project benefited immensely from the input of many other persons in one way or the other. I regret deeply the fact that I am unable to mention all by names. However I am obliged to express my sincere gratitude to particular people whose contributions were crucial to the completion of this work.

But first and foremost, I owe it all to God the Almighty. This work is a testimony of His faithfulness and His unending love.

I am greatly indebted to the capacity building Unit ICIPE for giving me a chance to be attached at ICIPE thus ensuring that I worked in the friendliest of academic atmospheres, with unlimited access to all the necessary facilities. Dr. Dapo Odulaja, the head of Biostatistics Unit, at ICIPE was one of my able supervisors. He was instrumental in the conceptualization of the research problem and assisted me in all the subsequent stages. Above all this, I hold as a treasure in my hearts the many experiences he shared with me on what it takes to make it in the statistics field. Not only has he introduced me to the world of ecological modeling he has also kindled a thirst to go for more and reach out to greater heights. For all this support, coupled with securing me a

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Mugo, my only classmate deserves special mention. He always spared time to have us exchange ideas and notes. To my colleagues Simon, Okello, Akinyi and all the K.U friends attached at ICIPE thanks for your company and encouragement during this period.

Communicating scientific ideas in a simple language is a problem every scientist has to grapple with. I equally fell prey to the temptations to write

long sentences and jargon. In this respect I am indebted to my cousin Jack for editing and proofreading my work.

The pressures of family commitment could have surely derailed this work were it not for the support of a loving husband, DALMAS and little angel, daughter, MICHELLE. They gave me the moral support and lifted my spirit above the pressure of a fledgling family.

More than their daughter, my parents have given all they have to enable me acquire this level of education. They have tirelessly shouldered the burden of paying school and college fees for over 20 years besides instilling a culture of excellence in me at a very tender age. I believe this is the fruit of their labour. In addition my younger sisters, Beatrice, Lucy and Elizabeth and brothers Onesmus and Fred were a great source of inspiration. Special tribute to my grandfather MZEE ALOYS OTIENO for holding dear to his heart my academic achievements even in his old age.

Last but not least, I pay tribute to the entire **Otieno** and **Origa** extended families. Built on a solid educational foundation, I have stood on unshakeable ground throughout my schooling. And for their solidarity of purpose, I could never wish I were born elsewhere.

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OVERVIEW

An ecosystem is a functional system or unit, which is able to sustain life, and includes all biological and non-biological variables in that unit. Spatial and temporal scales are not specified apriori, but are entirely based upon the objectives of the ecosystem study (Jorgensen, 1994).

Currently, there are several approaches (Likens, 1998) to the study of ecosystems:

- ❖ Empirical studies where bits of information are collected, and attempt is made to integrate and assemble them into a complete picture.
- ❖ Comparative studies where a few structural and a few functional components are compared for a range of ecosystem types.
- ❖ Experimental studies where manipulation of a whole ecosystem is used to identify and elucidate mechanisms.
- ❖ Modeling or computer simulation studies.

An ecological model must contain the features, of interest to the management or scientific problem that we wish to solve by using the model. The model might be a physical or a mathematical model, describing the main characteristics of the ecosystem and the related problem in mathematical terms.

The displacement of one species by another on economically important crops is of major economic and ecological concern. However, direct evidence of competitive displacement is difficult to obtain. This is partly due to the difficulty of measuring numbers and mortality in most natural populations and also because the population being eliminated may persist for a

relatively long period of time. The ecologist is therefore, compelled to seek for evidence of competitive displacement through the use of a mathematical model.

Reports of Over halt *et al* (1994a), Marthez (1972) and Warui and Kuria (1998) indicate a decrease in the absolute numbers of *C.orichalcociliellus* on the Kenyan Coast since the invasion by *C.partellus* in the early 1960's. This shift in species abundance over a period of 30 years suggests that the introduced *C.partellus* may be gradually displacing the indigenous *C.orichalcociliellus* in Kenya.

Interspecific competition is an important aspect of interaction between species. It plays a major role in the distribution, abundance and community structure of species (Schoener, 1974, Hutchinson, 1978). Competition is a factor in species extinction after the introduction of new species (Simberloff, 1981).

Our objective was to construct an appropriate competition model for the two species, *C.partellus* and *C. orichalcociliellus*, on four food resources found in the Kenyan coast. This model could be used to seek for the evidence of competition and to investigate the outcome of the competition between the two species.

We assumed that the wild grasses were in the field at the coast throughout the year while maize and sorghum were in the field during long and short rainy seasons in the year. The two *Chilo* species were therefore expected on the wild sorghum and Napier grass in the field throughout the year. Some of them, however, migrated to the maize and sorghum during the rainy seasons.

Chapter one introduces the fundamental concepts needed to understand the rest of the work in this dissertation. It briefly explains the bio-ecology of the two species and introduces the concept of competitive displacement, pointing out its outcome.

In Chapter two we outline two simple models for describing patterns of growth and decline or decay in biological populations and individual organisms.

In chapter three we present the Lotka-Volterra model, a simple descriptive model, from which many other competition models have been developed. We also, examine briefly various numerical methods available for solving differential equations. The fourth order, Runge Kutta method is discussed at length.

In chapter four we develop our competition model, for the two species on the four resources.

In chapter five we carry out an empirical study based on chapters three and four. It is in this chapter that we estimate the various parameters, fit them in the model, and carry out simulations to obtain the population density of the two species on the grasses for a period of 4000 days.

In chapter six we give an overview of what we have accomplished and suggest areas for further research.

CHAPTER ONE

FUNDAMENTAL CONCEPTS AND DEFINITIONS

1.1: General Introduction

Cereal crops, in particular, rice, *Oryza sativa L.*, Maize, *Zea mays L.*, sorghum, *bicolor L.*, *Pennisetum* species, are vital sources of human nutrition (Seshu Reddy and Walker, 1990). These crops are of low cash value, and are grown by a large proportion of the world's poorest people's (Ibid.). Maize and sorghum are staple foods for the majority people in the sub-Saharan Africa (Hill, 1983). They are also grown as feeds for poultry and livestock in the form of grain, forage, and fodder (Ofomata, 1998). Nearly 1,500,000 hectares are under maize in Kenya alone (FAO, 1991).

In the tropics, the yield of maize and sorghum is low. Damage by phytophagous insects is cited as one major constraint to increasing the production of maize and sorghum, (Ibid).

Stem borers are among the most damaging pests of cereal crops worldwide (Nye, 1960 Reddy, 1991). *Chilo partellus* (Swinhoe) and *Chilo orichalcociliellus* strand are among the most injurious noctuids and pyralids found in Africa (Seshu, 1991; Overholt *et al*, 1994a). With the exception of *C. partellus*, which is an Asian species, the rest are thought to be indigenous to Africa.

Larval feeding on the plant whorl, and later stem tunneling, causes plant damage. Infested plants have poor growth, low yields, and are susceptible to secondary infection and wind damage (Ofomata, 1991). Heavy infestations at the early stages of

plant growth cause 'dead heart' and, sometimes, total crop failure. Youdeowi (1989), and Reddy and Walker (1990) gave estimates of yield losses due to stem borers in the range of 20-40 percent of the potential yield (Ofomata, 1991).

Population dynamics of *C. partellus* and *C. orichalcociliellus* have been investigated in some African countries, including South Africa (Kfir, 1994), Madagascar (Delobel, 1975a) and Kenya (Warui and Kuria, 1983; Overholt *et al*, 1994). Evidence has shown that the introduced stem borer, *C. partellus*, is an efficient colonizer in many of the areas it has invaded. It often becomes the predominant and most economically important stem borer in maize and sorghum (Delobel, 1975a, Overholt *et al*, 1994) at elevations below 1500 metres (Reddy, 1983a,b).

In Kenya, studies have been conducted on the species composition of stem borers. Investigations by Overholt *et al* (1994a) on the distribution and sampling of *C. partellus* on maize and sorghum on the Kenyan coast from 1990-1993, indicated that it was the most abundant stem borer species in all the fields. It accounted for more than 80 percent of the total while *C. orichalcociliellus* and *S. calamists* accounted for less than 10 percent.

The reports of Overholt *et al* (1994a), Marthez (1972), and Warui and Kuria (1983), indicate a decrease in the absolute numbers of *C. orichalcociliellus* on the Kenyan coast since the invasion by *C. partellus* in the early 1960s. This shift in species abundance over a period of 30 years suggests that the introduced *C. partellus* may be gradually displacing the indigenous *C. orichalcociliellus* in Kenya.

The distributional shifts and changes can be explained by non-interactive and interactive processes. Non-interactive processes refer to situations in which ecological factors affect the population of the previously established species independently of the invading one. An example is the change of habitat availability in favour of the invading species (Black et al, 1989). Interactive processes refer to situations in which the invaders depress the population of the established species.

Interspecific competition is an important aspect of interaction between species. It plays a major role in the distribution, abundance and community structure of species (Schoener, 1974 Hutchinson, 1978). Like predation and habitat change, competition is a factor in species extinction after the introduction of new species (Simberloff, 1981).

Competition may be by interference, exploitation, or both. Exploitative competition occurs when individuals, using resources, deprive others of benefits gained from those resources (Schoener, 1983,1988).

Interference competition results when individuals harm one another directly by fighting or killing, or indirectly by aggressive maintenance of territory or production of chemicals to deter other individuals (Ibid). In all cases, the deprivation or harm decreases the victim's population size by limiting their survival, reproduction, or both.

Local displacements in 13 interactions involving stem borers were attributed to interference competition. Exploitative and interference competition in phytophagous insect species can be mediated through host plants, natural enemies, physical factors and interspecific competition (Ofomata, 1998). Ecological differences between

species which may influence the outcome of competitive interactions include, climatic factors, rate of development, food preferences, differences in courtship patterns, and equal insemination of female in both light and dark (Sturterant, 1929; Patterson, 1943).

Life history traits including fecundity, body size, voltinism and dispersal ability may contribute to the competitive success of a species (Denna *et al*, 1995).

Several attempts have been made to explain the competitive advantage of *C. partellus* over indigenous stem borers. Ofomata (1998), studied the biology of *C. partellus* and *C. orichalcociliellus* in Kenya and made the following conclusions;

- ❖ Since the invasion of *C. partellus*, crop damage has become greater due to the higher consumption by *C. partellus* as compared to *C. orichalcociliellus*.
- ❖ *C. partellus* and *C. orichalcociliellus* are ecological homologues, with close overlap in their niches.
- ❖ No evidence implicates direct interference or organism in the displacement of *C. orichalcociliellus* by *C. partellus*.
- ❖ Indigenous parasitoids are not important factors in the displacement of *C. orichalcociliellus*.
- ❖ Competitive displacement of *C. orichalcociliellus* appears to be due to superior characteristics of *C. partellus*, which give it a competitive advantage over *C. orichalcociliellus*.
- ❖ *C. partellus* is reproductively superior to *C. orichalcociliellus* in total fecundity and egg survival.
- ❖ *C. partellus* is a more efficient dispersant with a higher host-plant establishing success than *C. orichalcociliellus*.

- ❖ The relatively faster development of *C. partellus* compared to *C. orichalcociliellus* in cultivated and wild grasses may be an important factor in the competitive displacement of *C. orichalcociliellus*.
- ❖ The survival of *C. orichalcociliellus* in native wild grasses may have allowed the co-existence of *C. partellus* and *C. orichalcociliellus* at the coastal area of Kenya.
- ❖ Native wild grasses serve as refuges for re-infestation of other crops by these stem borers.
- ❖ Since the development and survival of these stem borers in wild grasses is slower and low, respectively, compared to the cultivated hosts, wild grasses may have value as trap crops for stem borers.
- ❖ Earlier termination of diapause in *C. partellus* compared to *C. orichalcociliellus* may allow *C. partellus* to complete more generations in a year, giving it more individuals to colonize crops after the onset of rains and thus, displace *C. orichalcociliellus* from their habitats.

The displacement of one species by another on economically important crops is of major concern both economically and ecologically. It is noteworthy, however, that direct evidence of competitive displacement is difficult to obtain. This is partly because of the difficulty of measuring numbers and mortality in most natural populations and also because the population being eliminated may persist on for a relatively long period of time. The ecologist is therefore compelled to seek for evidence of competitive displacement through the use of a mathematical model.

The most important use of mathematics in ecology is the adoption of mathematical models as the conceptual models underlying ecological research and management.

Mathematical models are also important in the formulation of new theories about ecosystems and ecology. Manipulating relationships expressed in mathematical models enables the relationships to be explored, and various hypotheses about the ways in which the relationships behave to be formulated.

Much time can be saved in the early stages of hypothesis formulation by exploring this hypothesis through mathematical models. Similarly, Mathematical models can be used readily to investigate phenomena from the viewpoint of existing theories, by integrating disparate theories into a single working hypothesis. Such models may quickly reveal inadequacies in the current theory and indicate gaps where new theory is required.

Modeling is always implicit in pest control. Faced with a pest situation, the pest control worker invariably creates a model of it either in his mind or in the form of a laboratory population or by taking a sample plot of a field. He then simulates control of this model producing a new state, which he compares with the actual pest situation that he desires. The advantage of mathematical models in this context is that they are more ordered, and more easily lend themselves to manipulation and simulation.

It is against this background that we seek to formulate a competition model for *C. orichalcociliellus* and *C. partellus*. Through its manipulation we shall be able to investigate the phenomena of competitive displacement between them and predicting the rate and implications in terms of crop yield in an area. A model of this kind can also form the basis of effective control of the two pests.

1.2: THE CONCEPT OF COMPETITIVE DISPLACEMENT, PRINCIPLE AND OTHER DEFINATIONS.

Competitive displacement involving ecological homologues is a unique and special type of interaction between species where one species brings about the extirpation or displacement of another ecologically homologous species, or prevents a second such species from successfully colonizing all or a part of its habitat (Ofomata-1998).

1.2.1: Principle

The competitive displacement principle may be hypothesized thus; different species having identical ecological niches cannot co-exist for long in the same habitat (Debach and Sunby, 1963). The principle is premised on the implicit understanding that all species differ biologically, no matter how closely related or similar they may be, in habitats (Hardin 1960). Although they may be ecological homologues, their inherent bio physiological differences will favor one species over another in a particular situation (Ofomata, 1998).

1.2.2: Definitions

The definitions of the following terms are as given in Ofomata (1998).

Habitat is the environment of a species' natural population unit. The essential physical and biotic factors in a locality where individuals of that population normally live and reproduce.

Ecological niche the role-played by an animal based on its precise food, spatial and habitual requirements in a particular habitat. This means habitation of identical ranges.

Competition ('together-seek') is the attempted or actual utilization of common resources or requisites by two organisms. Competition exists even if one does not directly harm the other in the process. Cole (1960) defined competition as that which eliminates one of two sympatric species occupying the same niche.

Competitive displacement; the elimination, in a given habitat, of one species by another species where one has the identical ecological niche of the other.

Effective progeny production(R); the number of female progeny per parental female, which are themselves capable of producing progeny, thus excluding males and sterile females.

1.3: THE IMPORTANCE OF COMPETITIVE DISPLACEMENT.

The occurrence of competitive displacement between ecological homologues, although not common, is thought to be more rare in nature and of less significance than it actually is.

Ofomata, (1998) gives the importance of competitive displacement as follows:

- Competitive displacement is important in explaining the failure of a species to establish in areas where the climate should be ideal for it,

and where it has colonized in large numbers, many sites with abundant food (hosts) present.

- Competitive displacement is an important part in evolutionary processes of adaptation and speciation. Just as there are expressed differences in the environmentally modified values (effective progeny production) between ecological homologues, there is expressed genetic variability within specific populations.
- The hypothesis of competitive displacement is of considerable importance in biological control where by species of natural enemies are frequently introduced in attempts to obtain efficient regulation of insect-pest populations.

We must note at this stage, however, that competition between two species does not always result in the displacement of one of the species. The consequences of competition between two species depend mainly on the per capita rate of population increase, r , of each species.

In competition, it is not the r of unimpeded growth, which is of interest, but rather the r , which occurs when the environment is saturated with individuals.

Take a case of two species A and B.

Suppose, now, that a few of both A and B were introduced into an environment. Initially both will be scarce and their growth unimpeded. However, as their combined population increases, and the r of each decreases, there comes a point when the r of one of the species, say A, drops

to zero for the first time. B retains a positive r and increases further, reducing A's r to make it negative. B, thus, increases as A decreases.

This is the mechanism of competition, in which "B has a competitive advantage over A", and thus increases at the expense of A. If B maintains its competitive advantage, even when A is rare, it will completely eliminate A. On the other hand, neither eliminates the other if A gains competitive advantage, when rare, and maintains it. In that case, both will *coexist* indefinitely.

MacArthur, R.H and Joseph H. (1966) adequately discussed, means of ensuring co-existence, pointing out that all such mechanisms so far imagined seem to rely on heterogeneity of the environment;

- If the environment is not completely uniform in space, one species may not be eliminated and both may co-exist indefinitely.
- If the environment changes in time, a somewhat prolonged co-existence of competitors is also possible. Suppose conditions were changed in the course of the above illustration, so that the r of A becomes greater than that of B. The direction of change of the proportions of the two species would be reversed. If the period between such fluctuations is shorter than the time required to eliminate any of the species, the two species will co-exist, at least, for some time. However, it will be more difficult for them to persist indefinitely.
- If there is enough variation in the resources to allow each population to specialize in one variety of the resource (Brown and Wilson, 1956).

- A species might specialize by utilizing an abundant resource, before another more efficient competitor arrives, and gain a temporary respite from extermination, If there is variation in time. Many "weedy" plants show this "opportunistic" specialization.
- In spatially homogeneous and temporally invariant environment the stable coexistence of two predators on a single resource is possible, although this coexistence is not at fixed densities (McGhee and Armstrong, 1976).

Co-existence may also occur in uniform conditions. For example, when each of the species in competition is favored when rare, and is placed at a disadvantage when common, neither would be eliminated. Thus, when a species was losing in competition, getting gradually more rare, it would be progressively favored over the winning species, which, in becoming commoner, was losing its advantage.

CHAPTER TWO

MODELS OF GROWTH AND DECLINE

2.1: INTRODUCTION

In this chapter, we describe two simple models for describing patterns of growth and decline or decay in biological populations and individual organisms. Later in chapter four we shall refer to this model to build more realistic model and in chapter five fit data to the models.

2.2: EXPONENTIAL GROWTH.

Exponential growth and decline are basic models for describing the change in size of biological populations. Essentially, this is because all organisms have an innate capacity to increase or decrease, at a rate directly proportional to their numbers. In many situations growth, or decline, appears as a continuous process. The mathematical tools for describing the dynamics of continuous growth through infinitesimal changes are differential equations. We begin by developing a differential equation for exponential growth, which we will then solve to find the mathematical equation for the size of the population at some specified time.

Take the case of a bacterial colony. The successive population sizes over a small increment of time dt are related by,

Colony size at time $t+dt$ = colony size at time t + growth increment in time $(t, t+dt)$

i.e., $N(t+dt) = N(t) + dN$.

The essential property of exponential growth is that the growth increment is directly proportional to the size of the population i.e., $dN = r N dt$.

where the parameter r is referred to as the rate constant of growth. It is implicit that the population size N is a function of time. Rearranging this expression gives $r = dN/Ndt$ as the fractional change in size per unit time. This is measured in units of reciprocal time for example 0.6 per hour or equivalently, 0.06 per minute. For this reason, r is sometimes referred to as the fractional growth rate, the relative growth rate or the specific growth rate. Dividing both sides of the above expression by dt gives the rate of change in size per unit time over the small time interval as

$dN/dt = rN$ letting Δt tend to zero the rate of change of population size is seen to satisfy the differential equation $dN/dt = rN$.

We solve this differential equation to obtain,

$$N(t) = N(0)e^{rt} \quad (2.2.1)$$

The population growth is called exponential from the function, which describes its form. An important property of exponential growth is that the logarithm of population size increases as a straight line with slope equal to the rate constant, r (using logarithm to base e). Note that for those populations with the same rate constant the increase in the logarithm of population size is a series of parallel lines separated by an amount depending only on their initial sizes.

For exponential growth the time taken to produce a doubling of population size is called doubling time. A characteristic property of exponential growth is that the doubling time does not depend on the initial population size but is determined solely by the rate constant of growth.

2.3: EXPONENTIAL DECAY.

In the model of exponential growth the rate constant is positive but the model can also have a negative rate constant. This case corresponds to a rate of loss or decay in direct

proportion to size or amount of material present. When the quantity of material present at time t can be described by a continuous variable $Q(t)$ the rate of change of the quantity at time t is given by the differential equation $dQ/dt = -kQ$.

The parameter k is called the rate constant of decay. It is measured in units of reciprocal time. By convention k is taken to be positive so that a negative sign appears on the right-hand side of the differential equation to represent a rate of loss.

The differential equation is solved in the same way as for the exponential growth to give the quantity of material present at time t as $Q(t) = Q(0)e^{-kt}$.

Where $Q(0)$ is the quantity present at time $t = 0$. The decline in the quantity is described by an exponential curve and its logarithm decreases as a straight line with slope equal to $-k$ (using logarithms to base e).

In exponential decay, the time taken to decay to half of the initial amount present is called THE HALF-LIFE. The quantity is analogous to the doubling time for exponential growth. It does not depend on the initial amount present and is determined solely by the rate constant of decay.

Although populations can increase exponentially, their food supplies usually increase arithmetically, so that the population growth will eventually be limited (Malthus, 1798). For plants and animals there are many ways in which population growth might be limited. Shortage of food, lack of space or the accumulation of toxic substances in the environment may lead to increased mortality rates or reduced rates of reproduction and thereby prevent further population increase. These changes may involve increased competition for resources, either directly through overt interactions between individuals, or indirectly via a more passive depletion of the environment. Whatever

the underlying processes, the result is limited population growth in which the relative growth rate decreases with increasing population size.

Many mathematical models for limited population growth, which apply to a wide range of biological processes and mechanisms, have been developed. However, we shall concentrate on the logistic model because of its relation with the competition models that we shall later discuss.

2.4: LOGISTIC MODEL FOR LIMITED POPULATION GROWTH IN CONTINUOUS TIME.

A basic pattern of limited population growth is sigmoidal or s- shaped curve. A particular case is the logistic model, which has been widely used, in theoretical work and in empirical studies to describe the growth of populations both in the field and in laboratory conditions. To develop the logistic model we begin by setting a differential equation for the growth rate and then solving the equation for the equation to find the pattern of growth in time.

We recall that the rate of growth of a population (for exponential growth) of size $N(t)$ at time t is given by $dN / dt = rN$ where r is the rate constant of growth. The characteristic feature of limited population growth is that the relative growth is not constant but decreases as the population size increases.

In the logistic model, the relative growth rate declines linearly with population size so that the rate of change of population size is then given by the differential equation;

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \quad (2.4.1)$$

The parameter r in this case, is the relative growth rate when the effects of limiting factors are negligible. K is called the carrying capacity or equilibrium level. When the population size equals K the growth rate is zero, and the population remains at that

level. As the population size increases, the relative growth rate is reduced in proportion to the fraction of the carrying capacity remaining. Note that the assumed linear decrease of relative growth rate with population size is a purely descriptive model for the effects of the factors, which limit growth. A more mechanistic model would involve postulates about the underlying processes and mechanisms associated with these factors. The differential equation for logistic growth can be solved using analytical methods to obtain;

$$N(t) = \frac{K}{1 + \left[\frac{K}{N(0)} - 1 \right] e^{rt}} \quad (2.4.2)$$

This is the logistic equation for population growth. This equation is sometimes written in the form

$$N(t) = \frac{K}{1 + e^{-r(t-h)}} \quad (2.4.3)$$

by substituting $K/(N(0)) - 1 = e^{hr}$. The parameter h is the time at which the population reaches half the carrying capacity, i.e., $N(h) = K/2$. This form assumes that the initial population size is less than the carrying capacity K since the exponential function is always positive.

2.5 PROPERTIES OF THE LOGISTIC GROWTH CURVE

- (i) The increase of population size with time follows a sigmoidal or s-shaped curve.

- (ii) The growth rate increase with size to a peak rate of $rK/4$ when the population reaches half the carrying capacity. This occurs at a point of inflexion on the growth curve where the slope is greatest.
- (iii) The logarithm of population size increases at a decreasing rate.
- (iv) The relative growth rate decrease linearly with population size with slope $-r/K$.

For logistic population growth, the carrying capacity K is reached when

$$N(t) = \underline{K} \text{ or } 1 + e^{-r(t-h)} = 1, \text{ where } h \text{ is the time to reach } \underline{K/2}$$

CHAPTER THREE

COMPETITION MODELS

3.1 INTRODUCTION

In this chapter, we present some simple descriptive models for competition between two species. There are a number of competition models that have been developed so far but we shall restrict ourselves to the Lotka –Volterra (L-V) model since it was the first competition model to be developed and all the other models are improvement of it.

3.2 THE LOTKA-VOLTERRA MODEL FOR TWO SPECIES

COMPETITION

A basic model for the interaction of two competing species was proposed by Lotka (1925) and, independently, by Volterra (1926). The approach extends the logistic model for limited population growth of a single species in which the growth rate is given by

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \quad (3.2.1)$$

where N denotes population density at time t , r is the intrinsic relative growth rate and K is the carrying capacity. The logistic model does not incorporate a specific mechanism for limited population growth but merely describes its effect as a relative growth rate, which decreases linearly with population density, i.e.

$$\frac{1}{N} \frac{dN}{dt} = r - r \frac{N}{K} \quad (3.2.2)$$

or

Relative growth rate

=Intrinsic relative growth rate-Reduction in relative growth rate due to effect of species on itself.

This reduction in the relative growth rate with increased density is a simple model for the effect of competition between individuals of the same species. Lotka-Volterra extended the approach to measure the effects of competition between species. He added a further reduction in the relative growth rate of one species, which is proportional to the density of other species and postulated the existence of two species competing for the same resource, R . Based on the assumptions that the specific growth rate of each of competing species increases linearly with the amount of resource present, and that the amount of resource available at time t , is diminished in proportion to the densities of the competitors so that for the interaction of species 1 and 2, Lotka-Volterra came up with the equation,

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 - r_1 \frac{N_1}{K_1} - r_1 \alpha_{12} \frac{N_2}{K_1} \quad (3.2.3)$$

When α_{12} exceeds one, species 1 suffers a greater competitive effect from species 2 than it does from itself. A similar coefficient α_{21} measures the competitive effect of species 1 on species 2.

This is the basis of the Lotka-Volterra model for two species competition.

Thus the Lotka- Volterra models for two species competition are

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1} \right) \quad (3.2.4a)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \alpha_{21} N_1}{K_2} \right) \quad (3.2.4b)$$

where N_1 and N_2 are the population density of species 1 and 2, r_1 and r_2 are the intrinsic relative growth rates, K_1 and K_2 are the carrying capacities in single population growth, and α_{12} and α_{21} are competition coefficients.

In the absence of competition from species 2, species 1 exhibits logistic population growth, increasing to its carrying capacity. Similarly with no competition from species 1, the density of species 2 will increase and stabilize at its carrying capacity. For specified values of the parameters and the initial population densities, the behavior of the model can be studied by solving the differential equations of population change using numerical methods.

For along time especially since the 1970's, more and more ecologists have pointed out that there exist many deficiencies in L-V equations. The authors' points are summarized as follows (Cui Qiwu *et.al*, 1991),

- ❖ L-V equations lack sufficient and reasonable theoretical foundation. Except for the direct extension of Logistic equation, they do not have any other theoretical backgrounds.
- ❖ The only theoretical basis of L-V equations, Logistic equation, has many deficiencies too (Pielou, 1969, Odum, 1983). It has been preliminarily proved that it is not a general theoretical model of single population growth (Cui and Lawson, 1982, Song, 1986).
- ❖ L-V equations oversimplify the process of interspecific competition (Neill, 1974; May, 1976). Lotka himself has always said that a correct interspecific competition model should be non-linear (Gilpin and Ayala, 1973).
- ❖ L-V model contains two restrictions on the mathematical form of the equations used: (a) the resource available at time t is a function of the population densities of the competitors at time t , and (b) the specific growth rate is a linear function of the resource (McGehee and Armstrong, 1975).

Meanwhile, as stated above, many theoretical models of interspecific competition have been constructed (MacArthur, 1968, 1972, May, 1971, Schoener, 1974 Armstrong and McGehee, 1975, Schoener, 1973, 1974a, 1976 Jensen, 1987). Since the 1980s Chinese Scholar Cui Qiwu together with his domestic and foreign colleagues, have constructed and studied a set of new ecological explanatory models based on the theory of Nutrition Kinetics (Cui and Lawson, 1982; Cui and Lu, 1985, 1988). In the following chapter we shall develop our model by modifying the explanatory model of interspecific competition based on the theory of Nutrition Kinetics established by Sun *et al*, 1991.

Looking at the various population models so far pointed out we note the importance of differential equations in them. It is imperative therefore that we discuss one method of solving differential equations. Numerical methods are usually employed in solving differential equations. Some of the numerical methods available for solving differential equations include Euler method, backward Euler method, Mid-point method, Taylor series method and the Runge Kutta methods. For the sake of the differential equations that we shall later need to solve, we briefly look at one of the Runge Kutta methods; the fourth order Runge-Kutta method for the system of equations which is often referred to as the standard method for solving differential equation because of its power of balance, precision and easy to compute.

3.3 THE FOURTH ORDER RUNGE-KUTTA METHOD FOR THE SYSTEM OF EQUATIONS

The fourth order classical Runge-Kutta method for the system of equations

$$\frac{du}{dt} = f(t, u)$$

$$u(t_0) = \pi$$

may be written as

$$u_{j+1} = u_j + \frac{1}{6}(K_1 + 2K_2 + 2K_3 + K_4) \quad (3.3.1)$$

where

$$K_1 = \begin{bmatrix} K_{11} \\ K_{21} \\ \cdot \\ \cdot \\ \cdot \\ K_{n1} \end{bmatrix}, \quad K_2 = \begin{bmatrix} K_{12} \\ K_{22} \\ \cdot \\ \cdot \\ \cdot \\ K_{n2} \end{bmatrix}, \quad \dots, \quad K_3 = \begin{bmatrix} K_{13} \\ K_{23} \\ \cdot \\ \cdot \\ \cdot \\ K_{n3} \end{bmatrix}, \quad \dots, \quad K_4 = \begin{bmatrix} K_{14} \\ K_{24} \\ \cdot \\ \cdot \\ \cdot \\ K_{n4} \end{bmatrix}$$

and

$$K_{i1} = hf_i(t_j, u_{1,j}, u_{2,j}, \dots, u_{n,j})$$

$$K_{i2} = hf_i\left(t_j + \frac{h}{2}, u_{1,j} + \frac{1}{2}K_{11}, u_{2,j} + \frac{1}{2}K_{21}, \dots, u_{n,j} + \frac{1}{2}K_{n1}\right)$$

$$K_{i3} = hf_i\left(t_j + \frac{h}{2}, u_{1,j} + \frac{1}{2}K_{12}, u_{2,j} + \frac{1}{2}K_{22}, \dots, u_{n,j} + \frac{1}{2}K_{n2}\right)$$

$$K_{i4} = hf_i(t_j + h, u_{1,j} + K_{13}, u_{2,j} + K_{23}, \dots, u_{n,j} + K_{n3}), i = 1(1)n$$

In an explicit form (3.3.1) becomes

$$U_{i,j+1} = U_{ij} + \frac{1}{6} (K_{i,j}^* + 2K_{2i}^* + 2K_{i+1}^* + K_{4,j}^*) \quad (3.3.2)$$

for each $i=1, 2, \dots, n$

CHAPTER FOUR

METHODOLOGY

4.1 INTRODUCTION

Sun *et al*, (1991) constructed a mathematical model of interspecific competition based on the theory of nutrition kinetics. Although the new model has the same qualitative behaviors, to some extent, as Lotka-Volterra competition equations, it gives the outcomes of interspecific competition a better explanation of nutrition kinetics, which conforms to the basic principles of ecology or biology (Sun *et al*, 1991). Their model, however, was for two species competing for one resource. We modify this to a model of two species competing for more than one resource.

For each resource let H be the food biomass available for the two species at time t , and M_i , the population density of the species i , $i=1,2$ at time t . We employ the basic modeling formula of nutrition Kinetics,

$$\frac{dM_i}{M_i dt} = \left(\frac{U_{mi}H}{K_i} \right) + H \quad (4.1.1)$$

where, U_{mi} is the maximum specific rate of growth of species i , when food is unlimited, K_i is the efficiency of food utilization. We now extend this model to include four distinct food sources; maize, sorghum, wild sorghum and Napier grass. We assume that the two wild grasses, Napier and wild sorghum are in the field throughout the year. Maize and sorghum are assumed to be in the field during long and short rainy seasons, that is, twice in a year. We assume, too, that the resources are independent.

The two species both have four stages in their life cycle. But our model is based specifically on the larval stage since it is at this stage that they are most injurious to the stated grasses. We therefore assume that the larval stage strongly influences each of these species population dynamics. Equation (4.1.1) may then be re-written as,

$$\frac{dM_i}{M_i dt} = \sum_{j=1}^4 \frac{U_{mij} H_j}{K_{ij} + H_j} \quad (4.1.2)$$

Where U_{mij} is the maximum specific rate of growth of species i on resource j and K_{ij} is the corresponding efficiency of food utilization. For each of this grass let the initial food resource be S_{mj} . Suppose each of this grass at any one time t , has the two species competing. After some time the limiting resource j decreases to H_j , while the size of competing population i , on j is M_{ij} which contains concentration S_{ij} of limiting nutrient j . Let α_{ij} represent the contained amount of limiting nutrient $j, j=1 \dots 4$, by per unit of population $i, i=1,2$.

Then;

$$H_j = S_{mj} - (S_{1j} + S_{2j}) \quad (4.1.3a)$$

$$S_{1j} = \alpha_{1j} M_{1j}, \quad S_{2j} = \alpha_{2j} M_{2j} \quad (4.1.3b)$$

We consider a case where there is only one species, i , on the resource j . We then define M_{mij} as the maximum size of population i when all the limiting nutrient j , is transformed into the biomass of population i . Then;

$$S_{mj} = \alpha_{1j}M_{m1j} = \alpha_{2j}M_{m2j} \quad (4.1.3c)$$

Putting this expression (4.1.3c) in (4.1.3a) we get,

$$H_j = \alpha_{1j}M_{m1j} - (\alpha_{1j}M_{1j} + \alpha_{2j}M_{2j}) \quad (4.1.3d)$$

Substituting (4.1.3d) into (4.1.2) we get,

$$\begin{aligned} \frac{dM_i}{M_i dt} &= \sum_{j=1}^4 \frac{U_{m1j}(\alpha_{1j}M_{m1j} - (\alpha_{1j}M_{1j} + \alpha_{2j}M_{2j}))}{K_{1j} + (\alpha_{1j}M_{m1j} - (\alpha_{1j}M_{1j} + \alpha_{2j}M_{2j}))} \\ &= \sum_{j=1}^4 \frac{U_{m1j}M_{m1j} \left(1 - (M_{1j} + \frac{\alpha_{2j}}{\alpha_{1j}}M_{2j}) \div M_{m1j} \right)}{\left(\frac{K_{1j}}{\alpha_{1j}} + M_{m1j} \right) \left(1 - (M_{1j} + \frac{\alpha_{2j}}{\alpha_{1j}}M_{2j}) \div \left(\frac{K_{1j}}{\alpha_{1j}} + M_{m1j} \right) \right)} \end{aligned} \quad (4.1.4)$$

$$\frac{dM_1}{dt} = \sum_{j=1}^4 U_{c1j}M_1 \frac{\left(1 - (M_{1j} + \frac{\alpha_{2j}}{\alpha_{1j}}M_{2j}) \div M_{m1j} \right)}{\left(1 - (M_{1j} + \frac{\alpha_{2j}}{\alpha_{1j}}M_{2j}) \div M'_{m1j} \right)} \quad (4.1.5a)$$

Likewise,

$$\frac{dM_2}{dt} = \sum_{j=1}^4 U_{c2j}M_2 \frac{\left(1 - (M_{2j} + \frac{\alpha_{1j}}{\alpha_{2j}}M_{1j}) \div M_{m2j} \right)}{\left(1 - (M_{2j} + \frac{\alpha_{1j}}{\alpha_{2j}}M_{1j}) \div M'_{m2j} \right)} \quad (4.1.5b)$$

where, $M_{mij} = \frac{K_{ij}}{\alpha_{ij}} + M_{mij}$ is a new parameter related to the amount of available nutrient j , and efficiency of nutrient utilization of population i .

$U_{cij} = \left(\frac{M_{mij}}{M'_{mij}} \right) \times U_{mij}$ is the parameter of specific rate of growth of population I on resource j . We now consider the mortalities of the two species on each of the resources. We denote the mortality by D_{ij} i.e. the mortality rate of species I on resource j . $j=1 \dots 4$; $I=1,2$. Then equation (4.1.5a) becomes,

$$\frac{dM_1}{dt} = \sum_{j=1}^4 U_{c1j} M_1 \frac{\left(1 - (M_{1j} + \frac{\alpha_{2j}}{\alpha_{1j}} M_{2j}) \div M_{m1j} \right)}{\left(1 - (M_{1j} + \frac{\alpha_{2j}}{\alpha_{1j}} M_{2j}) \div M'_{m1j} \right)} - D_{ij} \quad (4.1.6)$$

we manipulate the above equation to obtain,

$$\frac{dM_1}{dt} = \sum_{j=1}^4 U^*_{c1j} M_1 \frac{\left(1 - (M_{1j} + \frac{\alpha_{2j}}{\alpha_{1j}} M_{2j}) \div M^*_{m1j} \right)}{\left(1 - (M_{1j} + \frac{\alpha_{2j}}{\alpha_{1j}} M_{2j}) \div M'_{m1j} \right)} \quad (4.1.7)$$

Likewise (4.1.5b) becomes

$$\frac{dM_2}{dt} = \sum_{j=1}^4 U^*_{c2j} M_2 \frac{\left(1 - (M_{2j} + \frac{\alpha_{1j}}{\alpha_{2j}} M_{1j}) \div M^*_{m2j} \right)}{\left(1 - (M_{2j} + \frac{\alpha_{1j}}{\alpha_{2j}} M_{1j}) \div M'_{m2j} \right)} \quad (4.1.8)$$

where $M_{mij}^{\bullet} = \frac{1 - \frac{D_{ij}}{U_{cij}}}{1 - \left(\frac{D_{ij}}{U_{cij}}\right) \times \left(\frac{M_{mij}}{M'_{mij}}\right)} \times M_{mij}$ is the carrying capacity of resource j of

population i . $U_{cij}^{\bullet} = U_{cij} - D_{ij}$ is the parameter of specific growth rate of population i on resource j .

Thus equation (4.1.7) and (4.1.8) turn into the following more general forms respectively:

$$\frac{dM_1}{dt} = \sum_{j=1}^4 U_{c1j}^{\bullet} M_1 \frac{(1 - (M_{1j} + \alpha_{12j} M_{2j}) \div M_{m1j}^{\bullet})}{(1 - (M_{1j} + \alpha_{12j} M_{2j}) \div M'_{m1j})} \quad (4.1.9)$$

$$\frac{dM_2}{dt} = \sum_{j=1}^4 U_{c2j}^{\bullet} M_2 \frac{(1 - (M_{2j} + \alpha_{21j} M_{1j}) \div M_{m2j}^{\bullet})}{(1 - (M_{2j} + \alpha_{21j} M_{1j}) \div M'_{m2j})} \quad (4.1.10)$$

where α_{12} and α_{21} are competition coefficients of population 2 to 1 and population 1 to 2, respectively, and they are not reciprocal, for the two populations have different feeding habits. When $\alpha_{12} > 1$ then population 2 wins the competition and when $\alpha_{21} > 1$ the population 1 wins the competition.

CHAPTER FIVE
AN EMPIRICAL STUDY

5.1: INTRODUCTION

In this chapter we carry out an empirical study based on what we have discussed in the previous chapters. Having noted that our study is based purely on the larval stages of the two species, with the stated assumptions, we adopt equation (4.1.9) and (4.1.10) as the models representing the change in population density of *Chilo Partellus* and *Chilo Oricho* respectively with time. Before we can fit them, however, we first estimate the various parameters mostly derived directly from existing literature (Appendix A1), especially the work done by *Ofomata* (1998).

The parameter of maximum population density of each species on each resource M is among the parameters obtained directly from *Ofomata's* work and is given in table 2.1 (Appendix 2). To obtain the competition coefficients we refer to (Harper 1977) and define for each resource:

$$\alpha_{12} = ((\%M_1 \text{ at } 0:1) / (\%M_2 \text{ at } 0:1)) \div ((\%M_1 \text{ at } 1:1) / (\%M_2 \text{ at } 1:1)) \quad (5.2.1a)$$

Likewise,

$$\alpha_{21} = ((\%M_2 \text{ at } 0:1) / (\%M_1 \text{ at } 0:1)) \div ((\%M_2 \text{ at } 1:1) / (\%M_1 \text{ at } 1:1)) \quad (5.2.1b)$$

Table 2.2 (Appendix A2) gives the estimated competition coefficients on each of the resources. To obtain the other parameters U_{cij} and M'_{mij} , we assume a situation when there is no inter specific competition. Let us also assume a no death special case so that our models are reduced to,

$$\frac{dM}{dt} = \frac{U_c M (M_m - M) \div M_m}{(M'_m - M) \div M'_m} \quad (5.2.2a)$$

We proceed to get the integral form of the above equation,

$$U_c \frac{M'_m}{M_m} \int dt = \int \frac{M'_m - M}{M(M_m - M)} dm$$

$$U_c \frac{M'_m}{M_m} t + c = \int \frac{M'_m}{M(M_m - M)} dm - \int \frac{1}{(M_m - M)} dm \quad (5.2.2b)$$

Taking the first part of the second portion of equation (5.2.2) we express it as a partial fraction to obtain

$$A = B = \frac{M'_m}{M_m} \quad (5.2.3)$$

Substituting it back into equation (5.2.2) we get,

$$\begin{aligned} U_c \frac{M'_m}{M_m} t + c &= \frac{M'_m}{M_m} \int \frac{1}{M} dm + \frac{M'_m}{M_m} \int \frac{1}{M_m - M} dm - \int \frac{1}{M_m - M} dm \\ &= \frac{M'_m}{M_m} \ln M - \frac{M'_m}{M_m} \ln(M_m - M) + \ln(M_m - M) \end{aligned} \quad (5.2.4)$$

At time t_0 equation (5.2.4) becomes

$$U_c \frac{M'_m}{M_m} t_0 + c = \frac{M'_m}{M_m} \ln M_0 - \frac{M'_m}{M_m} \ln(M_m - M_0) + \ln(M_m - M_0) \quad (5.2.5)$$

Subtracting (5.2.6) from (5.2.5) we obtain;

$$t - t_0 = \frac{1}{U_c} \left(\ln \frac{M}{M_0} - \ln \frac{M_m - M}{M_m - M_0} \right) + \frac{M_m}{U_c \times M'_m} \ln \frac{M_m - M}{M_m - M_0} \quad (5.2.6)$$

$$\text{let } X_1 = \ln \frac{M}{M_0} - \ln \frac{M_m - M}{M_m - M_0}, X_2 = \ln \frac{M_m - M}{M_m - M_0} \quad y = t - t_0 \quad b_1 = \frac{1}{U_c}, b_2 = \frac{M_m}{U_c \times M'_m}$$

Then equation (5.2.6) becomes a linear equation as follows:

$$y = b_1 X_1 + b_2 X_2 \quad (5.2.7)$$

We then generated population data for each species on each resource using the logistic equation (2.4.2), for time t having fixed population at time t_0 . These we used to obtain the corresponding X_1 and X_2 which in regards to equation (5.2.7) we regressed using the SAS REG procedure (SAS institute, 1987) to obtain the parameters, U_{cij} and M'_{mij} . The results are presented in Tables 2.3 and 2.4 (Appendix 2). The estimated parameters are then substituted in the corresponding model equations (4.1.9) and (4.1.10) and the numerical solution for each of the models got by computer simulation of the fourth order Runge-Kutta method.

During our simulations we made the following assumptions;

- That Napier grass and wild sorghum are in the field throughout the year.
- That sorghum and maize are in the field during two rainy seasons in between which there is a dry season (Overhalt *et al*, 1994).
- That the two species infest the two wild grasses throughout the year. Some however, migrate to infest maize and sorghum during the rainy season.
- That since the larval of the two species preferred boring into young plants (Ofomata 1998) we assumed that the larval population in maize and sorghum grew constantly at the corresponding growth rates up to half the rainy season after which it decreased at the same rate until the end of the subsequent dry season.

Simulations were then done to obtain the population density of each species per plant in the four resources for a period of 4000 days.

Note that we fixed an arbitrary initial population for the two species on Napier grass and wild sorghum for the first year. The initial population on maize and sorghum at the beginning of any of the planting season was always taken as the average population density per plant of each species in the field at that time.

Figures 5.1...5.4 shows the time plot for the average population density on maize, sorghum, wild sorghum and the four grasses combined.

From the time plots, the population density of each of the species of the resources forever remain bounded away from the zero mark thus, neither of the species can ever approach extinction; the species coexist for a long period of time, though at fixed densities.

Fig 5.1

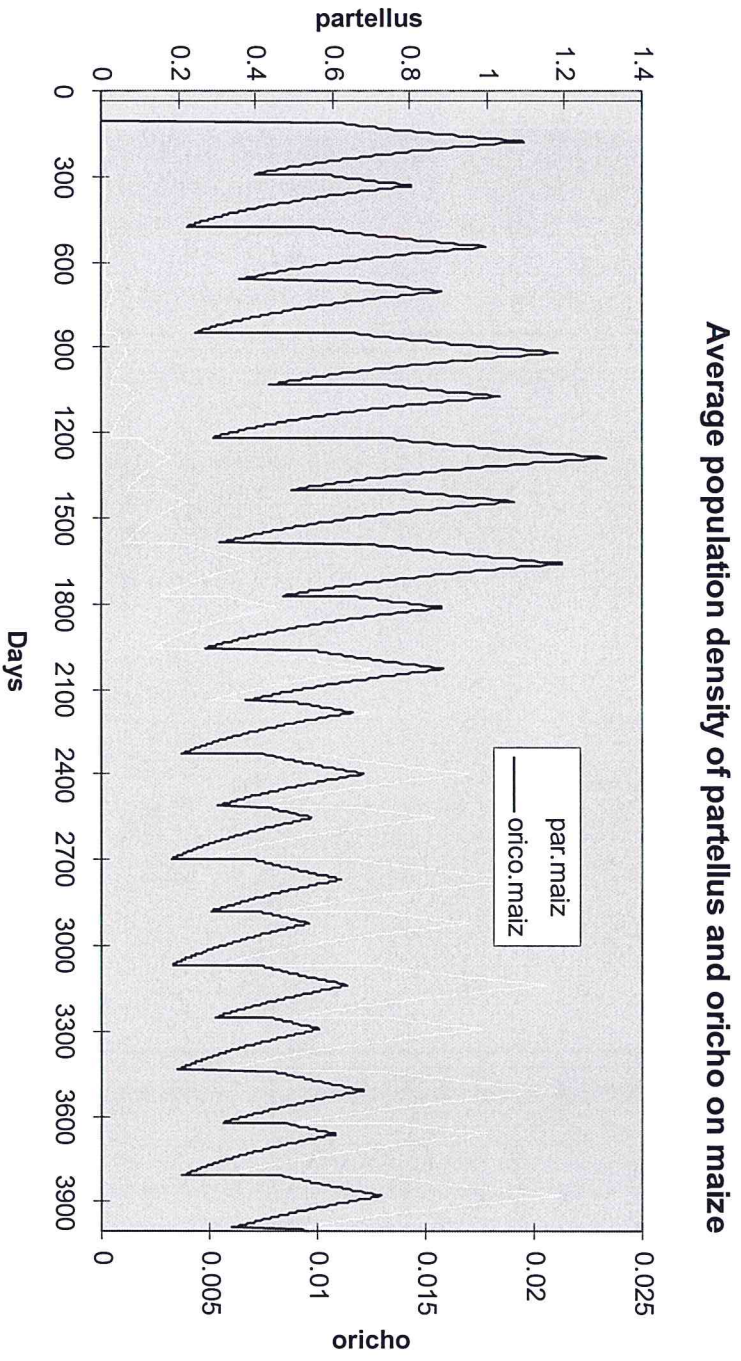
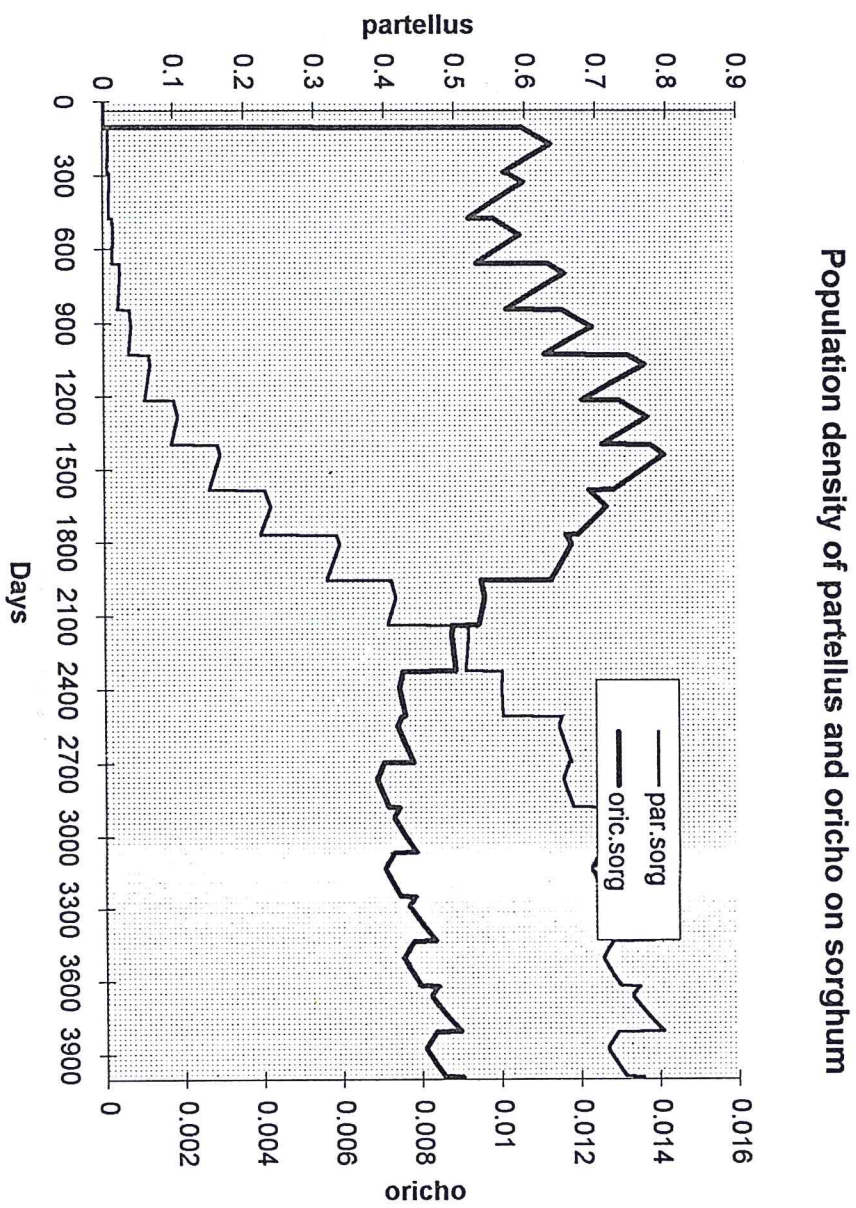


Fig 5.2



Population Density of partellus and oricho on wild sorghum

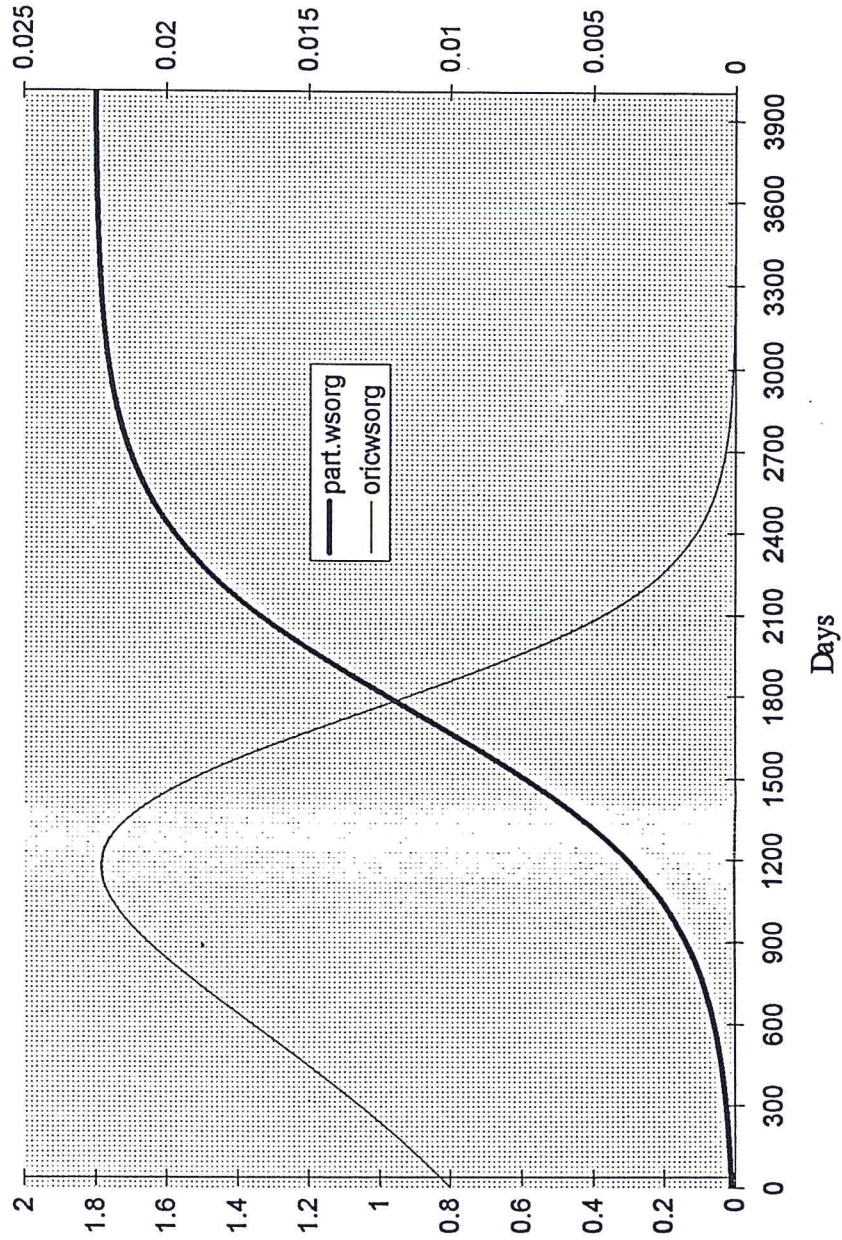
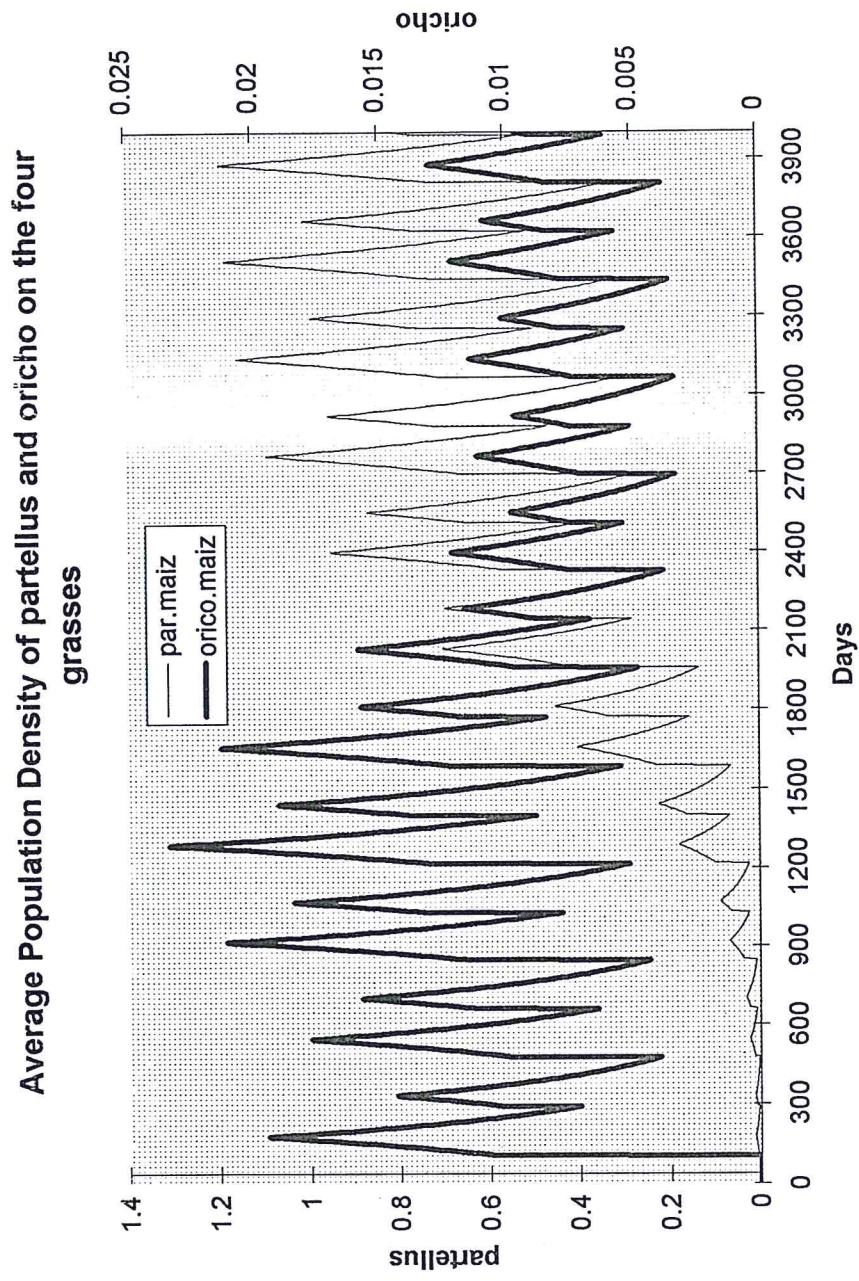


Fig 5.3

Fig 5.4



CHAPTER SIX

ACCOMPLISHMENTS AND CONCLUSIONS

6.1 INTRODUCTION

In this chapter we briefly describe the general achievements/conclusions we have made in this project. We also suggest areas, which have showed up during this project, for further research.

6.2 ACHIEVEMENTS/CONCLUSIONS

- a) We noted earlier that one of the things that hamper field researchers ability to make viable population projections for the two species is the difficulty to continuously carry out their field observations for reasonable length of time. Our model solves this problem because it enables one to make population projections for as many days as required as long as one has the initial population and the conditions remain constant. This saves time and resources.
- b) From our time plots one is able to deduce that despite the numerous inferior attributes of *Chilo orichalcociliellus* to those of *Chilo partellus*, it is able to persist in existence, though at very lower density, contrary to the expectation of extinction. This is deduced from the observation that at no time does the “oricho” curve hit the zero mark no matter the length of time. This could be attributed to the fact that the environment is spatially homogeneous and temporally invariant (McGhee and Armstrong 1975).

- c) We have been able to confirm that the wild grasses play a major role in the population dynamics of the two species and therefore any viable control of the two pests must emphasize the management of the wild grasses.
- d) We have been able to show from the competition coefficients that *chilo partellus* is superior in competition in the sorghum grasses. On the other hand, *Chilo oricho* is superior in competition in the Napier grass. The difference in competition, is, however, minimal in maize. This result is consistent with the information in the literature (Ofomata,1998).

6.3 SUGGESTIONS

- a) In our model we assumed that the birth rate and the death rate of each of the two species on each of the resources was constant. However it has been observed that the rate at which the larva establishes in the plant depends on the age of the plant and the time of the season (Ofomata, 1998). For example, at the beginning of the rainy season more adult species are expected to migrate to the maize and sorghum. We thus expect the growth rate (establishment rate) to be higher in them than in the wild grasses. The converse should also be expected. Similarly as the plants grow, we expect the establishment rate to be consistently reduced at a gradual rate. It is therefore necessary to investigate the concept of differential mortality and growth rates and incorporate them in this model.
- b) The two *chilo* species have a life cycle of four stages. We have concentrated our study on the larval stage only. It is necessary that we study the population dynamics of each of the stages separately before integrating them into a single population model. This would result in a more precise model.
- c) We need to carry out a sensitivity analysis of our model. In practice the sensitivity analysis is carried out by changing the parameter, forcing function, initial values

or sub models and observing the corresponding response on the important state variable. The relative change in parameters is chosen on the basis of our knowledge of the certainty of the parameters.

- d) It is necessary that we calibrate our model i.e., we test several sets of parameters by calibration and the various model outputs of state variables are compared with the measured or observed values of the same state variables. The parameter set, that gives the best agreement between model outputs and measured state variables, is chosen.

The need for calibration can be explained by use of the following characteristics of ecological models and their parameters (Jorgensen, 1994):

- i) Most ecological parameters are rarely known as exact values. Therefore all literature values for ecological parameters have some uncertainty.
- ii) All ecological models are simplification of nature. The process descriptions and the system do not account for all details. If the model is selected carefully it will include all the important processes and components for the problem in focus, but the omitted details might still have an influence on the result. This influence can to a certain extent be taken into account by the calibration.
- iii) An ecosystem is flexible system, which can meet changes in forcing functions by new properties of the state variables. This is either an adaptation of the present species or change in species composition. It is important in many modeling contexts to include this characteristic of ecosystems in our models.

e) We need to examine the consequences of periodic variation in r and/or K in our model. A small oscillation in the value of one parameter in a model equation usually cause a similar small oscillation in the population, the amplitude and phase of this oscillation being easily calculable from the transfer function . If, however, the imposed oscillation is of large amplitude, or if the undriven system itself oscillates, then the nonlinear effects may cause profound qualitative changes in the behavior of the population. For example, a population originally in stable equilibrium, when driven by a large oscillation in an environmental parameter, may oscillate at a frequency equal to a *subharmonic* of the driving frequency, and is thus conceivable that the annual climatic cycle could produce population cycles with a period of several years (Nisbet and Gurney, 1975). The effects of a periodically varying environment are also important for evolutionary theory, as the selective forces on a system of fluctuating environment differ from those in a stable environment. MacArthur and Wilson(1976) argued that, in a strongly varying environment, natural selection favors a species which can maximize its intrinsic growth rate (r -selection), while in a constant environment there is a selection for qualities which lead to the most use of available resources (K -selection)

f) We were unable to include guinea grass in our model yet it exists in the field among the other grasses (Ofomata,1998). This was due to lack of sufficient information on the growth parameters of the two-chilo species on it. Since partellus is not able to complete its life cycle on this grass, unlike oricho, it is vital to incorporate it in the model and see how it boosts further the population density of Oricho in the field.

REFERENCES

Black, W.C., Rai, K.S., Turco, B.J. and Arroyo, D.C. (1989). Laboratory study of competition between United States strains of *Aedes albopictus* (Diptera: Culcidae). *Journal Of Medical Entomology* 26: 839-850.

Brown, W.L., Jr., and E.O. Wilson (1956). Character displacement. *Sys. Zool.* 5:49-64

Cui, Q. and Lawson, G.J. (1982). Study on models of single populations: An expansion of the logistic and exponential equations. *J.Theor. Biol.*, 98: 645-659

Cole, L.C. (1960). Competitive exclusion. *Science* 132 (3423): 348-349

Cui Qiwu, Sun Guowei and Song Bo. (1986). Preliminary estimation of Logistics equation. *J. Ecol (China)*. 5(3): 57-62

Debach, P. (1966) and Sunby, L.A. (1963). Competitive displacement between ecological Homologues. *Hilgardia* 34(5) 105-166.

Food and Agricultural Organization (1991). Yearbook vol. 45.

Gilpin, M. E. and Ayala, F.J. (1973). Competition between species. Theoretical models and experimental tests. *Theor. Population Biol.*, 4: 331-356.

Hardin, G . (1960). The competitive exclusion principle. *Science* 131 (3409): 1292-1298

Hill, D.S(1983). *Agricultural insect pests of the tropics and their control* Cambridge University press. p 281-381

Hutchinson, G.E (1978). *An introduction to population ecology.* Yale University Press, New Haven, Connecticut, USA.

Kfir, R. (1994). Attempts at biological control of the stem borer *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) in South Africa. *African Entomology* 2: 67-68.

Likens, G.E.,(ed), (1985). *An Ecosystem Approach to Aquatic Ecology: Mirror Lake and its Environment.* Springer-Verlag, New York, 516 pp.

MacArthur, R. and Wilson, E.O. (1976). *The theory of Island Biogeography.* Princeton: Princeton University Press.

McGehee and Armstrong (1976). Coexistence of Two Competitors on One Resource.

J.theor. Biol.,56: 499-502.

Mathez, F.C. (1972). *Chilo partellus* Swinhoe, *C.orchalcociliellus* Strand (Lepidoptera). Crambidae) and *Sesamia calamistis* Hmps. (Lep Noctuidae) on maize

in the Coast Province Kenya. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 45: 267-289.

May, R.M., (1976) Theoretical Ecology. Blackwell Scientific Publications, Oxford.

Neill, W.E., (1974) The community matrix and interdependence of the competition coefficients. *Am. Nat.*, 108: 399-408.

Nisbet, R.M. and Guiney, W.S.C. (1975). Population Dynamics in a periodically varying Environment. *J. theor. Biol.* (1976) 56: 459-475.

Nye, I.W.B. (1960). *The insect pests of graminaceous crops in East Africa*. Colonial Research Study No. 31 London, Her Majesty's Stationary Office p 48

Odum, E.P., (1983) Basic Ecology. Sanders College Publishing, Winston.

Ofomata, V.C. (1998). Ecological Interactions Between *Chilo partellus* (Swinhoe) and *Chilo orichalcociliellus* Strand on the Kenya Coast.

Overhalt, W.A; K.Ogedah and P.M. Lammers (1994a). Distribution and sampling of *Chilo partellus* (Swinhoe)(Lepidoptera: Pyralidae) in maize and sorghum at the Kenya coast. *Bull. Ent Res.* 84: 367-378.

Overhalt, W.A; Ngi-Song, A.J. Kimani, S.W.; Mbapila, J.; Lammers, P. and Kioko, E. (1994b). Ecological considerations of the introduction of *Cotesia flavipes*

Cameron (Hymenoptera: Braconidae) for biological control of *Chilo partellus*(Swinhoe) (Lepidoptera: Pyralidae) in Africa. *Biocontrol News and information* 15(2): 19N-24N.

Patterson, J.T.(1943). Studies in the genetics of *Drosophila*.III. the Drosophilidae of the Southwest. Univ. of Texas pub, No.4313

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

Seshu Reddy, K.V., Walker, P.T. (1990). A review of the yield losses in graminaceous crops caused by *Chilo spp.* *Insect Sci. Appli.* 11 (4/5): 563-569.

Seshu Reddy, K.V. (1991) Insects pests of sorghum in Africa. *Insect Sci. Applic.* 12: 563-657.

SAS Institute (1987) *SAS/STAT guide for personal computers, version 6ed.* SAS Institute, Cary, NC.

Schoener, T. W., (1974). Competition and the form of habitat shift. *Theor. Population Biol.*, 6: 265-307.

Schoener, T.W. (1983). Field experiments on interspecific competition. *Am. Nat.* 122: 240-285

Schoener, T.W. (1988). Ecological interaction. In *Analytical Biogeography*. Ed. A.A.Myers, P.S. Giller. New York: Chapman and Hall pp. 255-97

Simberloff, D. (1981) Community effects of introduced species. In *Biotic crises in Ecological and Evolutionary Time* (ed.M.H. Nirecki), Academic Press, New York pp 53-81.

Song, B. (1986). Preliminary estimation of Logistic equation. *J.Ecol (China)*. 5 (3): 57-62

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

Youdeowi, A. (1989). Major arthropod pests of food and industrial crops of Africa and their economic importance. In Yaninek, J.S. and Herren, H.R (eds.). *Biological control: a sustainable solution to crops pest problems in Africa*. Ibadan, Nigeria, IITA pp. 31-50.

APPENDICES

APPENDIX A1

Table 1.1a: Larval establishment (std) of *C.partellus* while alone in different host plants.

Host plants	Percentage of larvae recovered		
	Number of days after infestation		
	3	10	21
Maize	76.4±22.5a	60.2±13.9a	50.4±16.7a
Sorghum	68.4±20.5a	42.4±12.7c	32.4±13.8b
Napier grass	36.2±15.1b	25.6±13.0d	19.4±9.1c
Wild sorghum	71.3±28.0a	49.7±21.4b	36.3±14.7b
F-value	27.89	38.01	33.18
Pr > F	0.0001	0.0001	0.0001

Means in the same column with different letters are significantly different $P \leq 0.05$

Source (Ofomata 1998)

Table 1.1b larval establishment (\pm std) of *C.partellus* while with
C. Orichalcociliellus in different host plants

Host plants	Percentage of larvae recovered		
	Number of days after infestation		
	3	10	21
Maize	66.7 \pm 31.2a	54.7 \pm 34.4a	36.7 \pm 15.8a
Sorghum	51.2 \pm 17.7b	41.2 \pm 11.0b	28.8 \pm 11.5b
Napier grass	36.3 \pm 12.5c	19.3 \pm 3.6c	18.0 \pm 6.1c
Wild sorghum	41.3 \pm 21.6bc	36.7 \pm 16.7b	26.7 \pm 14.2b
F-value	18.82	17.23	11.62
Pr > F	0.0001	0.0001	0.0001

Means in the same column with different letters are significantly different $P \leq 0.05$

Source (Ofomata1998)

Table 1.1c ; Larval establishment (std) of *C. Orichalcociliellus* while
alone in different host plants.

Host plants	Percentage of larvae recovered		
	Number of days after infestation		
	3	10	21
Maize	71.3±20.8a	53.0±22.9a	50.4±16.7a
Sorghum	66.0±21.2ab	43.4±10.6ab	32.4±13.8b
Napier grass	53.2±13.4b	32.5±17.7b	19.4±9.1c
Wild sorghum	62.0±11.1ab	47.0±10.0a	36.3±14.7b
F-value	5.13	4.99	8.60
Pr > F	0.0028	0.0033	0.0001

Means in the same column with different letters are significantly different $P \leq 0.05$

Source (Ofomata 1998)

Table 1.1d: Larval establishment (\pm std) of *C. Orichalcociliellus* while with
C. partellus in different host plants.

Host plants	Percentage of larvae recovered		
	Number of days after infestation		
	3	10	21
Maize	64.7 \pm 10.1a	54.7 \pm 34.4a	36.7 \pm 15.8a
Sorghum	48.8 \pm 16.2b	41.2 \pm 11.0b	28.8 \pm 11.5b
Napier grass	41.3 \pm 12.5c	19.3 \pm 3.6c	18.0 \pm 6.1c
Wild sorghum	41.3 \pm 14.8c	36.7 \pm 16.7b	26.7 \pm 14.2b
F-value	21.32	2.72	3.29
Pr > F	0.0001	0.0471	0.0226

Means in the same column with different letters are significantly different $P \leq 0.05$

Source (Ofomata 1998)

APPENDIX A2

Table 2.1: Maximum population density of *C. partellus* and *C. orichalcocillieus* on each host

species	Maize	Sorghum	Wild sorghum	Napier Grass
<i>Chilo partellus</i>	15	10	12	8
<i>Chilo orichalcocillieus</i>	15	8	12	14

Source Ofomata (1998)

Table 2.2: Competition coefficients of *C. partellus* and *C. orichalcocillieus* on each host

species	Maize	Sorghum	Wild sorghum	Napier Grass
<i>Chilo partellus</i>	1.495	1.18	2.056	0.93
<i>Chilo orichalcocillieus</i>	0.669	0.846	0.486	1.065

Table 2.3: Specific Growth rate (larval) of *C. partellus* and *C. orichalcocillieus* on each host

species	Maize	Sorghum	Wild sorghum	Napier Grass
<i>Chilo partellus</i>	0.019	0.017	0.017	
<i>Chilo orichalcocillieus</i>	0.018	0.013	0.019	0.015

Source Ofomata (1998)

Table 2.4: Parameter M'_{mj} .

species	Maize	Sorghum	Wild sorghum	Napier Grass
<i>Chilo partellus</i>	4.821	0.556	1.8	0.571
<i>Chilo orichalcocillieus</i>	5.0	0.572	0.6	0.571