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A MODEL OF PARASITISM BY *TRICHOGRAMMA* SPECIES NEAR *MWANZAI* SCHULTEN & FEIJEN (HYMENOPTERA: TRICHOGRAMMATIDAE) ON THE STALK BORER, *CHILO PARTELLUS* SWINHOE (LEPIDOPTERA:PYRALIDAE) ON SORGHUM.

BY

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THESIS SUBMITTED IN PARTIAL FULFILMENT

OF REQUIREMENT FOR THE AWARD OF THE DEGREE OF

MASTER OF PHILOSOPHY (M. Phil.)

IN APPLIED ENTOMOLOGY

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JANUARY, 1990

DECLARATION

I, ADELE JOSEE NGI-SONG, hereby declare that, the work presented in this thesis is my own and has not been submitted for a degree in any other University; it is original except where indicated otherwise and in which case full references are given.

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DEDICATION

This work is dedicated to my mother,

Mrs. Crescence Ndjee.

ACKNOWLEDGEMENTS

I acknowledge my employer, Ministry of Agriculture, Cameroon, for granting me the two years study leave to undertake this research project. This research was made possible with a fellowship from the International Centre of Insect Physiology and Ecology (ICIPE) in collaboration with the International Institute of Tropical Agriculture (IITA).

I am grateful to Professor Odhiambo, Director of ICIPE, to Dr. M.E. Smalley and Z.T. Dabrowski, the Academic Coordinators for the African Regional Postgraduate Programme in Insect Science (ARPPIS), who offered the opportunity to undertake my research at ICIPE.

I am most indebted to Dr. S. Nokoe, and Dr. M. Brownbridge (supervisors, ICIPE) who followed my progress through valuable discussions, comments and suggestions. I acknowledge Professor Ray Kumar (supervisor, RSUST, Port Harcourt, Nigeria) for his constructive criticisms and encouragement.

I wish to thank the staff of the Biomathematics Research Unit (BRU) (both in Nairobi and MPFS) for data analysis, and the Insect Mass Rearing Technology Unit (IMRT) staff, for the supply of *Chilo partellus* eggs. I also wish to thank Messrs. J. Asimba, J. Owino, J. Ouma and Kabiru for their assistance in rearing *Trichogramma* sp. and field work.

My sincere gratitude goes to Mr. S. E. Njomou (Director of CREPPHY, Yaounde, Cameroon) and J. Omange for their support. My thanks go to Dr. J.N. Perry (Rothamsted, U.K.) for his valuable contribution in the analyses of the data, and to Dr. J. Allotey for his advice and encouragement during the course work.

Finally, Many thanks to all friends who have contributed in one way or another to the success of this work.

ABSTRACT

Effects of the sequence of parasitoid release and three ecological factors, i.e. parasitoid densities, pest densities, and climatic conditions, on the rate of *Chilo partellus* (Swinhoe) egg parasitism by *Trichogramma* sp. nr. *mwanzai* Schulten and Feijen, were studied in caged experiments and in the field. Predictive models were developed using data generated from the above studies.

The five different parasitoid population densities used were positively correlated with the number of eggs and egg batches parasitised in the caged experiments. Mutual interference between the parasitoids was observed at the highest population density of the parasitoid (48).

The five different pest population levels were positively correlated with the number of eggs and egg batches parasitised. As pest density increased, significant variations were observed in the rate of parasitism. An inverse relationship was found between the formation of black heads and the parasitoid population size. The sequences of parasitoid release used in the study did not significantly affect the level of parasitism obtained.

For the caged experiments the maximum and minimum temperatures on the day of parasitoid release showed an inverse relationship with the number of eggs and egg batches parasitised, while the relative humidity of that same day was positively correlated.

T. sp. nr. *mwanzai* showed a Type II functional response in the caged experiments.

Field data confirmed the cage observations in several cases.

Data generated in the study were fitted into modified general host-parasitoid models for the prediction of parasitism rates if the pest and parasite population densities are known. A regression model was developed to express the proportion of egg batches parasitised as function of the climatic factors, number of parasitoids released and the number of pest egg batches exposed.

Variable types of fit were obtained when either the number of eggs parasitised or the number of egg batches parasitised were used as dependant variables. A model developed from the data generated in the caged experiments was validated using field data. Results indicated similarity in fits for the two cases.

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1 GENERAL INTRODUCTION

In the tropics, sorghum is one of the principal food crops. It is also used as a building material, fuel source, etc. Over 150 species of insect pests have been listed on sorghum (Young and Teetes, 1977; Seshu Reddy and Davies, 1979). *Chilo partellus* Swinhoe is one of the most serious lepidopteran stemborers of sorghum in East Africa and India (Young and Teetes, 1977; Hill, 1983; Pathak and Olela, 1983; Seshu Reddy, 1983; Teetes *et al.*, 1983). Damage is caused by early larval instars feeding in the leaf whorl and by later instars boring into the stem to cause "dead hearts" and "chaffy heads", (Dabrowski and Kidiavai, 1983; Seshu Reddy, 1983) contributing in this way, among other factors, to significant reductions in grain yield (Seshu Reddy, 1981; Alghali, 1986, 1987).

Several natural enemies of *C. partellus* have been observed. These include insects of the family Trichogrammatidae (Hymenoptera), a large group of minute parasitic wasps which attack eggs of various insects. The two well known genera of this family are *Trichogramma* and *Trichogrammatoidea*. The use of *Trichogramma* spp. as biological control agents for augmentative releases against graminaceous stalk borers began early this century particularly in the USA, USSR, Taiwan, South America and China (Stinner, 1977; Ables and Ridgeway, 1981). The earliest known attempt to utilise *Trichogramma* as a biological control agent occurred when a shipment of this parasite was sent from the USA to Canada in an attempt to control the sawfly, *Nematus ribesii* Scop. (Baird, 1956). Mass rearing and subsequent release of this entomophage has been described by Enock (1895) as "*Trichogramma* farming" because it was a practicable method for sugarcane borer

control in Louisana and Barbados in the early part of this century (Metcalfeand Breniere, 1969). *Trichogramma* have been successfully released many times to control the sugar cane borer, *Diatraea saccharalis* (Fab.) and other economic pests in the USA (DeBach and Hagen, 1970). Similarly, successful inundative releases of *Trichogramma* spp. against sugarcane borers (*Chilo* spp) have been reported from India (Sithanantham, 1980). So far, the major use of *Trichogramma* has been through inundative releases. This refers to the release of a large number of insects to cause an immediate and direct mortality in the pest population (Stinner, 1977). These parasitoids are used in this way, largely because of their inability to perpetuate their progeny in adequate numbers in subsequent generations after releases.

Parasitoids exert an important regulatory influence on borer populations (Appert and Ranaivosoa, 1970; Mohyuddin and Greathead, 1970; Rensburg and Hamburg, 1975; FAO, 1980). These include different species of *Trichogramma* which exert an influence in controlling various Lepidopteran pest species (Howard and Fiske, 1911; Somchoudhury and Dutt, 1980). In the USA, several species of this biocontrol agent were found effective against the European corn borer (ECB), *Ostrinia nubilalis* Hubner (Knipling and Mc Guire, 1968). *Trichogramma* spp. have also been successfully used for the biological control of the ECB in European countries including West Germany (Hassan and Heil, 1980, Hassan, 1981; Neuffer, 1982) and Bulgaria (Karadjov, 1982). In India *Trichogramma* spp. are used as effective control agents against sugarcane borers (Nagarkatti, 1980; Rao, 1980; Varadharajan, 1980; Sithanantham *et al.*, 1982). However, levels of successes attributed to the different parasitoids have been variable (Gupta, 1951; Breniere, 1965; Metcalfe

and Vand Whervin, 1967; Cueva, 1978; Hassan, 1981; Neuffer, 1982)

Theoretical models used to predict the effect of parasitoid releases for the biological control of pests have been developed (Thompson,1924; Nicholson, 1933; Nicholson and Bailey, 1935; Holling, 1959, 1966) and several aspects of host-parasitoid interactions have been studied. These include functional responses (Holling, 1959a, 1959b; Hassell *et al.*, 1976; Van Lenteren and Bakker, 1976, 1978), random searching abilities (Rogers, 1972; Hassell, 1978) and mutual interference (Hassell and Varley, 1969; Royama, 1971; Beddington, 1975). The winter moth, *Operophtera brumata* (L.) in Nova Scotia is one example of pest species where an empirical model has been developed for predicting a stable equilibrium obtained by introducing a parasitoid (Hassell, 1980). Several other models with implications for field applications have been developed and tested (Barclay *et al.*, 1985). Knipling (1972) developed a model for the control of *Diatraea saccharalis* F. by release of the parasite, *Lixophaga diatraeae* (Townsend). Similarly, successes in suppressing sugarcane borers have been reported by Summers *et al.* (1976) and King *et al.* (1981).

In Africa little work has been done on the biological control of graminaceous stalk borers. There is a need for such studies to be carried out, and so far only a number of species of exotic parasites have been released for control purposes (Mohyuddin and Greathead, 1970; Girling, 1972). Kumar (1984) reviewed the biocontrol attempts undertaken in Africa, and the movement of natural enemies from one country to another in the Ethiopian region. Records of the use of *Trichogramma* spp. in Africa are rather scanty, except for reports on their incidences. Available

records show that *T. papilionidis* Nagarkatti and Nagaraja were found on *Papilio desmodocus* in Angola while a *Trichogramma* sp. was observed on *Diopsis thoracica*, a rice pest in Ghana (Nagarkatti and Nagaraja, 1977). Similarly in Chad *Trichogramma* sp. was observed on *Diparopsis watersi* (Roths.) (Nagarkatti and Nagaraja, 1977). Other incidences of the parasitoids have been reported in Uganda, Kenya, Malawi, Malagasy, and Comoros (Nagarkatti and Nagaraja, 1977; Schulten and Feijen, 1982; Breniere *et al.*, 1985).

In Kenya some preliminary work has been done on indigenous parasitoids such as *Apanteles* sp., *Dentichasmias* sp., *Pediobus* sp., *Telenomus* sp., and *Trichogramma* sp. (Mathez, 1972; Bahana, 1985, 1987).

Studies on 3 ecotypes of *Trichogramma* found in Kenya are in progress at the Mbita Point Field Station of the International Centre of Insect Physiology and Ecology, Kenya (Oloo, G. W. pers. comm.). These include a strain from Rusinga Island which was tentatively identified as *Trichogrammatoides ? lutea* Girault, *Trichogramma* sp. nr. *exiguum* Pinto and Platner, a strain from Lambwe Valley, and *Trichogramma* sp. *minutum* group, nr. *mwanzai* Schulten and Feijen (Oloo G. W. pers. comm.), a coastal strain, which is used in the present study.

Most of the above studies concentrated on the bionomics and biology of the biocontrol agents. Very little work was done in determining the dosage, frequency and time of inundative releases for these parasitoids. Thus the need for developing functional response models cannot be over emphasized. The present project was therefore undertaken with the following objectives in mind:

(1) To develop a functional model for the prediction of optimal numbers of *Trichogramma* sp. to be

released for the effective control of known levels of *Chilo partellus* under laboratory conditions; and

(2) To test the effectiveness of this model under field conditions.

2 LITERATURE REVIEW ON MODELS FOR PEST CONTROL

2.1 Types of Models

Models are a convenient means of summarising large data base into a concise and practical format, commonly an equation. The equation simplifies calculations and facilitates some rationalization of the underlying biological process. Models mathematically describe our concept of nature (Streifer, 1974). Mathematical models which are useful in analyzing models of fluctuating populations are of three broad types:

a)-tactical models, or simulations, which are used for short term forecasts of population changes (Nisbet and Gurnet, 1982);

b)-strategic models which are simple mathematical models constructed with the aim of identifying possible ecological principles (Nisbet and Gurnet, 1982).

c)- and the testable models of laboratory data (Nisbet and Gurnet, 1982).

Models may also be classified according to their being deterministic or stochastic (Nisbet and Gurnet, 1982). A stochastic model describes both the trend and the fluctuation of the population, usually with a probabilistic component. The deterministic model only describes the trend of population fluctuation, and its most important property is that, if the history of population is known up to date, one can predict its exact value at any future time. The primary requirement of models in ecology, as in other fields, is to be realistic, the mathematical predictions of

total populations, or birth, for example should agree with field or laboratory observations (Streifer, 1974).

2.2. Host-parasitoid and predictive models.

Models presented here are based on host-parasitoid models (Barclay, 1987c). The original progenitor in this line was the Nicholson-Bailey model (Nicholson and Bailey, 1935), a density dependent model of host-parasitoid relationship.

There is an abundance of population submodels for insect parasitism (or predation) in ecological literature (Hassell and May,1973). Many of these have the general form:

$$N_s = N_t f[P_t, N_t]$$

$$P_{t+1} = N_t - N_s;$$

where N_s represents the survivor after P_t have searched for N_t hosts resulting in P_{t+1} parasite progeny. All assumptions about parasite searching behaviour are here contained in the function $f(P_t,N_t)$. If we consider the simplest case where the parasite population is specific and synchronized temporally with its host population, we can write the following generalized model for host-parasite interaction (Hassell and May, 1973):

$$N_{t+1} = FN_t f[P_t, N_t]$$

$$P_{t+1} = [N_t - N_{t+1}]/F$$

where N and P are now host and parasite densities in generations t and t+1, and F is the rate of increase of the host after allowing for all mortalities within the generation except parasitism (Hassell and May, 1973).

Hassell and May (1973) reported on the type of outcome from different models. These authors emphasized that in the latter case one should know the precise conditions which can lead to the population stability, since this may be a useful consideration in developing a theoretical basis to biological control. The practical objective is to be able to predict the type of outcome expected from different host-parasite interactions by measuring certain "key parameters" of the host and its parasite.

Hassell and Rogers (1972) discussed three basic parasite responses which can affect searching efficiency and should ideally form part of any general host-parasite (or predator-prey) model. These are: (1) the response to host density; (2) the response to other parasites; (3) and the distribution of searching parasites in relation to host distribution.

Table 1 provides a brief description of different host-parasite models (Hassell and May, 1973).

Several analytical models have also been developed to describe aspects of parasite behaviour as realistically as possible (Bakker *et al.*, 1967; Rogers, 1970). Bakker *et al.* (1967) and Rogers (1970) have developed models to describe the avoidance of super parasitism.

Holling (1964, 1966) developed detailed models to show the importance of the invertebrate functional responses of components such as movement and perception by the predator; the time the prey are exposed to predation; and the time spent handling the prey. More recent population models have included further parameters to describe parasitism. Holling (1959 b) included the effect of time wasting activity associated with attacking each host, but did not allow for host exploitation (Rogers, 1972). This model therefore generates the number of host encounters, but not the number

of host attacked. Watt (1959) developed a model which included a maximum attack rate by the parasite and also the parasite interference, but the properties of this model were not fully explored. Both of these models are difficult to test under field conditions. Hassell and Varley (1969) based their model on measurements of the outcome of search by known parasite populations, and showed interference to be an important component. This model is easily tested from field data provided that the adult parasite density and the percentage of hosts parasitized are known. Unlike the models of Holling (1959), it does not include any factors reducing the searching efficiency as host density increases.

The basis of these population models, as stated earlier, is a component which describes the number of host attacked (N_{ha}) and the searching parasite (P). Table 2 shows some of these equations which vary from the very simple to the complex.

A general host - parasitoid model was described by Perry (1987):

$$\text{Log } (-\text{Log}(Q_o)) = \text{Log } a + b \text{ Log } M$$

Where Q_o is proportion parasitised;
M = mean parasite density; a and b are constants.

This model agreed with models termed as "host - parasitoids models of inter mediate Complexity" (Hassel and May, 1973; Perry (1987) although the assumption in these models is that parasitoid search at random.

Table 1. Some models of host-parasite interaction (Hassell and May, 1973)

PARASITISM FUNCTION: ($N_s = N_t f(P_t, N_t)$) AUTHORS	MODELS	BRIEF DESCRIPTION
Nicholson(1933) Nicholson & Bailey(1935)	$N_s = N_t \exp(-aP_t)$	Random search, constant search efficiency.
Holling (1959b) Royama (1971) Rogers (1972)	$N_s = N_t \exp\left(-\frac{a'T_t P_t}{1+a'T_h N_t}\right)$	Random search, searching efficiency dependent on host density.
Hassell & Varley (1969)	$N_s = N_t \exp(-QP_t^{1-m})$	Random search, searching efficiency dependent on parasite density.
Hassell & Rogers (1972)	$N_s = N_t \exp\left(\frac{-a'T_t c P_t^{1-m}}{1+a'T_h N_t}\right)$	Random search, searching efficiency dependent on host and parasite density.
Hassell & May (1973)	$N_s = N_t \sum [a_i \exp(-ab_i P_t)]$	Non-random search, constant searching efficiency.
Hassell & May (1973)	$N_s = N_t \sum [a_i \exp(-Q(b_i, P_t)^{1-m}]$	Non-random search, searching efficiency dependent on parasite density.

Symbols: N_s=hosts surviving parasitism; N_t=host population at generation t; P_t=parasite population at generation t; a=area of discovery; T_h=handling time; T_t=total time initially available for search; a_i=the distribution of hosts; b_i=the distribution of parasites; m=mutual interference constant; c = constant; Q=area of discovery when P_t=1.

Table 2: Some models predicting the number of host encounter or attacked by insect parasites (after Hassell and Rogers, 1972)

MODEL	ATTACK COMPONENT	COMMENTS
Thompson (1924)	$N_{ha} = N(1-e^{X})$ where $N_a = CP$ $X = -\frac{N_a}{N}$	Random attack, parasite efficiency determined by the available egg performance.
Nicholson (1933)	$N_{ha} = N(1-e^{-aP})$	Random attack, % parasitism proportional to parasite density.
Watt (1959)	$N_{ha} = PK(1-e^{-a'NY})$ $Y=P^{1-b}$	Random attack, includes maximum attack rate per parasite and parasite interference.
Holling (1959)	$\frac{N_a}{P} = \frac{CaTtN}{1+CaThN}$	Describes the number of hosts encountered per parasite (not the number of hosts parasitised), includes handling time.
Hassell & Varley (1969)	$N_{ha} = N(1-e^{-QZ})$ $Z=P^{1-m}$	Random attack, includes parasite interference.

Symbols: N = number of hosts, P = number of parasites, N_a = number of attacks on N hosts by P parasites, C = eggs laid per parasite (a constant), a, a', Ca = attack coefficients (constants), b, m = interference constants.

Knipling (1972) employed hypothetical host-parasitoid models to calculate the impact of *Lixophaga diatraeae* (Townsend) to control *Diatraea saccharalis* (F.). These population models indicated that release of 1000 parasites per acre in the second generation of host would cause a subsequent accumulative suppression of the host population in the order of 97 % by the fourth or last host generation.

Goodenough *et al.* (1983) developed models to predict the developmental rate of the parasitoid *Trichogramma pretiosum* on eggs of four host species. The models agreed closely with observed data for temperatures from 20 to 30^0 C, but at 15^0 C the degree-day prediction of emergence were 5 to 7 days late. Similarly, a model of *Ooencyrtus kuvanae* (Howard) population dynamics was developed (Brown *et al.*, 1982). This model accurately simulated the behaviour of the observed *O. kuvanae* population. Predictions of the actual parasite abundance were very good in areas with outbreaks of gypsy moth population and poorer in less dense host population. This discrepancy indicated that the host-finding ability of *O. kuvanae* is less efficient in areas of low host density than in areas of high density (Brown *et al.*, 1982).

Barclay *et al.* (1985) studied several host-parasitoid models to assess the feasibility of parasitoid inundation as means of pest control. They found that in all these models, there existed a critical inundation rate, above which the host population was eradicated.

Whitfield et. al. (1980) developed a computer model to simulate the interaction between populations of onion maggots, *Hylemya antiqua* Meigen, and a Hymenopteran parasitoid, *Aphaereta pallipes* Say. When varying abiotic and biotic parameters were entered, the system produced an array of outputs that were used to elucidate the population

dynamics of these organisms in various environments. The model adequately simulated the development of the life stages of the onion maggot and was sensitive to changes in biotic and abiotic parameters. Interesting information and relationships about population dynamics of this insect and the effect of carefully timed insecticide sprays to avoid parasitoids mortality were revealed.

O'neil (1988) developed a model of predation by *Podisus maculiventris* (Say) on the Mexican bean beetle, *Epilachna varivestis* Mulsant, larvae on soybeans. The attack equation described the number of prey attacked as a function of the number of prey, soybean leaf area, and the searching behaviour of the predator:

$$Na = (N/A)x(C1e^{-C2\ N/A} + C3)$$

where Na = per capita predation rate; N = number of mexican bean beetle larvae; A = leaf area in square meters; C1 = maximum amount of area searched (m^2) above C3 when prey density is zero; C2 = rate of change in search inversely proportional to prey density; C3 = minimum area searched (m^2) at high prey density. To validate this model the predicted number of Mexican bean beetle attacked per predator were compared with an independant field data set.

Several other models for pest control have been studied including those of Sawyer and Haynes (1985), Barclay (1987a, 1987b, 1987c, 1988).

2.3. Functional response in host-parasitoid models

Functional response (Solomon, 1949; Holling, 1959a) is defined as any change in the number of hosts attacked per parasite (or prey attacked per predator) as the host density changes. Three forms of response are generally recognized: linear (type I); convex (type II), in which the curve rises at a decelarating rate towards some maximum values; and

sigmoid (type III) (Holling, 1959a). Of these, only type III can contribute to the stability of predator/prey population interactions (Holling, 1959a; Hassell and May, 1973; Murdoch and Oaten, 1975).

Functional response is central to the understanding of "prey death rates" and "predator rates of increase" (Lawton *et al.*, 1975) and in the consideration of optimal predator foraging behaviour (Charnov, 1976; Cook and Hubbard, 1977; Comins and Hassell,1979)

Kfir (1983) studied the effect of host density on parasitism by *Trichogramma pretiosum* Riley, by exposing groups of 150, 300, 600 or 1200 eggs of the potato tuber moth to 2, 4 or 8 female parasites per group. The parasite exhibited a type II functional response. As the host density increased, *T. pretiosum* parasitised more hosts, but at a decreasing rate. The attack coefficient (a') decreased as parasite density increased whereas handling time (T_h) remained almost constant. The search rate (a) decreased with the increasing host density.

The functional response of *Leptopilina boulardi* Barbotin *et al.* (1979) to variations in density of its host, *Drosophila melanogaster* Meigen was examined in the laboratory; result showed an ambiguous form of functional response, where parasitoid search time varied among patches changing the spatial frame of the functional response measurements (Hertlein and Thorarinsson, 1987). Stark and Whitford (1987) studied the functional response of third instar *Chrysopa carnea* Stephen larvae feeding on four densities of *Heliothis virescens* (F.) eggs on caged cotton. The authors suggested that the predators showed a type II functional response.

In most functional response experiments individual predators or parasitoids are confined in arenas (patches)

containing various densities of their prey for some fixed amount of time. However, recent studies have indicated that such "fixed-time" experiments may obscure a type III response by preventing natural enemies emigrating from patches containing low densities of hosts (Van Lenteren and Bakker, 1976, 1978; Collins *et al.*, 1981). Two variable time functional-response experiments have been conducted using insect parasitoids (Van Lenteren and Bakker, 1976, 1978, Collins *et al.*, 1981). In these studies, a behavioral assay was used as an indirect measure of emigration, and patch visits were terminated accordingly. In these cases, a comparison was made of the functional response obtained using this variable-time approach versus the equivalent fixed-time experiment. Results of both studies were similar. The design permitting parasitoid emigration generated a type III curve, while the fixed-time procedure resulted in a type II curve.

2.4. Model validation

Over the past decades, considerable effort has been directed towards the modelling of population processes (Feldman *et al.*, 1984). Models for integrated pest management (IPM) are used to assess biological control and host-parasite interactions, to evaluate sampling plans, to compliment other IPM decision-making methods, to train IPM personnel, and to codify and guide IPM research (Welch, 1979).

Given the importance of models to IPM, their outputs must be carefully compared to the observed behaviour of the real systems they are intended to represent. This comparison is termed "validation" and is one of the most perplexing aspects of modelling, due to the variety of techniques used (Welch *et al.*, 1981). Most complete

validation procedures involve graphical or tabular presentation of predicted versus observed results. Confidence limits may be shown, but often are not. Experimental expenses often limit the number of observations because, as model complexity grows, so does the amount of data required to characterize real system behaviour.

The general problem of validating population models involves the objective application of statistical tests. Some of the subjective aspects have been reviewed (Shannon, 1975). The standard statistical tests developed for simulation models (Shannon, 1975) are generally oriented towards validating the end result of the simulation. Feldman *et al.* (1984) have reported on the statistical procedure for validating a simple population model. He noted that the statistical validation of a time-dependent population processes model is a difficult task and that there is currently no adequate statistical methodology developed for complex population models that describe agricultural pest populations. Feldman *et al.*(1984) proposed a statistical procedure for such models and pointed out some present shortcomings in its application.

The validation process is essential to ascertain if the experimental data is sufficiently "close" to the predicted population means to have confidence in the model. Statistics are used to quantify the meaning of closeness in terms of true population means and variances. However, since the theoretical variances are not available, practitioners might fall into the trap of using the sample variance of the field data as their measure of closeness (Feldman *et al.*, 1984).

Some workers intensively document each model component, and then the present a small amount of data regarding overall model performance. Others present little data but

claim that model behaviour is "reasonable", or they appeal to the reader's judgement or conventional wisdom (Welch *et al.*, 1981). If the model does not provide predictions with a reasonable degree of accuracy the model may not be valid because one or more fundamental aspects of the ecosystem dynamics have been omitted (Shoemaker, 1980).

The result of improper validation may not be necessarily obvious, but the consequences of using invalid models in pest management may be catastrophic (Welch *et al.*, 1981). Welch *et al.* (1981) noted that validation is an essential stage in model development with at least two parameters which have to be considered in the validation process: (1). Risk-to-users or cost-benefit criteria for evaluating management models: and (2) rigorous statistical procedure to list research models. The authors further noted that the selection of inappropriate criteria could lead to unnecessary delays in the implementation or use of poorly validated models.

A common conception among modellers is that the development of practical field programs entails (1) creating detailed research models and then (2) simplifying them to form management models (Welch *et al.*, 1981).

3 MATERIALS AND METHODS

3.1 Rearing of the Pest.

Chilo partellus (Swin.) moths were reared in the Insect Mass Rearing Unit (IMRT) at ICIPE's Mbita Point Field Station (MPFS) following the methods developed by Ochieng *et al.* (1985). Eggs were deposited, in batches, on sheets of pleated wax paper. During the course of this study, sheets with egg batches were supplied by the IMRT unit for both laboratory and field experiments.

3.2 Collection and Identification of *Trichogramma* sp. *minutum* group nr. *mwanzai* Schulten and Feijen.

In December 1988, wax paper sheets carrying *C. partellus* egg masses, were exposed in farmers fields planted with maize or sorghum at Mtwapa in the coastal province of Kenya. The sheets, cut into strips of four pieces, were hung on the plants with masking tape. Three days later, all the sheets were collected and brought to the laboratory at MPFS. Parasitised egg batches were carefully cut and put into test tubes which were later corked with cotton wool and kept under ambient laboratory conditions.

This species of *Trichogramma* was tentatively identified as *Trichogramma* sp. *minutum* group nr. *mwanzai* Schulten and Feijen by Dr. A. E. Polaszek of the Commonwealth International Institute of Entomology (CIE), Departement of Entomology British Museum (Natural History), London, UK, in August 1988. According to his observations, this species belongs to the *minutum* group. He further stated that species belonging to the *minutum* group are extremely difficult to differentiate. The specialist added that the rather short flagellum of the male antennae appears to be charasteristic of both this species and *mwanzai*, but

that this species differs from *mwanzai* in having much longer hairs on the male flagellum. Schulten and Feigen (1982), however, observed no parasitisation of *C. partellus* eggs by *T. mwanzai*.

3.3 Rearing of the Parasitoids

Cages measuring 28 cm x 17 cm x 17 cm were made from plexiglass or perspex sheets. A circular hole, 12 cm in diameter, was made in each of two opposite faces of the cage and a sleeve made of fine black cotton cloth glued onto the hole in one of the faces. A circular piece of the same cloth was used to seal the hole in the other face of the cage (Plate 1). Two larger cages measuring 50 cm x 25 cm x 25 cm, made in the same way, were later constructed as the colony grew larger (Plate 2).

The first generation of the parasitoids emerging from the field collected samples in the test tubes were offered freshly laid *Chilo* eggs to parasitize. The parasitized eggs were then transferred to the rearing cages where the second and succeeding parasitoid generations were reared. At emergence, the parasitoids were exposed to fresh *Chilo* eggs.

A 20% sucrose solution was presented to the parasitoids as diet. The solution was put in a small test tube (7.5 cm long and 1 cm diameter) which was corked with cotton wool. The sucrose solution was then suspended from the inner wall of the rearing cage so that the parasitoids could feed from the moist cotton wool. The sucrose solution was changed regularly, particularly after the death of the preceeding generation.

3.4 Laboratory Study

Twenty cages measuring 1 m x 1 m x 1 m were constructed with wooden frames covered with fine mesh netting on five

Plate 1: Cage used for the rearing of T. sp. nr. mwanzai

Plate 2: Cage used for rearing a larger colony of T. sp. nr. mwanzai

sides. The bases of the cages were made of wood which supported the potted sorghum plants. One side of each cage was provided with a lockable door (Plate 3). Fifteen of the cages were used for the main experimental work and the remaining five were used to grow plants, free from insect damages for use in the experiments. There was one potted plant per cage.

At weekly intervals, a local sorghum variety (Serena) was sown in each of the fifteen buckets filled with garden soil. For each experiment, buckets containing three plants aged 17-20 days after emergence (DAE) were placed singly into a cage and artificially infested with a known number (Cx) of day 0 old *C. partellus* egg masses. There were fifteen cages per experiment. For the 15 buckets, a total of 90 egg batches of similar sizes were excised and attached to the plants, using small pieces of masking tape. Egg batches were attached at specific points of the plant, namely the upper and lower surfaces of the first and second sorghum leaves, close to the stem (Plate 4 and 5).

When two egg masses were used per bucket, the central plant and one other were chosen and one egg mass attached to each. In the cases where four egg masses were used, the central plant had two and the other two plants carried one each. There were two egg masses per plant, one at the same point of both sides of the same leaf, when six egg batches were used. For 8 egg batches, three egg masses were placed on each of the central and one other plant and the two remaining batches placed on the third plant. Finally, for ten egg masses, 3 were attached to each plant, with the central plant carrying an additional egg mass. Thus there were five populations of *Chilo* egg batches, viz: C1, C2, C3, C4 and C5, being 2, 4, 6, 8, and 10 egg masses, respectively, attached to the plants.

Plate 3: Experimental cage.

Plate 4: Experimental site for the caged experiments.

Five *Trichogramma* populations were also used, viz: T0, T1, T2, T3, and T4, representing releases of 0, 6, 12, 24, and 48 adult *Trichogramma* respectively.

Schemes of Parasitoid Release

Three schedules of adult *Trichogramma* releases were followed:

i-All adults were released simultaneously;

ii-Half the number of adults was released at 12 o'oclock and the other half released at 3 pm; and

iii-One third the number of adults was released at 9 am, another third releasd at twelve noon; and the remaining third released at 3 pm.

Two other perspex cages measuring 17 cm x 17 cm x 28 cm were constructed for the collection of parasitoids to be used in the release experiments. As in the rearing cages, two holes, 12 cm in diameter, were made on the 2 opposite faces (the larger ones) of the cages, one covered by a circular black cotton cloth (front face), while a sleeve was glued on the other face. On the upper portion of the cage, in the extreme left corner of the front face, the cage opened into a tube, 6 cm in length and 1 cm in width, onto which a test tube of 7 cm length and 2.5 cm diameter could easily be fitted. The front face of the cage was then exposed to light, which stimulated the insects to move to the back of the cage away from the light. From there, they entered the collection tube where they would be counted (Plate 6). Only females were used and excess were removed using an aspirator. The insects were restricted to 8 per tube. For releases of 48 *Trichogramma* females simultaneously, 6 test tubes were placed in the bucket. The same principle was followed for releases involving the other *Trichogramma* densities.

Plate 5: Eggs fixed on plants with tubes positioned during release of parasitoids in a cage.

Plate 6: A cage used for counting T. sp. nr mwanzai for releases.

Egg batches were removed from the cages after 3 days and placed in marked test tubes corresponding to the experimental cage. These were observed on the fifth day, using a binocular microscope at a magnification of 250x and the following parameters recorded:

i-the number of eggs parasitised;

ii-the number of black heads formed;

iii-the number of eggs which did not change into black heads and which were not parasitised;

iv-the total number of eggs; and

v-the number of egg masses parasitised per cage.

The experimental design was a 5 x 5 x 3 factorial arrangement. This gave a total of 75 units per replicate, replicated three times, and thus the total number of experimental units was 225.

Fifteen units were taken at a time and these included all the *Chilo* egg populations, the release sequences and the *Trichogramma* populations.

Temperature and Relative Humidity.

The daily maximum and minimum temperatures and relative humudity were recorded on day one, day two, and day three, from the day insects were released. The first part of the data was obtained using a thermohygrograph with no protection from a Stevenson's screen (Plate 7), while the second part of data came from a thermohydrograph placed in a Stevenson screen adjacent to the experimental cages. Two types of adjustment were made to these climatic data. One was done by calculating the mean daily maximum and minimum temperatures and relative humidities for the protected apparatus and for the research station thermohydrograph; the mean difference in the values of the two sources of data was thus established. From these mean differences and from the

station readings on the same days, values of the maximum and minimum temperatures and relative humidities of the unprotected apparatus were deduced.

The second method was to establish a relationship between the readings from the station and those from the protected apparatus, using regression analyses.

3.5 Field Study

A local variety of sorghum, Serena, was planted in a field measuring 54 m x 15 m using a split split plot design. Plants were spaced at 20 cm between plants and 50 cm between rows. The land was divided into 9 plots. Each of the 9 plots was subdivided into two sub-plots and 6 sub-sub-plots measuring 2.5 m x 4.5 m each. These gave a total of 54 sub-sub-plots.

There were three replications, each consisting of three plots which were planted on the same day. The three plots of each of the other two replicates were planted later at four day intervals.

In each replicate, the following treatments were applied:

i. one *Trichogramma* population (Tx) per main plot;

ii. one sequence of release (R) per sub-plot;

iii. one *Chilo* egg population (Cx) per split split plot.

These were completely randomised. Thus in total, for each replicate, there were:

i. three parasitoid populations, viz: 0, 48, and 96 per plot.

ii. two sequences of release for the sub-plots, viz:

(a) simultaneous release at 9 a.m.

(b) half the number released at 9^{00} a.m. and the other half at 3 p.m.

iii. three *Chilo* egg batches populations per sub-plot, viz: 6, 12, and 24 egg batches.

Three weeks after planting, plants were randomly selected from each split split plot. 24 plants were selected for *Chilo* population level of 24 egg masses, 12 plants for the level of 12 egg masses and 6 plants for the level of 6 egg masses. One week later, the selected plants were artificially infested with one *Chilo* egg mass by fixing them with masking tape as described above for the caged experiments. the parasitoid releases were also carried out as stated above (Plate 8). Two days after infestation, eggs were collected and brought to the laboratory for observation on the levels of parasitism obtained.

Temperature and relative humidity were also recorded, using a thermohydrograph which was kept in a Stevenson's screen throughout the experiment.

3.6 Analyses of Data and Model Development

Laboratory and Field Data Analyses

Data collected for both the field and laboratory experiments were analysed using the SAS Institute package (1987). The data were subjected to correlation and regression analyses, the analyses of variance using the general linear model procedure, and means separation using the Duncan's multiple range test. There were a total number of 10 variables, for the laboratory data:

1. The sequence of release of *Trichogramma* (SEQ)
2. *Chilo partellus* egg population (CHILO)
3. The *Trichogramma* population (TRICHO)
4. The number of egg batches used (BATCH)
5. The total number of black heads formed (BH)
6. The number of eggs parasitised (EPAR)

Plate 7: Stevenson's screen used for the protection of the thermohygrograph.

7. The number of egg batches parasitised (BPAR)
8. The average height of the plants (AVPL).
9. The daily mazimum and minimum temperatures (MTMP and XTMP)
10. The daily maximum and minimum relative humidities (MRH and XRH).

Only variable 8 was not available for the field data.

Correlation analyses were performed on all 10 variables.

An ANOVA test was run to evaluate the effects of three main factors, including: five Trichogramma population levels, the number of egg batches exposed in the field plot or in the experimental cage, and the sequences of parasitoids release; on the number of Chilo eggs parasitised, the number of egg batches parasitised, and the number of black heads formed.

Functional response

Functional response curves were plotted using data collected from caged experiments for each parasitoid population density, i. e. for 6, 12, 24, and 48 parasitoids. The mean number of eggs or egg batches exposed in the cage (host density). The curves obtained were compared to Holling's (1959a,b) type I,II, III functional response.

In the laboratory, to determine the handling time T_h of individual females parasitoids, newly emerged females *T.* sp. *mwanzai* were enclosed with freshly laid *C. partellus* egg in 4-ml vials, stoppered with cotton wool. The time taken by each female to locate an egg was recorded using a stop-watch. Similarly, the time taken by individual females after settling on an egg was recorded. The total handling time was therefore determined by summing the average of the two measurements, including host location time and the taken to complete oviposition. This, in practice, is the total time taken by a female on an egg before resuming the same behavioural pattern on a different egg.

Model development

The major factors identified from the above analyses were later fitted into a general host-parasitoid model described by Perry, (1987):

$$\text{Log}[-\text{Log}(Q_0)] = \text{Log } a + b \text{ Log } M.$$

(where Q_0 = proportion parasitised, M = mean parasite density, *a*, and *b*, are constant). The dependent variables used in the equations were EPAR and BPAR. Appropriate log transformation of the data were carried out to enable the use of the linear least squares fitting procedure. The following models were tested:

$$\text{LNPEPAR} = a + b \text{ TRICHO}$$

$$\text{LNPEPAR} = a + b \log_e (\text{TRICHO})$$

Similar models were tested using LNPBPAR;

where $\text{LNPEPAR} = \log_e(-\log_e(\text{PEPAR}))$ and

$\text{LNPBPAR} = \log_e(-\log_e(\text{PBPAR}))$, PEPAR and PBPAR being the proportion of eggs and egg batches parasitised, that is the ratio of eggs parasitised to the total of eggs available or the ratios of batches parasitised to the total of egg batches exposed, respectively.

3.7 Model Validation

To validate models obtained from the laboratory experiment, a Chi Square analysis was performed using the values of the Log of the proportion of egg batches parasitised, (LNPBPAR), that were obtained from :

1. a model developed using field data,
2. a model developed using laboratory data,

In both models the values of the independent variables were those obtained from the field experiment for the second method of insect of release (sequence 2)

4 RESULTS

4.1 Factors Affecting the Survival of *C. partellus* and its Parasitism by *Trichogramma* sp. nr. *mvanzai*

4.1.1 Factors Affecting Egg Parasitism in *C. partellus*

4.1.1.1 Caged Experiments

Parasitoid Density

Correlation analyses showed a positive relationship between the number of eggs parasitised and the number of adult *Trichogramma* sp. released in the cages ($p < 0.01$, $r = 0.49$) (Appendix 1).

The analyses of variance (ANOVA) showed a lack of significance in the interaction of the size of *Trichogramma* population released and the sequence of release but suggested that there were significant differences in *Trichogramma* and batch levels for the number of eggs parasitised ($P < 0.01$, $R^2 = 0.516$, Table 1). There were differences in parasitisation rate when 0, 6, 12, 24, or 48 parasitoids were released (0, 8.97, 19.82, 76.57, 63.46 eggs parasitised respectively).

The Duncan's multiple range test comparison for host and parasitoid levels are given in Table 2, while changes in linear patterns are illustrated in Fig 1.

Pest density

Considering *C. partellus* egg populations, correlation analyses showed a strong positive linear relationship between *C. partellus* egg populations and the number of eggs parasitised ($p < 0.01$, $r = 0.301$, Appendix 1), some differences in *C. partellus* egg population levels were observed ($p < 0.01$, Table 1). The number of eggs

parasitised increased with the density of *C. partellus* eggs in the cage. The mean number of eggs parasitised in batch 2 was not significantly different from that of batch 4, but was significantly different from that of batch 6, 8 and 10. Similarly, the mean number of eggs parasitised in batch 4 was significantly different from that of batch 6, 8 and 10, the mean numbers of eggs parasitised for batches 6, 8, and 10 were not significantly different (Table 2, Fig 2).

When the effect of pest density on the number of eggs parasitised was studied for different batch level the same trend was noticed with $p < 0.01$ (Appendix 2 ,3).

Single degree of freedom component analyses suggest that the relationship between the level of egg parasitism and *Trichogramma* populations had significant linear, cubic and quartic components ($P<0.01$, Appendix 4).

Sequences of Parasitoid Release

The sequence of parasitoid release did not show any correlation with the number of eggs parasitised (Appendix 1). The analyses of variance (ANOVA) and the DMRT showed that there was no difference between the mean numbers of eggs parasitised for the three sequences of release (Table 1 and 2).

Climatic conditions

The relationships between field and cage climatic variables were obtained by making two adjustements on the caged experiments weather data. For the first adjustement, these relationships are given in Table 3 and for the second adjustement they are as follows:

Adjusted maximum temperature (Y1) = 10.737086

+ (0.0579479) x maximum field temperature (X1)

Adjusted minimum temperature (Y2) = 5.9227495

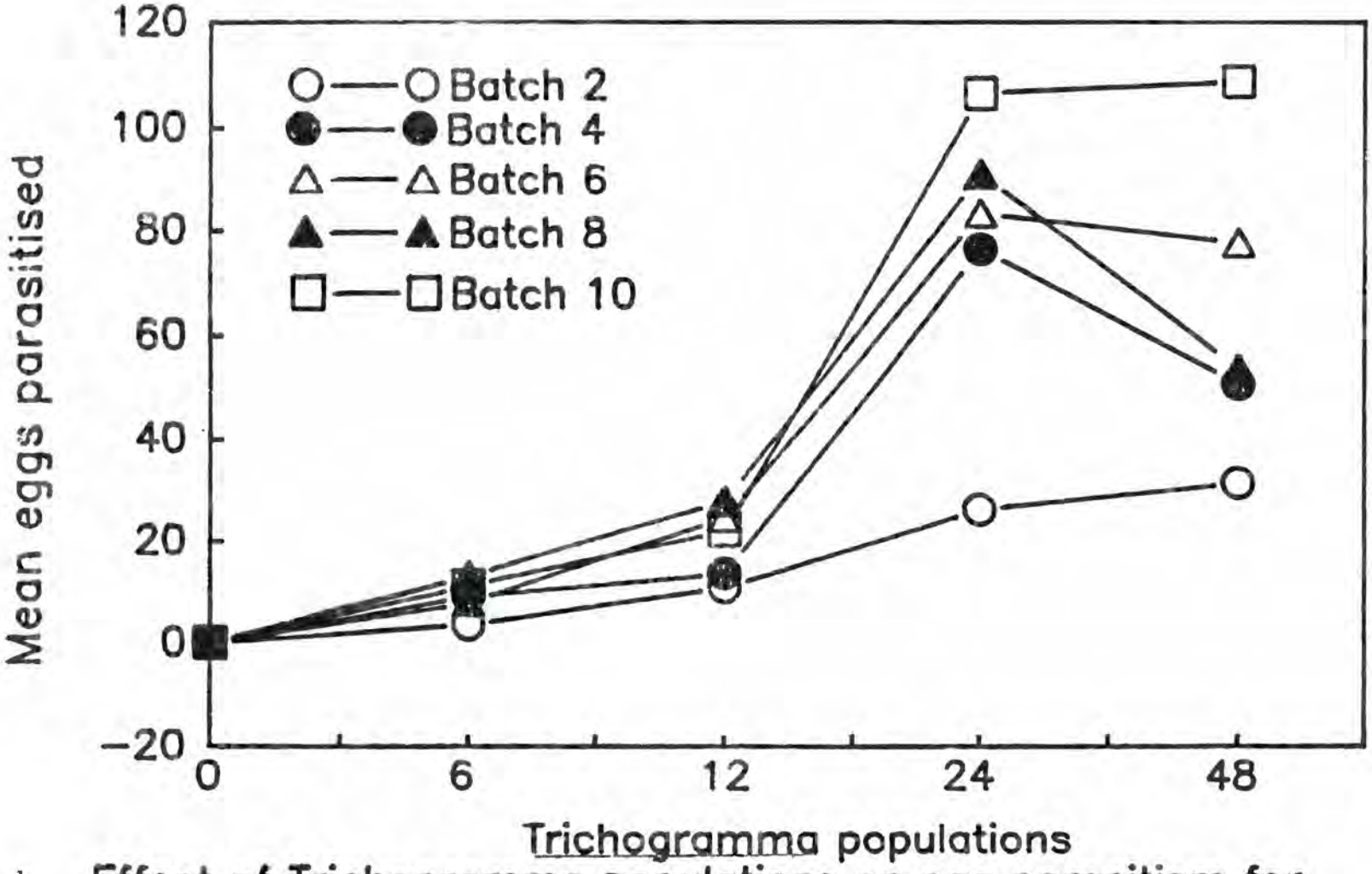
TABLE 1:ANOVA for *Trichogramma* sp. nr. *mwanzai* populations, number of egg batches and sequences of parasitoid release on the number of eggs parasitised in the cages.

SOURCE	DF	MS	P>F
MODEL	42	6861.5749	0.0001
TRICHO	4	51530.4796	0.0001
SEQ	2	2130.8492	0.2499
BATCH	4	7280.4165	0.0011
TRICHO*SEQ	8	764.6443	0.854
SEQ*BATCH	8	983.6389	0.7389
TRICHO*BATCH	16	2119.914	0.1508
ERROR	177	1524.646	
	R^2	0.516418	
	CV	115.1203	

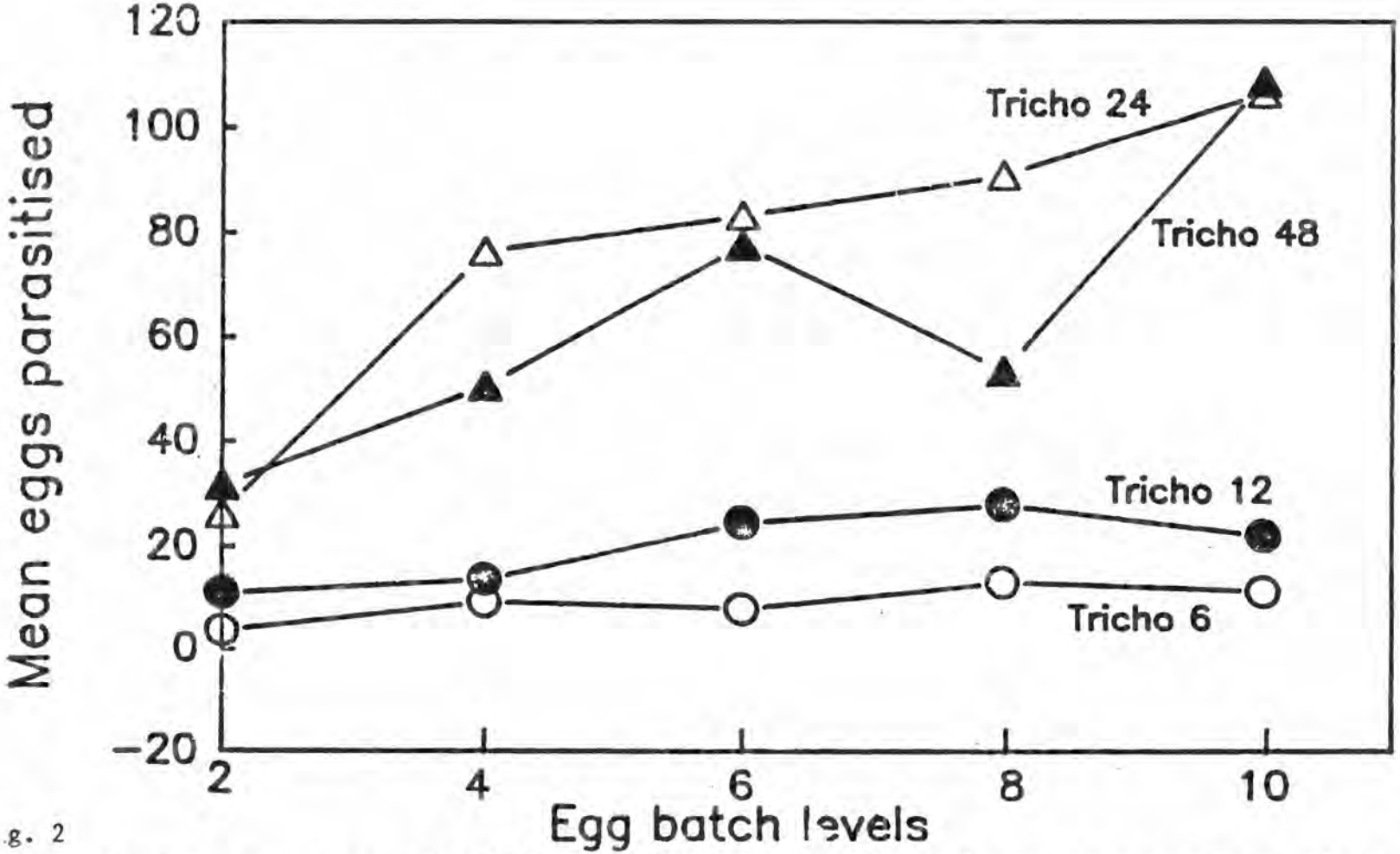
TABLE 2: Duncan's multiple range comparison for the number of eggs parasitised in cages according to a number of parameters.

SEQUENCE GROUPS	n	Means
SEQ 1	72	30.417 A
SEQ 2	74	30.851 A
SEQ 3	74	40.392 A
TRICHO LEVELS		
0	43	0.000 C
6	44	8.977 CB
12	45	19.822 B
24	45	76.578 A
48	43	63.465 A
BATCH NUMBERS		
2	45	14.467 C
4	45	29.956 CB
6	44	36.682 AB
8	44	39.500 AB
10	44	50.262 A

NOTE: means with the same letter, within a particular group, are not signficantly different



1 Effect of Trichogramma populations on egg parasitism for different batch levels in caged experiments



g. 2

ect of the number of Chilo partellus egg batches exposed on the rate of egg parasitism for different Trichogramma sp. populations

+ (0.813442) x minimum field temperature (X2)

Adjusted maximum RH (Y3) = 47.298639

+ (0.506110) x maximum field RH (X3)

Adjusted minimum RH (Y4) = 30.508688

+ (0.695765) x minimum field RH (X4) (appendix 5).

Further analyses showed that the maximum temperature had an effect on the rate of egg parasitism. There was a negative correlation between maximum temperature and parasitism when the maximum was on either the first or second day. There was a positive correlation when the maximum temperature occured on the third day ($r = -0.305$, $r = -0.338$, $r = 0.435$, respectively). When the minimum temperature was recorded on day 1, there was a negative correlation with the number of eggs parasitised. When the the minimum temperature was obtained on either day 2 or day 3, there was no correlation. When the maximum relative humidity was recorded on day 1, it appeared to positively influence the rate of parasitism. Similarly there was a positive correlation between the rate of egg parasitism and the minimum Rh for all 3 days of eggs exposure. There was no such correlation when the maximum Rh was recorded on day 2 or day 3 of the experiments (Appendix 1).

4.1.1.2 Field Experiments

Parasitoid Density

There was no correlation between the number of eggs parasitised and the size of the *Trichogramma* sp. population (Appendix 6). The ANOVA did not show any significant effect of *Trichogramma* sp. population size on the rate of parasitism, while the other factors (BATCH, SEQ) were highly significant (Table 4). However, excluding the sequences of release, the ANOVA model for *Trichogramma* sp. populations

and number of egg batches exposed, the Trichogramma population did not significantly influence the number of eggs parasitised (Table 5). The DMRT showed no significant difference in the number of eggs parasitised for different parasitoid densities, but that there was a difference between the number of eggs parasitised in the control plot and the plots where parasitoids were released (Table 6).

Pest Density

There was no correlation between the number of eggs parasitised and the *C. partellus* egg populations (Appendix 6). As the in caged experiments parasitism increased with the increasing pest density at a decreased rate, but there was no significant difference in the number of eggs parasitised for the different batch levels, except between BATCH 25 and the rest (Table 6). The ANOVA for *Trichogramma* sp. populations, number of egg batches, and sequences of release, however, showed that the effect of batch numbers was highly significant ($P < 0.01$, $R^2 = 0.859$, Table 4).

The number of eggs parasitised was very low compared to the pest population exposed to parasitism. The maximum number of eggs parasitised was 142.50 (for a pest population of 25 egg batches) while the lowest number of eggs parasitised was obtained for a pest density of 5 egg batches found in the field (the lowest) (4.67 eggs parasitised) (Table 6).

Sequences of Parasitoid Release

No correlation between the number of eggs parasitised and sequences of parasitoid release was observed (Appendix 6). However, the two sequence of releases differed significantly ($P < 0.01$, $R^2 = 0.859$, Table 4). But, according to the DMRT, there was no significant difference

Table 3: First adjustment of weather data for caged experiments

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Max T^0 of day x in cage = Max T^0 of day x in the field - 0.58

Min T^0 of day x in cage = Min T^0 of day x in the field + 2.5

Max Rh of day x in cage = Max Rh of day x in the field + 7.6

Min Rh of day x in cage = Min Rh of day x in the field + 20

Note: 0.58, 2.5, 7.6, and 20, are $T^0$and Rh mean differences. (T°= Temperature)

TABLE 4: ANOVA for *Trichogramma* population levels, batch number, and sequences of release on the number of eggs parasitised in the field.

SOURCE	DF	MS	P>F
MODEL	33	2329.5057	0.0015
TRICHO	2	1216.1969	0.1694
SEQ	1	9811.9431	0.0008
BATCH	10	2855.1098	0.0019
TRICHO*SEQ	2	485.2679	0.4739
SEQ*BATCH	6	5004.7629	0.0002
TRICHO*BATCH	10	543.7206	0.5749
ERROR	20	625.8819	
		R^2 0.859968	
		CV 111.3728	

TABLE 5: ANOVA for *Trichogramma* population level, and the number of egg batches exposed on the number of eggs parasitised in the field

SOURCE	DF	MS	P>F
MODEL	24	1894.4518	0.2804
BATCH	2	2306.9215	0.2350
TRICHO	10	2775.9704	0.0989
TRICHO*BATCH	12	398.5536	0.9910
ERROR	29	1514.6408	
	R^2	0.5086	
	CV	173.2558	

between the mean number of eggs parasitised of the two sequences of release (Table 6).

Climatic Conditions

Unlike the cage experiments, there was no correlation between the climatic conditions and the number of eggs parasitised (Appendix 6).

4.1.2 Factors Affecting Egg Batches Parasitism in *C. partellus*

4.1.2.1 Caged Experiments

Parasitoid Density

The total number of egg batches parasitised showed a strong positive relationship with the size of the *Trichogramma* sp. population ($P < 0.01$, $r = 0.523$) (Appendix 1). Levels of this factor differed significantly, $P < 0.01$ (Table 7 and 8).

The mean number of egg batches parasitised was directly proportional to the number of parasitoids released, peaking at a parasitoid population of 24 (3.444 egg batches parasitised). At a parasitoid density of 48, there was a slight decrease in the number of batches parasitised (2.75 egg batches parasitised) (Fig. 3). The DMRT showed that there was no significant difference in the number of batches parasitised between the control treatment and the release of 6 parasitoids. There were differences in the rate of batch parasitisation attained when 6, 12, 24 and 48 parasitoids were released (Table 8).

When individual cases were considered, the DMRT for each batch level showed that for BATCH 2, the means could be separated into two significantly different groups. The maximum number of egg batches parasitised was 1.111 when 24

Table 6 : Duncan's multiple range comparison for different levels of factors on the number of eggs parasitised in the field

Sequence groups	n	Means
SEQ 1	27	24.259 A
SEQ 2	27	20.667 A
TRICHO LEVELS		
0	18	3.444 B
48	18	38.944 A
96	18	25.000 A
BATCH NUMBERS		
5	3	4.67 B
6	15	17.07 B
8	1	0.00 B
10	5	4.20 B
11	4	25.75 B
12	8	30.62 B
18	1	0.00 B
22	3	18.67 B
23	5	24.00 B
24	7	17.86 B
25	2	142.50 A

Note: means with the same letter, in the same column within a particular group, are not significantly different at $P > 0.05$

parasitoids were released. For BATCH 4, the maximum number of egg batches parasitised was 2.889 when 24 parasitoids were released. These means were also classified into two groups. In BATCH 6, at a parasitoid population density of 24, the maximum number of egg batches parasitised was 4.111. Three significantly different groups of means were therefore identified. The maximum number of 4.222 batches parasitised for a release population of 24 parasitoids was found for a pest population of 8 egg batches per cage (BATCH 8). Finally, for BATCH 10, the maximum number of batches parasitised was 5. The means were also separated into three main significantly different groups depending on the parasitoid population released (Appendix 8).

Single degree of freedom contrasts confirmed the presence of linear, cubic and quartic components (Appendix 4)

Pest Density

There was a positive correlation between the number of egg batches exposed and the number of batches parasitised ($P < 0.01$, $r = 0.382$) (Appendix 1). As the number of egg batches exposed increased, there was an increase in the rate of parasitisation. The DMRT showed no differences in the number of egg batches parasitised for BATCH 6 and 8, but there were differences for BATCH 2, 4, 6, (or 8) and 10 (Table 8). A linear relationship was evident (Fig. 4) (Appendix 4).

Sequences of Parasitoid Release

The sequence of release of adult *Trichogramma* sp. nr. *mwanzai* showed no correlation with the number of egg batches parasitised (Appendix 1). From the DMRT, it appeared that all the mean numbers of egg batches parasitised for all the

TABLE 7: ANOVA for *Trichogramma* sp. nr. *nvanzai* populations, effect of the number of egg batches and the sequence of parasitoid release on the number of batches parasitised in caged experiments.

SOURCE	DF	MS	P>F
MODEL	42	13.4269591	0.0001
TRICHO	4	96.0727049	0.0001
SEQ	2	0.9047638	0.5893
BATCH	4	22.7682339	0.0001
TRICHO*SEQ	8	0.5660235	0.9529
SEQ*BATCH	8	0.9710024	0.8023
TRICHO*BATCH	16	4.8530711	0.0004
ERROR	179	1.7060756	
	R^2	0.648705	
	CV	81.68151	

TABLE 8 : Duncan's multiple range comparison for various levels of factors on the number of egg batches parasitised in caged experiments.

SEQUENCE GROUPS	n	Means
SEQ 1	72	1.500 A
SEQ 2	75	1.573 A
SEQ 3	75	1.720 A
TRICHO LEVELS		
0	43	0.000 D
6	45	0.511 D
12	45	1.244 C
24	45	3.444 A
48	44	2.750 B
BATCH NUMBERS		
2	45	0.578 D
4	45	1.244 C
6	44	1.909 B
8	45	1.822 B
10	43	2.488 A

NOTE:means with the same letter, within a particular group, are not significantly different at P > 0.05.

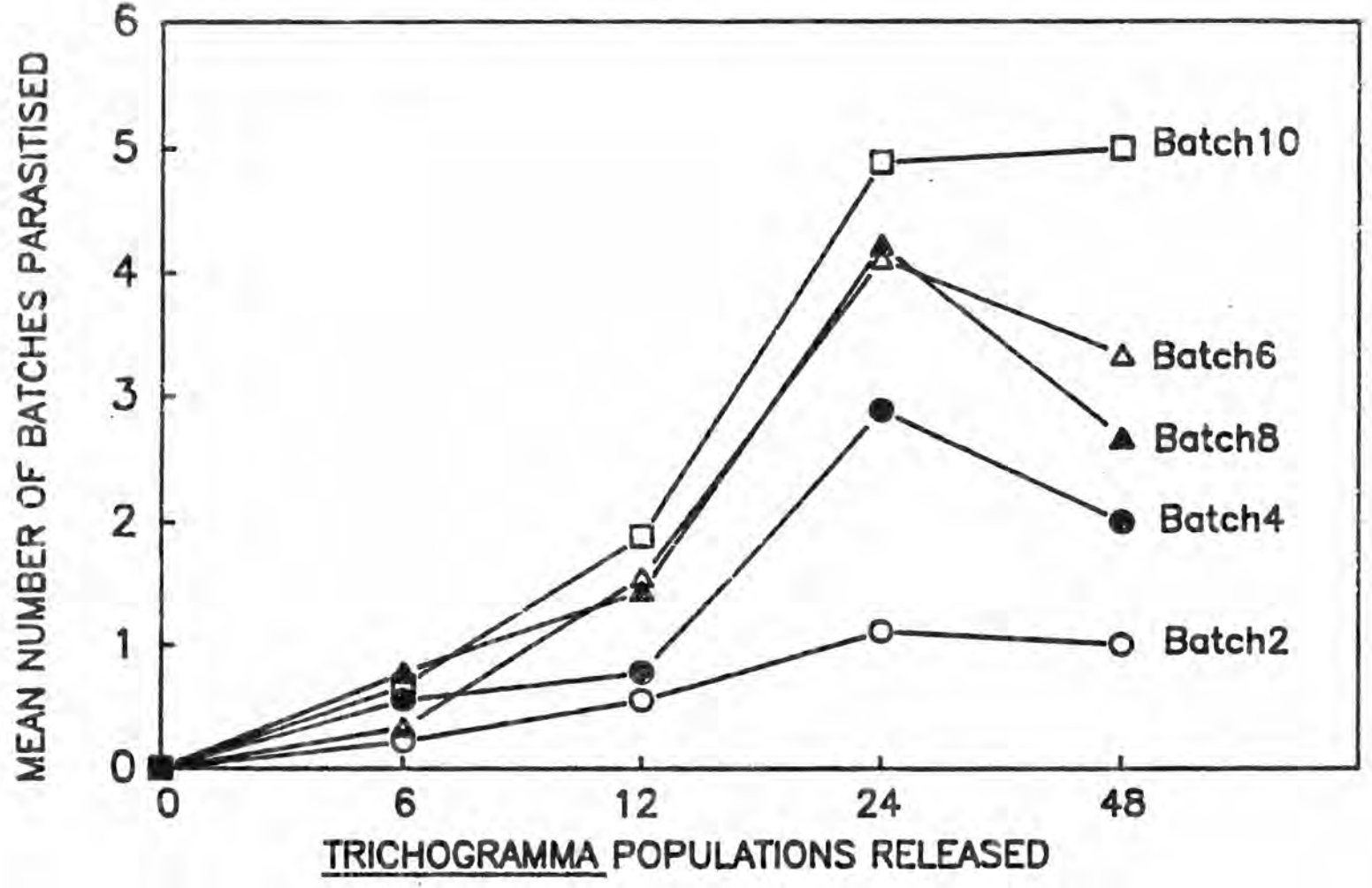

Fig. 3 EFFECT OF TRICHOGRAMMA POPULATIONS ON EGG BATCH PARASITISM FOR DIFFERENT BATCH LEVELS IN CAGED EXPERIMENTS

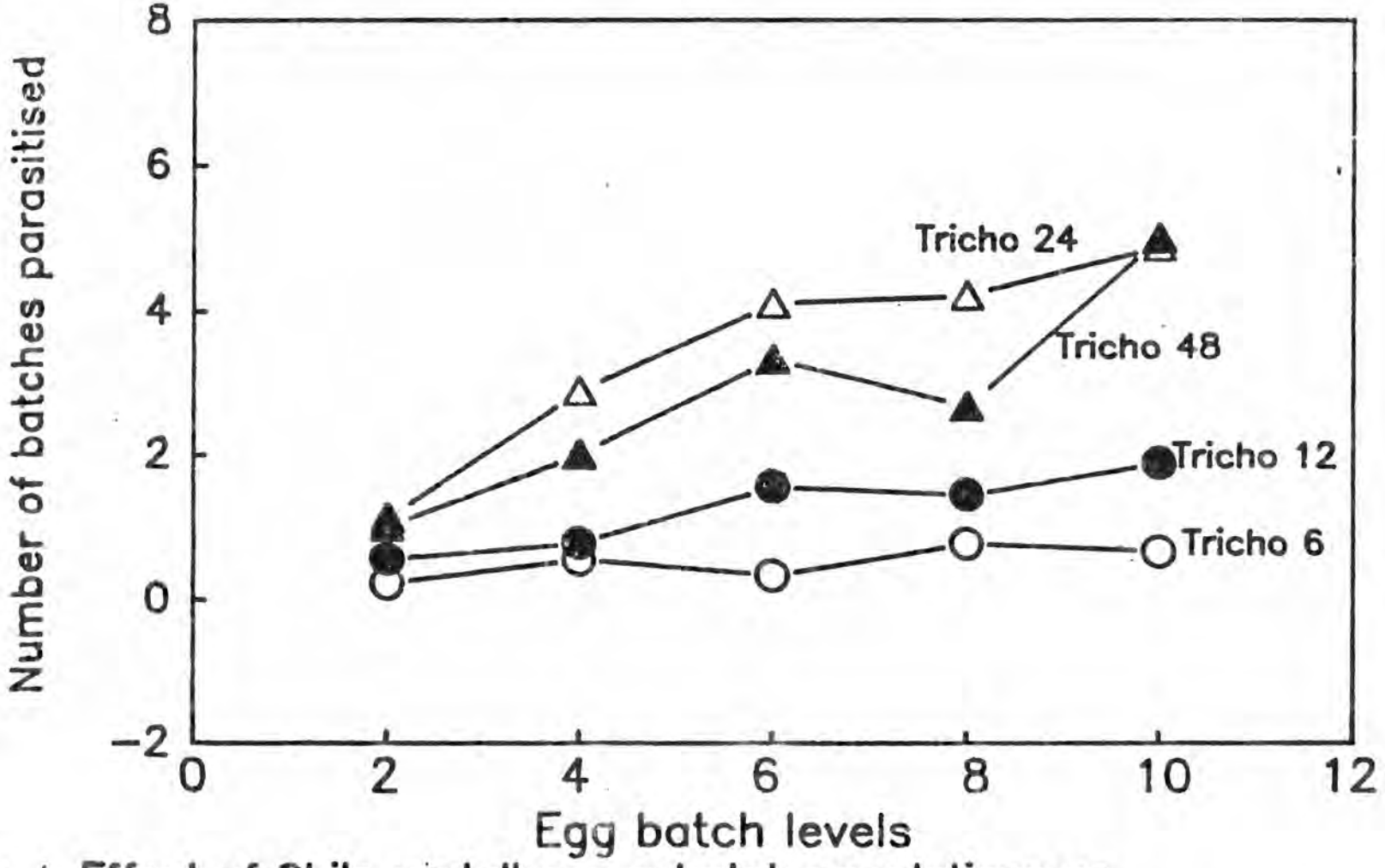

Fig. 4 Effect of Chilo partellus egg batch populations on batch parasitism for different Trichogramma sp. population levels

sequences of parasitoid release, were not significantly different (Table 8 and Appendix 8).

Climatic Conditions

Using the second adjustment of the weather data it appeared that, the maximum temperature of all the three days of exposure, and the minimum temperature the first day of exposure were negatively correlated with the number of egg batches parasitised. The maximum Rh of day 1 and the minimum Rh of day 2 and 3, showed a positive correlation with the egg batch parasitism (Appendix 1).

4.1.2.2 Field experiments

Parasitoid Density

As with the caged experiments, the number of egg batches parasitised in the field was positively associated with the parasitoid population density, ($0.01 < P < 0.05$, (Appendix 6). The ANOVA for TRICHO, SEQ, and BATCH effect on the rate of egg batch parasitism, showed that parasitoid density significantly affected the number of egg batch parasitised ($P < 0.01$), with the combined effect of SEQ and BATCH being equally highly significant (Table 9). When the release sequence factor was ignored the ANOVA did not reveal any significant differences in the parasitisation achieved (Table 10). When 48 parasitoids were released, the mean number of egg batches parasitised was not significantly different from the number parasitised when 96 parassitoids were released, both levels, however, were significantly different from the control (0 parasitoids) (Table 11).

TABLE 9 : ANOVA for *Trichogramma* population levels, number of egg batches exposed, and sequences of release on the number of batches parasitised in the field.

SOURCE	DF	MS	P>F
MODEL	33	5.6672	0.0009
TRICHO	2	7.6014	0.0138
SEQ	1	21.1273	0.0010
BATCH	10	7.3926	0.0009
TRICHO*SEQ	2	0.2456	0.8428
SEQ*BATCH	6	9.9050	0.0004
TRICHO*BATCH	10	1.8101	0.3079
ERROR	20	1.4203	
	R^2	0.868136	
	CV	81.46358	

TABLE 10: ANOVA for *Trichogramma* population levels,and the number of egg batches exposed on the number of batches parasitised in the field.

SOURCE	DF	MS	P>F
MODEL	24	4.9809	0.1456
TRICHO	2	8.3277	0.0980
BATCH	10	7.02359	0.0555
TRICHO*BATCH	12	1.5268	0.9209
ERROR	29	3.3063	
	R^2	0.5549	
	CV	124.2909	

Pest Density

The number of egg batches parasitised in the field was positively associated with the number of egg batches exposed ($0.01 < P < 0.05$, Appendix 6). The rate of parasitisation increased with an increase in the egg batches population. There was no difference in the number of egg batches parasitised for all batch sizes except between BATCH 25 and the others (Table 11).

Sequences of Parasitoid Release

The mean numbers of egg batches parasitised in the field following the two sequences of parasitoid release were not significantly different (Table 11).

Climatic Conditions

The number of egg batches parasitised in the field was positively associated with the maximum and minimum temperatures experienced on days 2 and 3, and the minimum Rh of days 1 and 2 ($0.01 < P < 0.05$, Appendix 6).

4.1.3 Factors Affecting the Formation of Black Heads in *C. partellus* Eggs

4.1.3.1 Caged Experiments

Parasitoid Density

Correlation analyses showed that there was a negative correlation between *Trichogramma* sp.population levels, and the number of black heads formed ($r = -0.24$, $P < 0.01$) (Appendix 1).

The *Trichogramma* sp.population levels had an inverse effect on the number of black heads formed ($P < 0.01$, Table 12): as the number of parasitoids increased the number of black heads formed reduced. The lowest BH was obtained when

Table 11: Duncan's multiple range comparison for levels of factors on the number of egg batches parasitised in the field.

	MEANS	N
SEQUENCE GROUPS		
SEQ 1	1.519 A	27
SEQ 2	1.407 A	27
TRICHO LEVELS		
0	0.389 B	18
48	2.222 A	18
96	1.778 A	18
BATCH NUMBERS		
5	0.333 B	3
6	0.933 B	15
8	0.000 B	1
10	0.800 B	5
11	1.500 B	4
12	1.875 B	8
18	0.000 B	1
22	1.667 B	3
23	1.800 B	5
24	1.571 B	7
25	7.000 A	2

Note: means with the same letter, within the same teatment group, are not significantly different at $P > 0.05$.

the number of parasitoids was 48, irrespective of the number of egg batches exposed in the cages. The highest number of BH was formed in the control, (no parasitoids released).

The general DMRT showed that there was a significant difference in the formation of black heads between the control plot and plots where parasitoids were released, it did not show differences between releases of 6 and 12 parasitoids, while there was a significant difference in the number of black heads formed for all other release populations (Table 13). The groupings through DMRT showed 2 significantly different groups of means for batch sizes of 2, 4, and 8 egg batches, three groups when 6 batches were exposed, and 4 when 10 egg batches were exposed (Appendix 10) according to the size of the *Trichogramma* population released.

The relationship between the *Trichogramma* sp.population levels and the number of black heads formed was only linear (Appendix 4).

Pest Density

Correlation analyses showed that there was a strong positive relationship between the levels of *C. partellus* egg batch exposed and the number of black heads formed ($r = 0.88$, $P < 0.01$) (Appendix 1). The *C. partellus* population levels, represented by the batch number in Table 18 contributed significantly, $P < 0.01$, in the ANOVA model to the formation of black heads. The general DMRT showed five significanly different groups of means in the number of black heads which were formed for the five pest populations used (Table 13).

Single degree of freedom contrast showed a significant linear relationship (Appendix 4).

Sequences of Parasitoid Release

There was no significant association between the sequence of release of adult *Trichogramma* sp. nr. *mwanzai* used and the number of black heads formed (Appendix 1). The DMRT showed no differences in the number of black heads formed for the three sequences of parasitoid release used (Table 13).

Climatic Conditions

The effect of weather was minor in this case, and only the maximum temperature and the minimum Rh of day 2 appeared to exert a significant effect on the number of black heads formed (Appendix 1).

4.1.3.2 Field Experiments

The number of black heads formed in the field did not show any significant relationship to any of the factors tested, including the climatic conditions, with the exception of the number of egg batches exposed (Table 14). There was no significant difference between the number of black heads formed when release sequence 1 and 2 were used, nor for the parasitoid population levels of 0, 48,and 96 (Table 15). The number of eggs reaching the black head stage was only associated with the *C. partellus* egg density (Appendix 6).

4.2 Functional Response

Functional response curves were obtained by plotting the mean number of eggs parasitised (and mean number of egg batches parasitised) against *C. partellus* host densities for parasitoid densities of 6(Fig. 5), 12 (Fig. 6), 24 (Fig. 7), and 48 (Fig. 8). A general combined curve were also plotted for eggs and egg batches parasitised (Fig. 9 and 10).

TABLE 12: ANOVA for *Trichogramma* sp. nr. *mwanzai* population size, number of egg batches and sequences of parasitoid release on the number of black heads formed in caged experiments.

SOURCE	DF	MS	P>F
MODEL	42	52508.913	0.0001
TRICHO	4	42104.400	0.0001
SEQ	2	541.901	0.7845
BATCH	4	486808.301	0.0001
TRICHO*SEQ	8	1628.837	0.6645
SEQ*BATCH	8	3135.200	0.197
TRICHO*BATCH	16	3173.040	0.1357
ERROR	173	2229.951	
	R^2	0.851116	
	CV	25.36185	

Table 13: Duncan's multiple range comparison for levels of factors on the number of black heads formed in cages.

SEQUENCE GROUPS	n	Means
SEQ 1	70	181.571 A
SEQ 2	74	188.824 A
SEQ 3	72	187.986 A
TRICHO LEVELS		
0	42	222.67 A
6	43	201.26 B
12	43	197.02 B
24	45	167.62 C
48	43	144.12 D
BATCH NUMBERS		
2	45	58.98 E
4	43	117.44 D
6	43	182.00 C
8	43	257.14 B
10	42	324.55 A

NOTE: means with the same letter are not significantly different at P > 0.05.

TABLE 14: ANOVA for *Trichogramma* population level, number of egg batches exposed and sequence of parasitoid release on the number of eggs turning into black heads in the field.

SOURCE	DF	MS	P>F
MODEL	33	70313.600	0.0001
TRICHO	2	2082.037	0.8041
SEQ	1	6962.386	0.4008
BATCH	10	177259.751	0.0001
TRICHO*SEQ	2	5931.935	0.5439
SEQ*BATCH	6	11489.476	0.3390
TRICHO*BATCH	10	8720.180	0.5325
ERROR	20	9446.957	
	R^2	0.924704	
	CV	30.76166	

Table 15: DMRT for *Trichogramma* population level, number of egg batches exposed and sequence of parasitoid release on the number of eggs turning into black heads in the field.

SEQUENCE GROUPS	n	Means
SEQ 1	27	337.70 A
SEQ 2	27	294.22 A
TRICHO LEVELS		
0	18	289.94 A
48	18	338.67 A
96	18	319.28 A
BATCH NUMBER		
5	3	131.00 B
6	15	125.00 B
8	1	155.00 B
10	5	244.80 B
11	4	209.50 B
12	8	299.87 B
18	1	114.00 B
22	3	644.00 A
23	5	582.60 A
24	7	545.86 A
25	2	699.00 A

Note: means with the same letter, within a particular group are not significantly different at $P > 0.05$

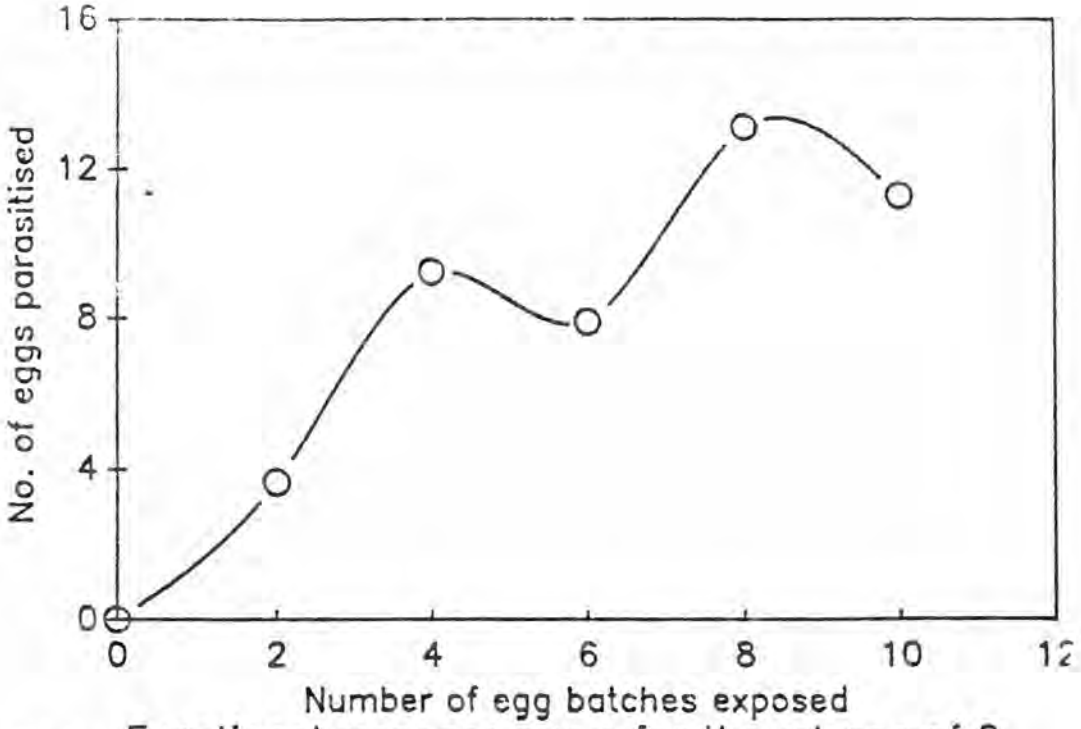

Fig.5: Functional response curve for the release of 6 Trichogramma sp.

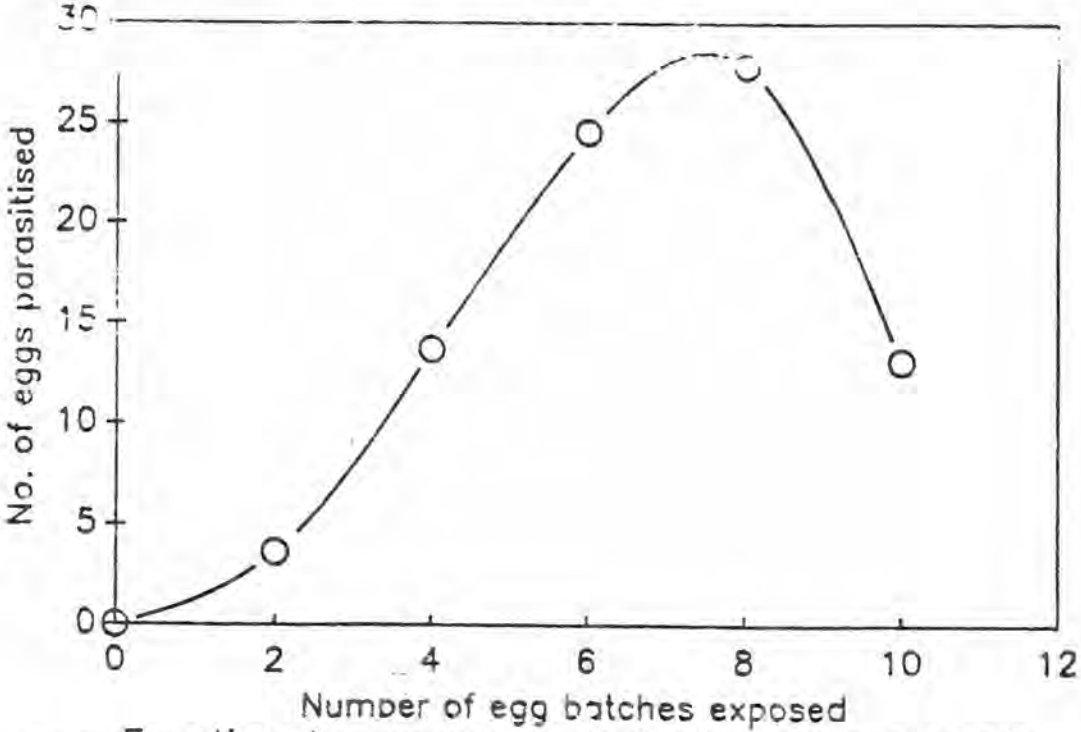

Fig. 6: Functional response curve for the release of 12 Trichogramma sp.

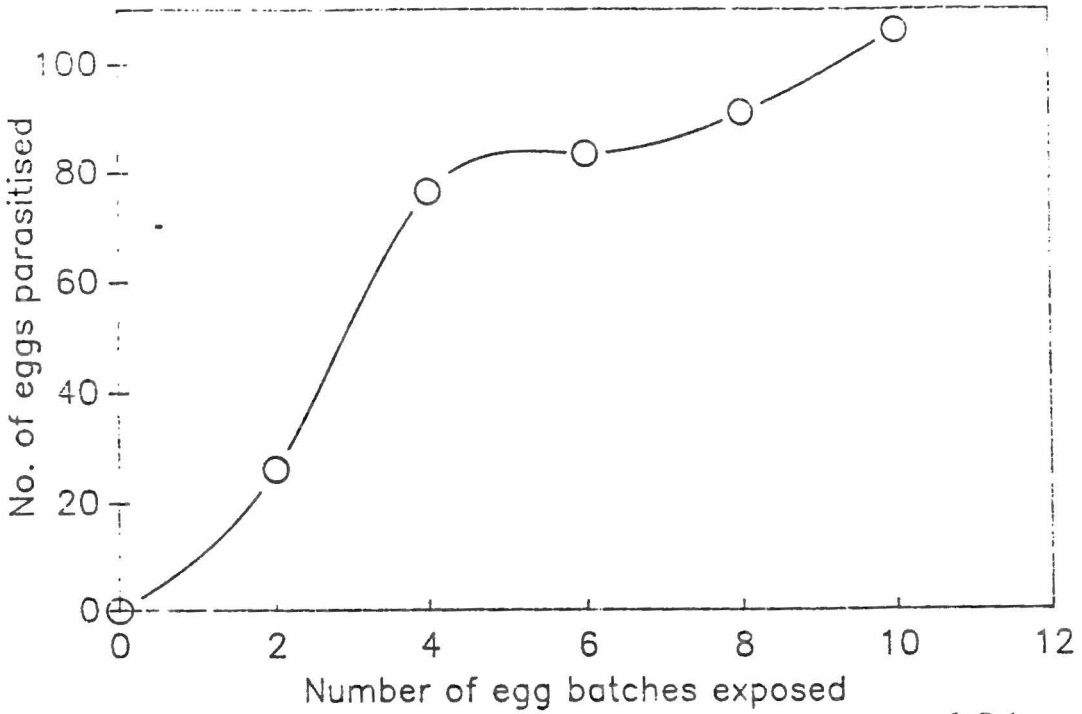

Fig.7 Functional response curve for the release of 24 Trichogramma sp.

Fig.8 Functional response curve for the release of 48 Trichogramma sp.

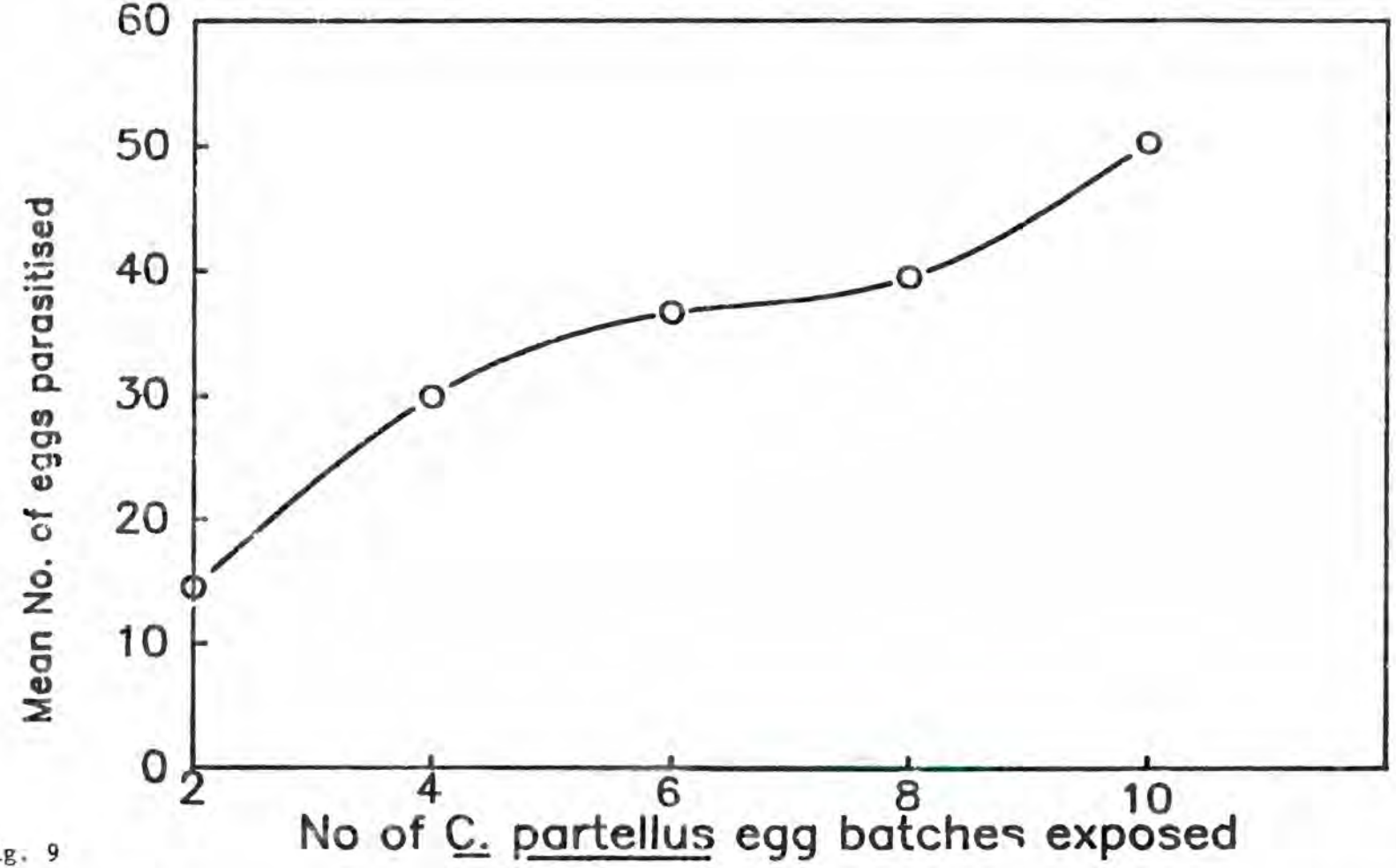

Fig. 9

Functional response curve of Trichogramma sp. nr. mwanzai in cages

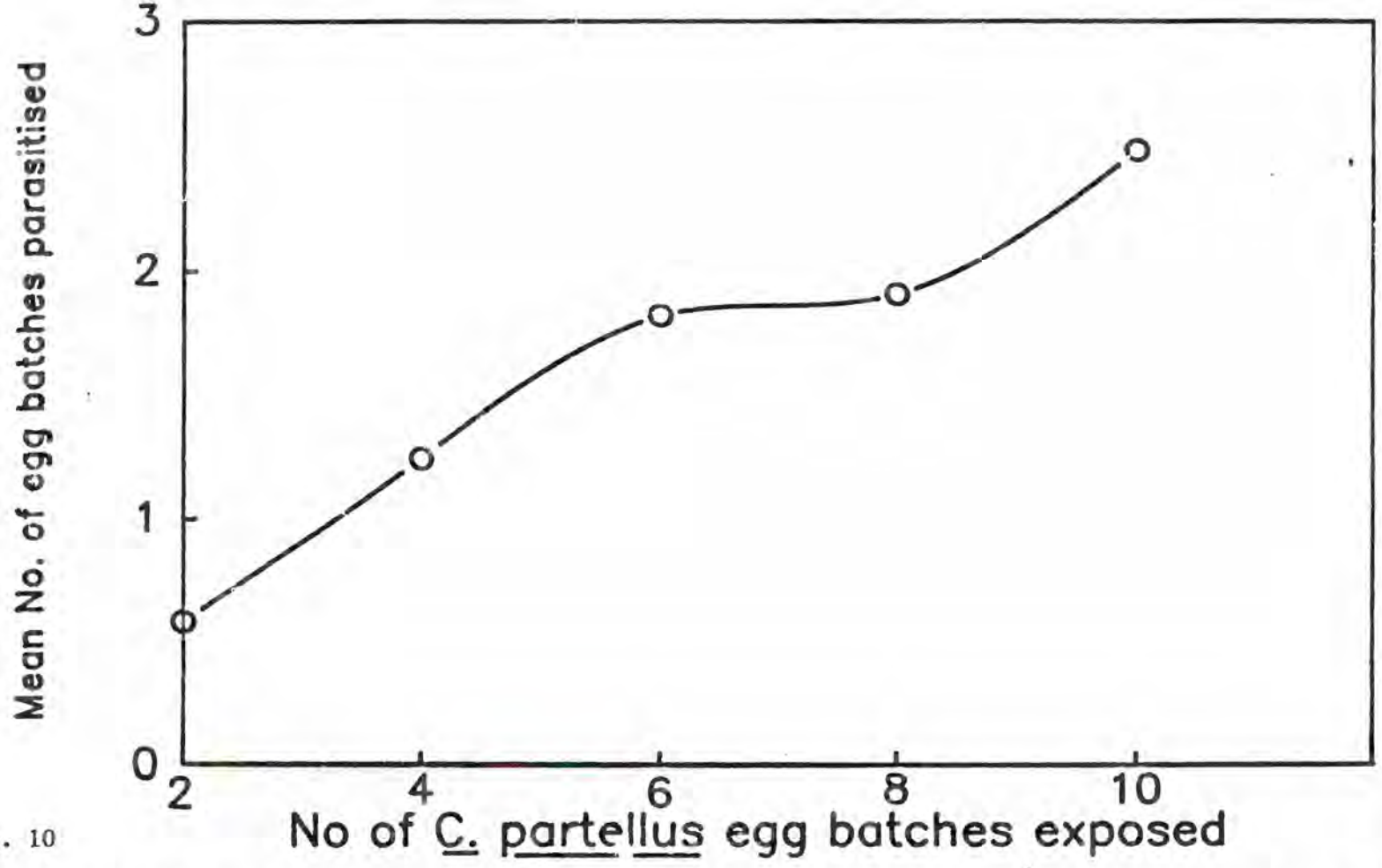

Fig. 10

Functional response curve of Trichogramma sp. nr. mwanzai in cages

The handling time was calculated and found to be T_h = 3.73 minutes (Appendix)16).

4.3 Fitting Host-Parasitoid Models

4.3.1 Fitting Host-Parasitoids Models for Egg Parasitism

Laboratory Data

Using the dependant variable EPAR the following models were tested:

$$LNPEPAR = a + b\ TRICHO \qquad (I)$$

$$LNPEPAR = a + b\ \log(TRICHO) \qquad (II)$$

Where LNPEPAR is the Log of the proportion of the number of eggs parasitised, that is the ratio of the number of eggs parasitised to the total number of eggs available; log(TRICHO) is the natural log of TRICHO (the parasitoid population), a and b are constants determined using the least squares procedure. The results are provided in Tables 16 to 19.

The data did not adequately fit these models (Table 16). Similarly, considering the different egg batch levels, i.e., 2, 4, and 6 batches, the data could not fit the models. For BATCH 8 and BATCH 10, model (II) was fitted significantly although the $^{100}R^2$ were low, being 9.91 and 12.76 respectively (Table 17).

When the number of egg batches exposed, the maximum and minimum temperatures and Rh's of day 1 (parameters found to be correlated with EPAR) were added, the following models were well fitted ($P < 0.01$, and the $^{100}R^2$ were,7.42, 16.98, 5.09 and 14.64, respectively):

$$LNPEPAR = a + b(TRICHO) + c(batch) + d(XRH1) + e(XTMP1) \qquad (III)$$

$$LNPEPAR = a + b(TRICHO) + d(XRH1) + e(XTMP1) \qquad (IV)$$

LNPEPAR = a + bLog(TRICHO) + d(XRH1) + e(XTMP1) (V)

LNPEPAR = a + bLog(TRICHO) + c(batch) + d(XRH1) + e(XTMP1) (VI) (Table 18)

When replacing the parameter BATCH by SEQ, the data did not fit any of these models (Table 19).

Using the Genstat program the log-log link transformation of the proportion of unparasitised egg was chosen to conform to the model of Perry (1987). In this case, the transformed proportion was regressed on the log. density of parasitoids, these models were fitted,

$a + b \log_e(TRICHO)$ (model VII)

$a + b \log_e(TRICHO) + c \log_e(TRICHO)^2$ (Model VIII)

$a_{batch} + b \log_e(TRICHO) + c \log_e(TRICHO)^2$ (Model IX)

The linear relationship showed a positive slope (i.e. as the parasitoid density increased, the proportion parasitised increased, the proportion unparasitised decreased, and transformed proportion unparasitised increased). There was an indication of curvilinear relationship in the fitted values (for each batch), and so a quadratic term was added, giving model VIII. When the linear ($\log_e(TRICHO)$) and the quadratic ($\log_e(TRICHO)^2$) terms were allowed to vary with BATCH, no improvement of the fit was observed. The quadratic term allow us to estimate the density for which parasitism is maximal. This occured when $\log_e(TRICHO) = - {}^*b / 2\,{}^*c = - 5.65 / 2(-0.783) = 3.61$ ($^*b$ and $^*c$ being estimates of parameter b and c) $\log_e(TRICHO) = 3.61$. For the highest density tested, this value is roughly midway between the two largest densities. Postulating a model in which parasitism is maximal at the highest density tested, which was $\log_e(TRICHO) = 3.871$, the following model was obtained:

$a + b \log_e (TRICHO) (1-(\log_e TRICHO/7.742))$ (X).

(equivalent to $a + b \log_e (TRICHO) - b \frac{(\log_e TRICHO)^2}{7.742}$)

Which by putting

$dt(TRICHO) = b \log_e (TRICHO) (1-(\log_e TRICHO/7.742))$

is a linear model $a + b\ dt(TRICHO)$ with two parameters. This model was fitted (assuming no difference between batches).

Field Data

The field data significantly fitted the model

$$LNPEPAR = a + b \log_e(TRICHO) + c\ BATCH$$

with a $^{100}R^2$ of 23.73 (Table 25)

4.3.2 Fitting Host-Parasitoid Models for Batch Parasitism

Laboratory Data

Using BPAR as the dependent variable in models I and II where the proportion of egg batches parasitised was given as a function of the parasitoid density, models were significantly fitted ($P < 0.01$) (Table 20). The $^{100}R^2$ values were 19.78 and 19.32 respectively.

With three additional independent variables, i.e.: BATCH, XRH1, XTMP1, the models were of the form model III and VI, where LNPBPAR is the Log of the proportion of batch parasitised.

The data fitted these models well at the 1% level of significance, with R^2 values of 0.317 for model (10) and 0.365 for model (11) (Table 21).

When the main effect BATCH was removed from equations (III) and (VI), the resulting model IV and V were fitted, but the R^2 value dropped to 0.297 and 0.343 respectively. Splitting the models into their different components, i.e. LTRICHO, XRH1, XTMP1, and BATCH, showed that each of the

components contributed significantly to the model (Table 21).

Testing the main effects TRICHO, SEQ, and climatic parameters, the model fitted the data for all the batch levels used (2, 4, 6, 8, and 10) (Table 22). Splitting the models, TRICHO and LTRICHO were again the main contributing factors, with XTMP1 contributing, in some cases, to the models.

When the effect of TRICHO and the weather parameters were tested for a particular batch number and sequence of release, the model

LNPBPAR = a + b LTRICHO + c XRH1 + d XTMP1

showed significant fits for:BATCH2 SEQ3, BATCH4 SEQ3, BATCH6 SEQ2, BATCH8 SEQ1 and SEQ2, BATCH10 SEQ1, SEQ2, and SEQ3 (Table 23). For other BATCH-SEQ combinations, there were no significant fits. Splitting the model in the latter case showed that the variables TRICHO and LTRICHO contributed significantly to the model. Simlarly, temperature contributed significantly for BATCH1 SEQ3, BATCH4 SEQ1, BATCH4 SEQ3, BATCH6 SEQ3, BATCH8 SEQ1, and BATCH10 SEQ1. The significant effects of the relative humidity were only manifested for BATCH8 SEQ3.

The R^2 values of the models in Table 23 were the highest calculated for all models tested.

All the models, from sequence of release 1 to sequence 3, fitted Perry's (1987) general model at the 1% level of significance, when fitted for each sequence. The main factors to be considered were the parasitoid population levels and the maximum temperatures (Table 24).

These results were later compared with those for field data.

Field Data

The field model LNPBPAR = a + b(BATCH) + clog(TRICHO) significantly fitted the field data with $P < 0.01$ and a $100R^2$ value of 23.38 (Table 25)

Three dimensional curves were obtained firstly by plotting a range of maximum temperatures (22 to 30^0 C), the parasite density and the proportion of egg batches parasitised for a fixed average maximum relative humidity and for fixed number of egg batches and sequence of release (batch2 seq3 and batch10 seq1) (fig 11 and 12) (equations were taken from Table 23). Secondly for no specific batch numbers or sequences of parasitoid release were considered (Table 21). The results showed the same trend for the three plottings (fig 13)

4.4 Model Validation

The selected model for validation (from the models developed with laboratory data (Table 24)), was model number3:

$$1- LNPBPAR = 3.082504 + 0.060892(BATCH) - 0.060228(TRICHO) - 0.079245(XRH1) + 0.193824(XTMP1)$$

where the LNPBPAR (=LNPBPARE ,expected value) was calculated by replacing BATCH, TRICHO, XRH1, and XTMP1, by field values of sequence 2 of these variables. The observed LNPBPAR (LNPBPARO) were directly calculated, using the field data and model of sequence 2 (see SAS program in Appendix 15)

The Chi-Square test showed that there were no significant differences between LNPBPARO and LNPBPARE suggesting that the model selected was valid (Table 26).

Fig. 11 Plot of Predicted PBPAR for Batch2 seq3 for varying TRICHO and temperature

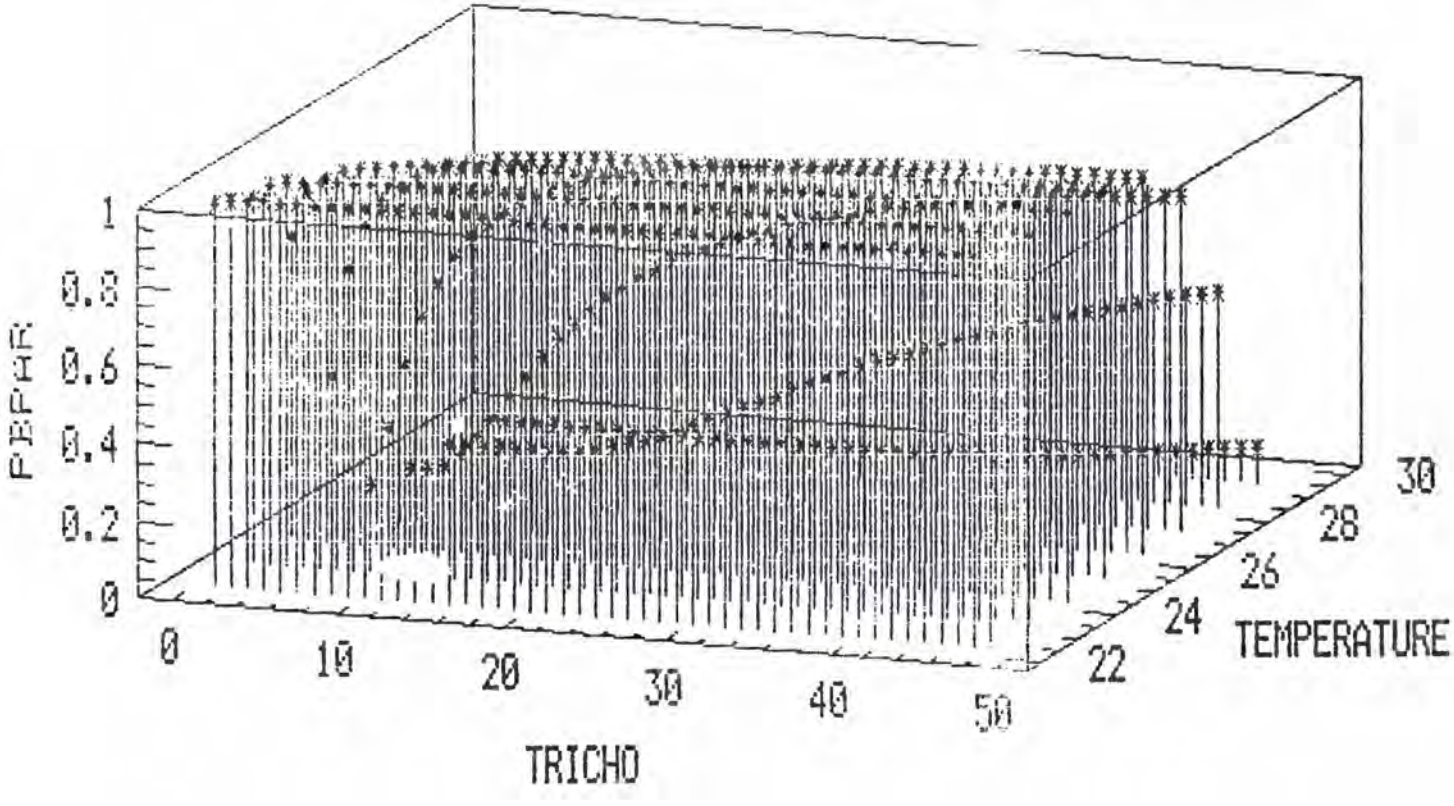

Fig. 12 Plot of Predicted PBPAR for Batch10 seq1 for varying TRICHO and temperature

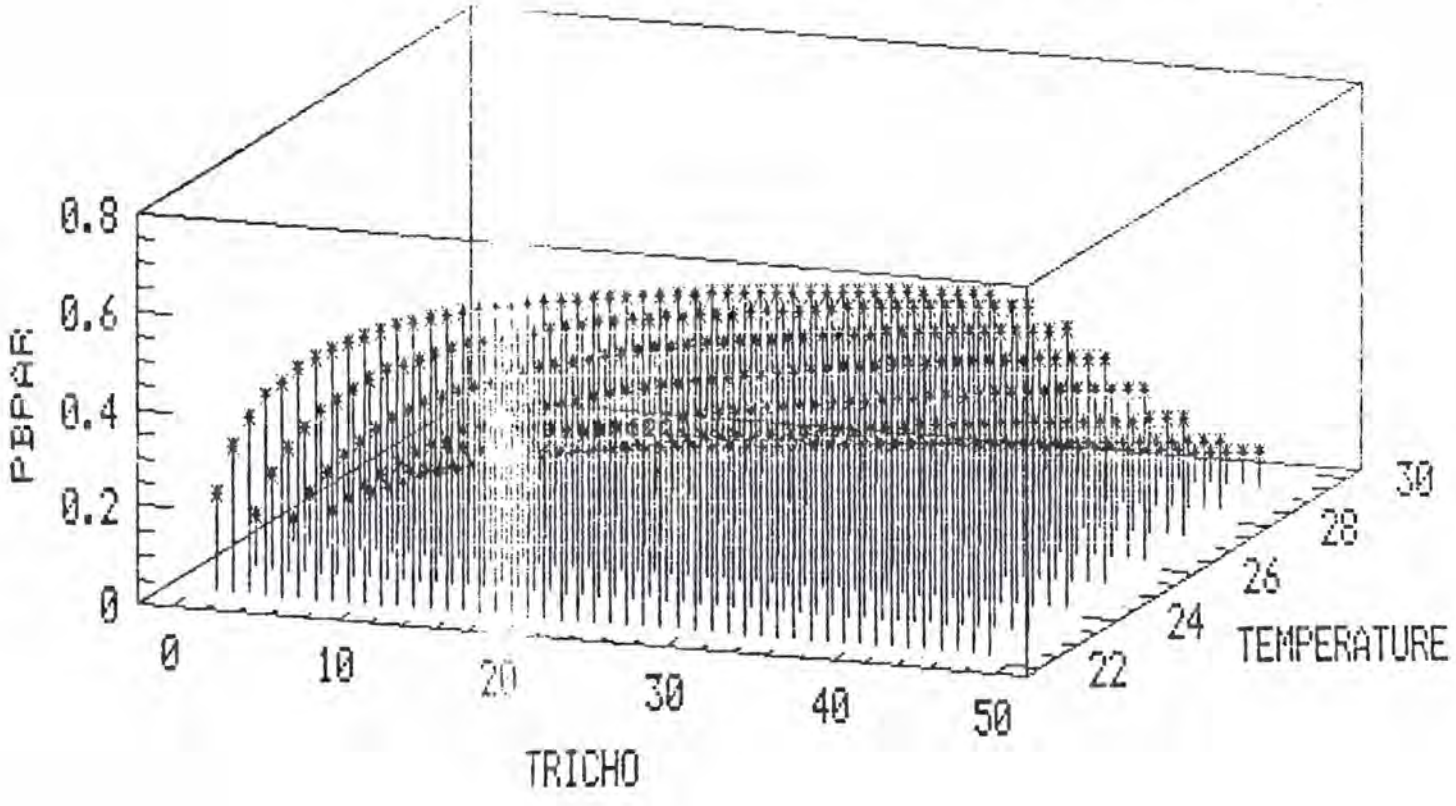

Fig.13 Plot of Predicted PBPAR for varying TRICHO and temperature

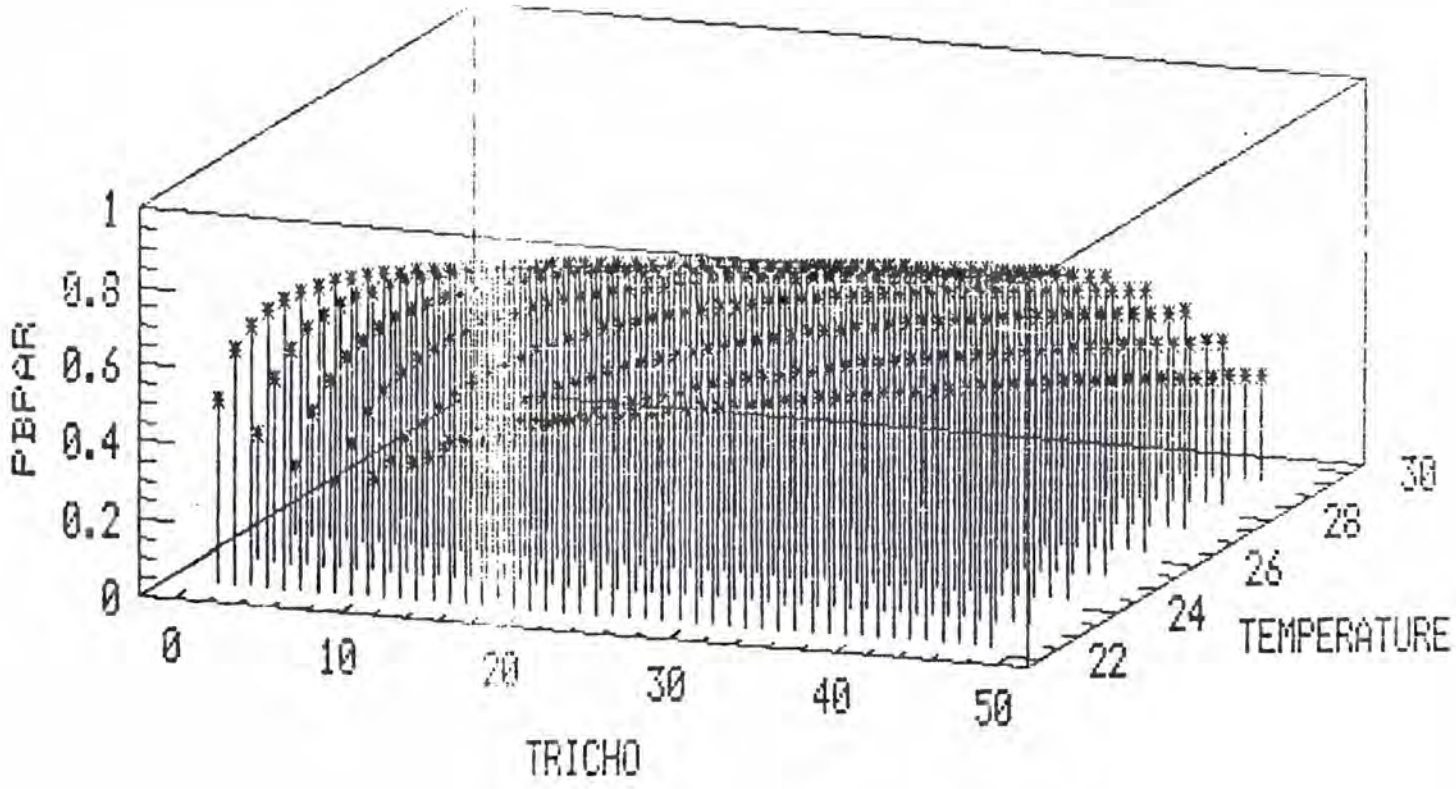

TABLE 16: Models relating the proportion of eggs parasitised to *Trichogramma* population levels used in the caged experiments.

DEPENDANT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDANT VARIABLES				
	INTERCEPT	TRICHO	LTRICHO	100_{R^2}	SSE
LNPEPAR	0.256411	-0.004036	--	1.17^{n}	0.63
LNPEPAR	0.146722	--	0.021399	0.67^{n}	0.63

Note: n means not significant at $P < 0.05$

TABLE 17 : Models relating the proportion of eggs parasitised to *Trichogramma* population levels in caged experiments for different number of egg batches exposed.

DEPENDANT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDANT VARIABLES				
LNPEPAR	INTERCEPT	TRICHO	LTRICHO	100_R2	SSE
BATCH LEVELS					
BATCH 2	0.132436	-0.013681	--	7.71^n	0.82
BATCH 2	-0.030818	--	-0.049730	2.09^n	0.84
BATCH 4	0.131866	-0.006930	--	6.67^n	0.45
BATCH 4	0.028388	--	-0.014639	0.62^n	0.47
BATCH 6	0.283202	-0.002373	--	0.51^n	0.57
BATCH 6	0.179831	--	0.033743	2.00^n	0.57
BATCH 8	0.367262	0.001920	--	0.39^n	0.51
BATCH 8	0.284555	--	0.067620*	9.91*	0.49
BATCH 10	0.359421	0.002482	--	0.66^n	0.51
BATCH 10	0.273549	--	0.075690*	12.76*	0.48

Note: n means not significant at $P < 0.05$, * = significant at $0.01 > P > 0.05$

TABLE 18 : Models relating the proportion of eggs parasitised to *Trichogramma* population levels, the number of *C. partellus* egg batches exposed and the maximum Temp. and Rh on the day parasitoids were released in the caged experiments.

DEPENDENT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDENT VARIABLES							
	INTERCEPT	TRICHO	LTRICHO	BATCH	XRH1	XTMP1	100_R2	SSE
LNPEPAR	1.042589	-0.005720*	--	--	-0.020070**	0.038099	7.42**	0.61
"	0.537500	-0.005709*	--	0.69353**	-0.0197459**	0.040568	16.98**	0.58
"	1.285054	--	0.003254	--	-0.020486**	0.026086	5.9**	0.62
"	0.761104	--	0.001409	0.069361**	-0.020166**	0.029394	14.64**	0.59

Note: * = 0.05 > P > 0.01
** = P < 0.01

TABLE 19: Models relating the proportion of eggs parasitised to *Trichogramma* population levels, day 1 max Temp. and Rh, and the sequences of parasitoid release for different number of egg batches exposed in caged experiments.

DEPENDENT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDENT VARIABLES							
LNPEPAR	INTERCEPT	TRICHO	LTRICHO	XRH1	XTMP1	SEQ	100_r2	SSE
BATCH 2	0.846536	-0.015479	--	-0.019542	0.055444	-0.204451	15.80	0.84
BATCH 2	0.731337	-	-0.072822	-0.020572	0.057295	-0.204451	10.30	0.87
BATCH 4	0.506555	-0.008621	-	-0.016138	0.035137	0.068886	16.89	0.45
BATCH 4	0.413236	--	-0.035641	-0.016224	0.035227	0.067893	9.68	0.47
BATCH 6	1.761610	-0.004381	--	-0.031373	0.046653	0.041944	16.47	0.55
BATCH 6	1.959660	--	0.007218	-0.031367	0.035253	0.045427	14.79	0.56
BATCH 8	1.163901	0.000313	--	-0.019418	0.034104	0.01878	8.62	0.51
BATCH 8	1.710578	--	0.054447	-0.019920	0.012213	0.006179	14.51	0.49
BATCH 10	0.588226	0.000836	--	-0.012219	0.035075	-0.029268	5.36	0.52
BATCH 10	1.080230	--	0.062581	-0.011596	0.0100801	-0.023011	13.22	0.50

NOTE : None of the above models was significant

TABLE 20: Models relating the proportion of egg batches parasitised to the *Trichogramma* population level in caged experiments.

DEPENDANT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDANT VARIABLES				
	INTERCEPT	TRICHO	LTRICHO	$100_{R}2$	SSE
LNPBPAR	1.444322	-0.066925	--	19.78**	2.28
LNPBPAR	1.027986	--	-0.464436	19.32**	2.29

Note: *, ** = Levels of significance. * = 0.05 > P > 0.01 and ** = P < 0.01

BLE 21: Models relating the proportion of egg batches parasitised to *Trichogramma* population levels, number of *C. partellus* egg batches exposed and the maximum Temp. and Rh on the day the parasitoids were relaesed in the caged experiments

PENDENT RIABLE	PARAMETER ESTIMATES FOR INDEPENDENT VARIABLES							
	INTERCEPT	LTRICHO	TRICHO	BATCH	XRH1	XTMP1	100_{R^2}	SSE
PROP	0.048079	--	-0.074194**	0.127824*	-0.074278**	0.286926**	31.70**	2.14
"	0.701721	--	-0.074278**	--	-0.073901**	0.286166**	29.72**	2.16
"	-2.320923	-0.601197**	--	--	-0.079046**	0.406683**	34.33**	2.10
"	-3.125700	-0.602735**	--	0.134137**	-0.079435**	0.408303**	36.51**	2.07

e: * = 0.05 > P > 0.01
** = P < 0.01

TABLE 22: Models relating the proportion of egg batches parasitised to *Trichogramma* population levels, day 1 Max Temp. and Rh, and the sequence of parasitoid release, for different number of egg batches in caged experiments.

DEPENDENT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDENT VARIABLES							
LNPBPAR	INTERCEPT	TRICHO	LTRICHO	XRH1	XTMP1	SEQ	100_R2	SSE
BATCH 2	5.592247	-0.092750**	-	-0.162037*	0.427493	-0.431351	38.78**	3.01
BATCH 2	1.291538	-	-0.773418**	-0.165202*	0.587576*	-0.431351	39.61**	2.88
BATCH 4	-4.808450	-0.108170**	-	-0.054214	0.503413*	-0.838568	41.52**	2.67
BATCH 4	-8.702226	--	-0.797258**	-0.058838	0.643811	-0.838563**	41.59**	2.66
BATCH 6	0.354271	-0.075567**	--	-0.075593	0.293931	0.134477	33.08**	2.17
BATCH 6	-2.124758	--	-0.638774**	-0.086312	0.419358	0.074279	39.23**	2.07
BATCH 8	2.177995	-0.038484**	--	-0.048927	0.124158	0.194025	39.19**	1.01
BATCH 8	-0.117201	--	-0.368591**	-0.049815*	0.211656**	0.194025	59.46**	0.82
BATCH 10	1.977065	-0.054732**	--	-0.027063	0.089233	-0.129881	61.76**	0.79
BATCH 10	0.136186	--	-0.419817**	-0.033063	0.176430**	-0.204594	65.72**	0.75

Note:
* = 0.05 > P > 0.01
** = P < 0.01

TABLE 23: Models relating the proportion of egg batches parasitised to *Trichogramma* population levels, maximum Tem. and Rh on the day of parasitoid release for different number of egg batches and sequences of parasitoid release in caged experiment.

DEPENDENT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDENT VARIABLES						
LNPBPAR	INTERCEPT	TRICHO	LTRICHO	XRH1	XTMP1	100_{R^2}	SSE
BATCH2 SEQ1	1.768599	-0.091437	--	-0.087428	0.290647	26.82	3.30
" " 1	-1.494343	--	-0.671266	-0 091361	0.408151	26.69	3.31
" " 2	19.259752	-0.056350	--	-0.171832	-0.098715	33.62	2.42
" " 2	17.060681	--	-0.431257	-0.174099	-0.018534	34.79	2.40
" " 3	-6.839716	-0.130461*	--	-0.226851	1.090547*	58.13*	3.28
" " 3	-14.279830	--	-1.217731**	-0.230145	1.373110**	74.45**	2.56
BATCH4 SEQ1	-3.349193	--	-0.559577	-0.046015	0.346462	26.86	2.64
" " 1	-2.011812	-0.108417	--	-0.039246	0.311603	52.32	2.13
" " 2	4.733915	-0.038925	--	-0.195918	0.509852	27.46	3.32
" " 2	-1.184615	--	-0.708658	-0.193823	0.746798	48.19	2.80
" " 3	-22.178861	-0.177169**	--	0.076522	0.688782*	73.80**	2.19
" " 3	-26.604076	--	-1.123538**	0.063323	0.838173	55.81*	2.84
BATCH6 SEQ1	9.336226	-0.069089	--	-0.211672	0.415971	30.80	3.34
" " 1	8.53452	--	-0.939074	-0.262632	0.640022	50.57	2.82
" " 2	-7.778511	-0.106713**	--	0.016468	0.323098	58.36	1.83
" " 2	-10.081229	--	-0.642874*	0.010625	0.398113	39.39	2.21
" " 3	1.660338	-0.054156*	--	-0.043552	0.135878	50.30	1.14
" " 3	-1.226110	--	-0.487379**	-0.045081	0.245167	72.62**	0.85
BATCH8 SEQ1	0.729788	-*0.46581*	--	-0.043419	0.176127	46.55	1.10
" " 1	-1.945986	--	-0.436591**	-0.044579	0.277812*	70.52**	0.82
" " 2	-1.276455	-0.036238	--	-0.012904	0.143622	29.09	1.19
" " 2	-3.805052	--	-0.381375**	-0.013435	0.241173	56.76*	0.93
" " 3	8.244803	-0.03263	--	-0.090457	0.052724	50.11	0.93
" " 3	6.563586	--	-0.287808*	-0.091431*	0.115983	60.91	0.83
BATCH10 SEQ1	-3.707178	-0.055163**	--	0.003510	0.197979	70.96*	0.74
" " 1	-5.347972	--	-0.438523**	-0.012257	0.310334*	76.20**	.67
" " 2	2.300567	-0.062915**	--	-0.032037	0.091264	68.61**	0.88
" " 2	0.511191	--	-0.419331**	-0.035123	0.153308	56.78*	1.03
" " 3	5.796542	-0.043376*	--	-0.047573	-0.011535	55 71*	0.87
" " 3	3.489030	--	-0.389357	-0.048807	0.075554	77.36**	0.62

Note: * = 0.05 > P >0.01 and ** = P < 0.01

LE 24: Models relating the proportion of egg batches parasitised to the *Trichogramma* population levels, number of egg batches and weather conditions in caged experiments for different sequences of parasitoid release.

ENDANT RIABLE	PARAMETER ESTIMATE FOR INDEPENDANT VARIABLE							
BPAR	INTERCEPT	TRICHO	L/TRICHO	BATCH	XRH1	XTMP1	100_{R^2} ,	SSE
1	0.978045	-0.075072**	--	0.080369	-0.077087	0.274798*	30.90	2.20
1	-1.590409	--	-0.593911**	0.100832	-0.087596	0.392060**	33.23**	2.17
2	3.085204	-0.060228**	--	0.060892	-0.079245	0.193824	26.26**	2.05
2	0.134805	--	-0.516699**	0.060892	-0.081171*	0.304172*	33.36**	1.95
3	-4.111944	-0.087559**	--	0.241694*	-0.067182	0.391279**	40.59**	2.23
3	-7.861645	--	-0.701163**	0.241694**	-0.070428	0.529598**	45.81**	2.13
1	1.425623	-0.075234**	--	--	-0.076340	0.273319*	30.12	2.20
1	-0.995482	--	-0.589895**	--	-0.086582	0.388258**	32.00**	2.17
2	3.447854	-0.060228**	--	--	-0.079245	0.193824	25.71**	2.04
2	0.500155	--	-0.516699**	--	-0.081171*	0.304172**	32.80**	1.90
3	-2.661779	-0.087559**	--	--	-0.067182	0.391279**	34.59**	2.33
3	-6.411480	--	-0.701163**	--	-0.070428	0.529598**	39.28**	2.23

te: *, ** = level of significance. * = 0.05 > P > 0.01 and ** = P < 0.01

TABLE 25: Models relating the proportion of egg batches and eggs parasitised to the *Trichogramma* population level and number of egg batches exposed in the field.

DEPENDANT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDANT VARIABLES				
	INTERCEPT	BATCH	LTRICHO	100_{R^2}	SSE
LNPBPAR	1.474457	-0.009075	-0.114651**	23.38**	0.74
LNPEPAR	0.064654	0.035580*	0.042553	23.73**	0.56

Note: *, ** = Levels of significance. * = 0.05 > P > 0.01 and ** = P < 0.01

TABLE 26: Model validation

OBS	LNPBPARO	LNPBPARE	CELLCHI	SUMCHI
1	2.02827	0.95901	1.19220	1.1922
2	0.58487	1.93194	0.93926	2.1315
3	0.58487	4.82288	3.72406	5.8555
4	2.02827	1.26347	0.46295	6.3185
5	2.02827	1.68837	0.06843	6.3869
6	0.83621	4.57931	3.05960	9.4465
7	2.02827	1.68971	0.06784	9.5143
8	1.14647	0.89677	0.06952	9.5838
9	0.73402	3.72683	2.40335	11.9872
10	2.02827	0.91509	1.35413	13.3413
11	2.02827	1.97585	0.00139	13.3427
12	2.02827	4.86679	1.65555	14.9983
13	2.02827	1.28045	0.43675	15.4350
14	0.91265	1.61050	0.30238	15.7374
15	2.02827	4.62323	1.45652	17.1939
16	2.02827	2.01115	0.00015	17.1941
17	1.14647	0.94069	0.04502	17.2391
18	0.87689	3.89252	2.33629	19.5754
19	2.02827	0.95901	1.19220	20.7676
20	-0.36507	1.93194	2.73107	23.4986
21	2.02827	4.88377	1.66959	25.1682
22	2.02827	1.26347	0.46295	25.6312
23	0.58487	1.56659	0.61520	26.2464
24	0.18701	4.57931	4.21293	30.4593
25	0.89532	1.99417	0.60550	31.0648
26	-0.30787	0.77499	1.51303	32.5778
27	0.42419	3.78772	2.98684	35.5647

NOTE: CALCULATED CHI-SQUARE = 35.5647**
TABULATED CHI-SQUARE = 38.885 (N = 26, c'= 0.05)
= 45.652 (N = 26, C'= 0.01)
LNPBPARO = OBSERVED LNPBPAR (FROM FIELD MODEL)
LNPBPARE = EXPECTED LNPBPAR (FROM LABORATORY MODEL)

5 DISCUSSION

5.1 Factors Affecting Parasitisation in *C. partellus*

In Cages

Parasitoid Density

In the caged experiments a good relationship was obtained between the number of eggs (or batches) parasitised and the number of parasitoids released in different cages. *Trichogramma* sp. nr. *mwanzai* appears to respond numerically to its own population density and the results showed differences in the levels of egg parasitisation for different parasitoid population levels. However, due to the small differences in the number of parasitoids released, the difference in parasitisation rates between the control and the release of 6 parasitoids was not significant. Similarly, there was no significant difference in parasitisation rate when 6 and 12 parasitoids were released, or between the parasitisation rates when 24 and 48 parasitoids were released.

Egg parasitism increased with the parasitoid density in similar fashion for batch 2 and batch 10, with the peak number of eggs parasitised at a parasitoid density of 24. For double that density, i.e. 48 parasitoids, the number of eggs parasitised did not change significantly, suggesting a decrease in the searching efficiency of the parasitoid possibly due to mutual interference in overcrowded patches. Parasitoids have been observed to react markedly to the presence of other searching individuals nearby, leading to a reduction in the time spent searching the hosts and/or an increase tendency for dispersal (Hassell, 1978) and the same tendency may also be observed after a female detects a host

that has already been parasitised (Rogers, 1972; Hassell and Waage, 1984). Observations made for batch sizes of 4, 6 and 8 seemed to confirm this effect of mutual interference, as demonstrated by a decrease in the number eggs parasitised for the parasitoid density of 48.

Price (1972), studying the behavior of the parasitoid *Pleolophus basizonus* (Gravenhorst) in response to changes in host and parasitoid density, found that the parasitoid showed mutual interference in egg-laying at high parasitoid:host ratios, and a density-dependent escape reaction to adult parasitoid density. Similarly, Hassan (1981) has observed that the degree of parasitism by *T. evanescens* on the European corn borer *Ostrinia nubilalis*, was affected positively by the number of parasitoids released in the field. An increase in parasitoids density from 2 to 8 reduced the mean number of parasitised *C. partellus* eggs from 53.8 to 48.5, as host density increased from 100 to 200 (Ochiel, 1989). The effect of parasite density in the host-parasitoid relationship was also studied by Cook and Hubbard (1977).

Pest Density

The number of *C. partellus* eggs (or egg batches) parasitised was proportional to the density of egg (or egg batches) exposed in cages, and the parasitoid responded functionally by finding more hosts. Cave and Gaylor (1988) obtained the same type of response with *Telenomus reynoldsi* Gorh and Coker. They found that the density of eggs parasitised by *T. reynoldsi* was linearly correlated with the host density (*Geocoris punctipes* (Say) and *G. uliginosus* (Say), pests of cotton). Gross *et al.* (1984) found that higher *Heliothis zea* Boddie densities intercept and retain

proportionally more *T. pretiosum*, which in turn led to higher rates of parasitisation.

The effect of host density upon the number of hosts parasitised have been studied experimentally by a number of workers (DeBach and Smith,1941b; Ullyett, 1949 a and b; Burnett, 1951 and 1954). In each case, the number of hosts attacked per parasite increased with an initial increase in host density but tended to level out with a further increase (Holling 1959a). Ochiel (1989) observed that increasing *C. partellus* egg batches and egg density led to an increase in mean number of egg batches and eggs parasitised by parasitoid females.

As noted above, the non-significant differences in the number of eggs (or egg batches) parasitised may have been the result of small differences in the number of egg batches exposed, including 2 and 4, then 6, 8, and 10 batches.

Sequence of Parasitoid Release

There was no effect on the rate of eggs and egg batches parasitism according to the sequences of parasitoid release used in this study. The timing of parasitoid release, and methods of release rather than the sequence of parasitoid release seemed to have had some effect on the rate of parasitism. Varadharajan (1980) estimated the best time for the release of the parasitoid in India, on the basis of larval activity which he observed to be higher in the hotter months, so two releases of *T. australicum* Girault per month from third month after planting and specially in May and June, reckoned to be the hottest months in the year, gave a better control of sugar cane borer, *Sacchariphagus indicus* (Kapur). Somchoudhury and Dutt (1980) have shown that for effective control of *C. partellus* using *T. perkinsi* and *T. australicum* in India the best time for the release of the

parasitoid was from July onwards. Gross *et al.* (1981), have suggested other times of release based on the ecological adaptability of the biological control agents.

Most releases of *Trichogramma* sp. are made using parasitised eggs from which adults parasitoids will emerge the following day (Kanour and Burbutis, 1984; Ochiel, 1989; Lu, Q.G., pers. comm.). In this study the actual adult parasitoids were counted and release the day following their emergence in the rearing cages, this might have affected their longevity and therefore had a negative effect on the number of eggs or egg batches parasitised.

Climatic Conditions

From this study, it appeared that climatic conditions affect parasitisation. The maximum temperature of the first 2 days had an inverse effect on the rate of parasitism, while that of the third day had a direct effect on parasitism. The average maximum temperature for each of the three days of exposure was almost equal (26.1^0 C) suggesting an inconsistency in the effect of temperature on parasitism. On the other hand, observations made during the experiments indicated that most parasitisation occurred on the day of parasitoid releases, especially within the first few hours after releases with most of the insects dying soon afterwards. The maximum temperature of that same day (26.1^0C) showed an inverse relationship with the number of eggs and batches parasitised, while the maximum and the minimum Rh showed a positive one, therefore the effect of climatic conditions should not be overlooked.

Cave and Gaylor (1988) had observed that high temperature and low humidity reduce the survival time of developing immature parasitoids, while Smith (1988) (citing Biever (1972)) reported that the rate of search by *T.*

minutum was highly dependent on air temperature. However, Ochiel (1989) found no consistent relationship between temperature and rates of parasitisacion by *Trichogramma* sp. nr. *exiquum* on *C. partellus*.

Observations made during the experiments showed that, under bright sun light, the parasites moved a lot resulting in a decrease in the rate of parasitisation, as compared to parasitisation rates on cloudy days. Cheng (1986) working on *T. chilonis* Ishii and its utilisation for the control of sugar cane borers in Taiwan, also found that the parasites moved more actively under bright sun light. Neuffer (1982) stated that the number of *T. evanescens* Weswood required to be released in sweet corn fields to control the corn borer *Ostrinia nubilalis* depended, among other factors, on the prevailing weather conditions.

In the Field

Parasitoid Density

In the field, variations in parasitoid density did not seem to affect the rate parasitism. The effects of releasing different parasitoid populations were not conspicuous due to the general low egg parasitism obtained.

Pest Density

As observed in the caged experiments the parasites responded functionally to host density. The higher the density of the pest in the field, the higher the rate of parasitisation obtained, confirming that parasitism, in this case, was density dependent.

Much experimental work has in the past been aimed at investigating whether or not parasites act as density dependent factors. This has been done by allowing a known

number of hosts and parasites to interact and then scoring the percentage of parasitism achieved. Takahashi (1968) using single individuals of the ichneumonid *Nemeris canescens* (Grav.) searching for larvae of *Ephetia cautella* (Walk.), showed that parasitism was density dependent. On the other hand, DeBach and Smith (1949a) who used a constant number of the chalcid *Mormoniella vitripennis* Walk., searching for different densities of housefly puparia showed that the percentage decrease in the rate of parasitism which occured with an increase in host density, was a result of the long "handling time" (Holling, 1959) which prevented a *Mormoniella* female from attacking more than two host puparia in a day. In this case, the action of the parasites was inversely density dependent (Smith, 1935; Varley and Gradwell, 1974).

Sequences of Parasitoid Release

As in the caged experiments, correlation analyses did not show any linear relationship between the sequence of parasitoid release and the number of egg batches parasitised. The ANOVA, however, showed some significant differences when different numbers of parasitoids were released in different sequences, but this appeared to depend on the number of egg batches exposed due to an observed significant batch-sequence interaction.

Climatic Conditions

In the field study, the effects of weather on the rate of parasitisation was not conspicuous owing to the general low levels of parasitisation obtained. On the other hand, the climatic conditions may have been the cause of the low rates of parasitism observed. Plants were infested three weeks after emergence and the shelter they provided may have

not been enough to protect parasitoids from the sun and from the wind. Furthermore the wind could have enhenced parasitoid dispersal out of the experimental plot, although it is known that in the field, *T. sp. nr. mwanzai* can parasitise eggs up to five meters away from the point of release (Lu, Q.G., Pers. Comm.)

5.2 Factors Affecting the Formation of Black Heads

This study, which was restricted only to observing the effect of host density, parasitoid density and the sequences of parasitoid of release on the rate of black heads formation, showed a clear linear but inverse relationship between parasite density and the number of black heads formed. This suggests that parasitism is a density dependent factor. The natural egg mortality, other than parasitism, was apparently low in cages, i.e. 11.68%, but in the field is was found to be around 36.56 %. The average maximum temperature of about 26 degree appeared to be favorable for egg development.

As shown in the caged experiments, the sequence of parasitoid release did not have any effect on the survival of the pest.

In the field, whilst there was no apparent relationship between the number of parasitoids released and the number of black heads formed, as a result of a low rate of parasitism obtained, such relationship would not be clear. It is possible that if high numbers of parasitoids had been released, such a relationship would have been observed.

The number of host eggs surviving parasitism (in this case the number of black heads formed) depends upon the number of parasitoids searching and their individual effectiveness, determined by the degree of heterogeneity that renders some hosts more suceptible to the parasitism

that others (Hassell and Waage, 1984). Heterogeneity can be manifested in many ways: for example, by spatial distribution of parasitism from host patch to host patch by temporal asynchrony between host and parasitoid or by differencial suceptibility of individual hosts to parasitism (Hassell, 1969, Hassell and Waage, 1984). The variability in fertility of *C. partellus* eggs, in this study, might have brought a certain degree of heterogeneity in the egg population which was therefore observed in the level of parasitism, and subsequently in the number of black heads formed. The number of hosts surviving parasitism is also influenced by the parasitoid functional response.

5.3 Functional Response

Many authors claimed that the typical functional response in host-parasitoid relationship is a Type II response (Holling, 1959a). In this study when 6 or 48 parasitoids were released type of response was not clear due to deflection at a host density of 6, and 8 respectively. The analyses showed no difference in the number of eggs or egg batches parasitised for host densities of 6, 8, and 10. This allows us to say that the observed response is type II. This is supported by observations made for the parasitoid releases of 12 and 24 (Fig. 6 and 7). Ochiel (1989) studied the response of *T.* sp. nr. *exiguum* to *C. partellus* eggs and also a type II functional response (Holling, 1959a).

The combined functional response curves showed a kind of Nicholsian type of response (Type I), but due to the fact there was no statistical difference between batch 6, 8 and 10 this could simply be a type II response. The deflection in batch 8 may be attributed to experimental error, as no other apparent reasons could be advanced. According to Perry (1987) the lack of data at the extreme of the range

may make a truly curved line appear to be straight. Stark and Whitford (1987) studying the functional response of the third instar of *Chrysopa carnea* (Stephens) larvae feeding on 4 densities of *Heliothis virescens* (F.) eggs, on caged cotton found a Type I functional response (Hassell, 1978); search rate and the proportion of prey attacked did not vary with the prey density. However, the number of eggs attacked by *C. carnea* increased at a declining rate at higher egg densities and the proportion of eggs attacked was not constant. This suggested a possible Type II response due to predator satiation or handling time limitation. Other studies have indicated Type I functional responses for parasitoids such as *Geocoris punctipes* (Say) (Hutchison and Pitre, 1983), *Chrysopa signata* (Schneider) (Samson and Blood, 1980) feeding on *Heliothis* spp..

5.4 Models Development and Validation

Models from Cage Studies

The host-parasitoid models used in this study were derived from Perry's (1987) general host-parasitoid model

$$\text{Log}(-\text{Log}(Q_0)) = \text{Log } a + b \text{ Log } M$$

but considerably improved through additional factors in some cases and showed significant fits in most cases. Other host-parasitoid models, termed as "host-parasitoids models of intermediate complexity" (Hassell and May, 1973; Perry, 1987) designed for the classical type of biocontrol programmes, equally conformed to Perry's (1987) general model. These models incorporated some other parameters such as the parasitoid area of search (a), the mutual interference coefficient (m) (Hassell and Varley, 1969; Hassell and May, 1973); , and from these general models the above parameters can be deducted. As from Hassell and

Varley (1969) the area of discovery (a) (Nicholson, 1933) can be derived if the parasite density (P), the initial host density (UI) and the number of hosts surviving (U) are known : $a = (1/P)\log_e (UI/U)$ (Hassell, 1971). Models in this study are, therefore, somehow specific, as most of the above factors were fixed.

When Q_0 is equal to PEPAR and M equal to TRICHO, the data did not fit the model. However, when this model was tested for different batch levels, the data showed significant fits at higher egg batches densities suggesting that the model was best expressed when higher batch densities were used.

Brown *et al.* (1982), in developing a population model for the gypsy moth egg parasite *Ooencyrtus kuvanae*, obtained a good fit when the gypsy moth population was in outbreak. The fit of the model by the field data became poorer as the gypsy moth density decreased.

Additional parameters such as the maximum temperature and relative humidity of the day when the insects were released improve the fit of the models. The best models were selected on the basis of a high coefficient of determination, R^2, being obtained for the fitted data.

The models did not work when the sequence of release was added as one of the independant variables, confirming that this type of sequence of parasitoid release is an unnecessary consideration for the development of such models.

When Q_0 was equal to the proportion of egg batches parasitised, the model significantly fitted the general model ($P < 0.01$), $^{100}R^2$ values being 19.78 and 19.32. The use of the number of egg masses exposed in the model seemed to have improved the fit. More improvements were obtained when batch number, and maximum temperature and relative

humidity, were added to the general equation as independent variables.

Removing the variable BATCH from the model reduced the R^2, suggesting that the effect of egg batch density is of great value, although the splitting of the model into its component also showed the contribution of other additional parameters. In general, a variable contribution was noted for the climatic parameters showing a certain inconsistency of their effect on parasitism in this study.

The accuracy of prediction using the variable BPAR, in the laboratory, was as high as 77.36 (Table 32). Using the second adjustement of weather data the R^2 were even higher (Appendices 12, 13, and 14)

Analyses of models obtained using Genstat program, showed that the consistency of differences between batches in model IX seem to imply a progression such that the higher number of batches suffer less parasitism (this was also noticed in the previous analyses). The proportion of parasitised eggs, in the quadratic model, declined from a maximum value of $\log_e$(TRICHO) when density is increased further, particularly at highest density. This is an unsual implication (Perry, pers. comm.). Three dimensional plots from three regression equations (Fig. 11, 12, and 13) confirmed this observation. Comparison of models tested showed that the biologically more meaningful hypothesis that parasitism is maximal at the highest tested density can be accepted. Also, runs showed that there was no need for more complex models, because, the models in which the linear and quadratic terms were allowed to vary with batches did not produce any improvement of the fit and that the heterogeneity found was not unusual for such data.

Field Models

The field data fitted the models well, if an additional parameter, BATCH, was incorporated. Both field models with Q_0 equal to PEPAR and PBPAR could be used in prediction of the degree of parasitism.

The climatic variables were not incorporated due to lack of correlation observed with the number of eggs parasitised. However, Biever (1972) found that a single input of temperature appears to have a significant effect on the searching activity, and thus on the potential effectiveness, of *Trichogramma* in the field therefore its incorporation in the models should be considered.

Validation

The validation results, which showed that there were no differences in the models developed in the laboratory and in the field, suggesting that predictions can be made for field experiments using laboratory-based models. Then the following regression model developed with data from cage studies and incorporating parasites density, pest density temperature and relative humidity as independent variables appeared to agree with all situations, and could therefore be selected :

$$LNPBPAR = -3.125 - 0.602\ (LTRICHO) + 0.134\ (BATCH) - 0.079\ (XRH1) + (XTMP1)^{0.408}$$

($^{100}R^2 = 36.51$, Table 21)

During this study, the experimental conditions used tried to simulate natural conditions as closely as possible. For example the age of the plants used (20 DAE) was such that borer infestation at this stage can cause important yield losses (Seshu Reddy *et al.* 1989; Sharma and Sharma, 1987a, and b); and simulation of the *C. partellus* oviposition site (Alghali, 1988) by specific placement of

the egg batches. However, the manipulation of the parasitoids, especially during release, might have brought about great variations in their behavioral response which could subsequently have affected the reliability of the models obtained. Therefore the applicability of these models obtained from either cage or field data remain questionable. This calls for additional field studies, to define more precisely the parasitoid release rates and release methods required with regard to sorghum plant growth stage, oviposition time of *C. partellus* (knowing that under natural conditions the peak oviposition of by *C. partellus* females occurs at 4 to 9 weeks after plant emergence (Alghali, (1988); ICRISAT, (1988)), and the influence of climatic factors (such as wind, sunshine, temperature and humidity) on parasitisation in the field. Determination of the area of search by individual females and the effect of mutual interference would further increase the accuracy of the model.

6 SUMMARY

The effect of varying pest and parasitoid densities, the sequence of parasitoid release and climatic conditions on the rate of *C. partellus* egg and egg batches parasitism, were investigated in both caged and field expariments. Data collected were analysed using the analys of variance and linear regression models. The study highlights are summarised as follows:

Caged experiments:

1. The release of different *Trichogramma* sp. nr. *mwanzai* population densities (6, 12, 24, 48) showed a proportional increase in the number of *C. partellus* eggs and egg batches parasitised. Maximum parasitisation was obtained following the release of 24 parasitoids.
2. The number of eggs and egg batches parasitised by densities of 24 and 48 parasitoids were not significantly different, suggesting a reduction in the searching capacity of the parasitoid due to mutual interference. In general, at varying *C. partellus* eggs and egg batches densities (2, 4, 6, 8, 10), there was variation in the numbers parasitised. The number of eggs and egg batches parasitised increased with pest density. However, there was a reduction in percentage parasitism rate at Pest population higher than 4.
3. There was no significant difference between the number of egg or egg batches parasitised when 2 and 4 or 6, 8, and 10 egg batches were exposed for parasitisation.
4. The highest increase in parasitisation rate was observed at the highest pest population and for a parasitoid density of 24.

5. In the cage, the relationship between the number of eggs or batches parasitised, with the parasitoid population had linear, cubic, and quartic components.

6. The sequences of parasitoid release did show any significant difference in the number of eggs or egg batches parasitised.

7. The maximum temperature of DAY 1 (26.1^{0}C) was inversely correlated with the number of eggs and egg batches parasitised.

8. The maximum relative humidity of DAY 1 (87.2%) and the minimum relative humidity of DAY 1 (58.7%) were positively correlated with the number of eggs and egg batches parasitised.

9. An inverse relationship was noted between parasitoid density and the number of *C. partellus* black heads formed in the caged experiments, while a positive relationship was obtained between the size of the pest population and the number of black heads formed.

10. The sequences of parasitoid release did not appear to influence the number of black heads formed in the caged experiments.

11. The maximum temperatures of DAY 2 showed a positive effect on the number of black heads formed in cages, while the minimum temperature of the same day showed a negative effect.

12. A type II functional response curve was obtained from the caged data.

Field Experiments

13. Low levels of parasitism were observed in the field, hence no effect of varying parasitoid populations on the rate of parasitism could be determined.

14. There was no significant difference in the number of egg batches parasitised, between the releases 48 and 96

parasitoids. There were significantly higher number of egg batches parasitised by both release population size than the control.

15. By increasing the pest population an increase in the number of egg batches parasitised was achieved although there was no significant difference in the number of egg batches parasitised for most of the batches collected, except for the batch size of 25

16. There were no differences in the number of eggs or egg batches parasitised according to the two sequences of parasitoid release used in the field.

17. No relationship was found between climatic conditions and the number of eggs parasitised in the field, but the number of egg batches parasitised was positively correlated with the minimum relative humidity of DAY 1 (55.0%).

18. A linear relationship was obtained between the parasitoid population densities and the number of black heads formed.

19. In general, climatic conditions showed an inconsistent effect on the rate of parasitism achieved.

20. There was no difference in the number of black heads formed for the two sequences of release used in the field. There was no correlation between the number of black heads formed and the parasitoid population density. The climatic factors also did not seem to affect the formation of black heads in this experiment.

Models development and validation

21. Caged and field data were fitted into a modified general host-parasitoid model developed by Perry (1987) ($\log[-\log(Q_0)]=\log a + b \log M$, where Q_0 is the proportion parasitised, M the parasitoid mean density, while a and b are constants). The modified general model incorporated factors such as the maximum temperature and relative

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Appendix 1: Pearson correlation coefficient for (a) *Trichogramma* population levels, (b) number of egg batches exposed, (c) sequence of parasitoid release, (d) Temp. and Rh, on the levels of parasitism for (1) eggs and (2) batch, under caged conditions.

	BH	EPAR	BPAR
TRICHO	-0.24375**	0.49840**	0.52323**
BATCH	0.86728**	0.21928**	0.31856**
CHILO	0.88362**	0.30102**	0.38251**
SEQ	0.02360	0.08101	0.05758
XTMP1	-0.01131	-0.30557**	-0.23833**
MTMP1	-0.01425	-0.22643**	-0.14417**
XTMP2	0.15792*	-0.33867**	-0.29004**
MTMP2	-0.05343	0.08733	0.12440
XTMP3	0.10914	0.43587**	-0.36550**
MTMP3	-0.00675	-0.13104	-0.04238
XRH1	-0.09505	0.44.027**	0.41090**
MRH1	0.4946	0.13754*	0.08871
XRH2	-0.00436	0.00986	0.05216
MRH2	-0.16609*	0.45059**	0.39799**
XRH3	-0.06171	0.7754	0.04315
MRH3	0.10938	0.24396**	0.22002*

note * = $0.05 > p > 0.01$, ** = $P < 0.01$

d.z 2: ANOVA for Trichogramma sp. nr. nvanzai populations and sequences of parasitoid release on the number of eggs parasitised for different numbers of egg batches exposed in caged experiments.

	BATCH2			BATCH4			BATCH6			BATCH8			BATCH10	
OU CE	df	ms	P>F	df	ms	P>F	df	ms	P>F	df	ms	P>F	df	ms	P>F
DEL	14	756.752	0.1986	14	3543.184	0.0012	14	5525.452	0.0875	14	3900.301	0.0342	14	7860.163	0.0094
SEQ	2	598.867	0.3353	2	1318.757	0.2663	2	1001.297	0.597	2	1102.2875	0.5415	2	1874.531	0.515
TRICHO	4	1719.856	0.0248	4	9377.533	0.0001	4	13299.853	0.0005	4	11797.617	0.0006	4	32165.322	0.0002
SEQ*TRICHO	8	314.672	0.7737	8	1182.117	0.3189	8	2698.1327	0.2321	8	766.661	0.8896	8	1387.3802	0.843
ROR	30	528.356		29	953.378		29	1986.781		29	1759.2184		27	2756.364	

Appendix 3: Duncan's multiple range test for *Trichogramma* sp. nr. *nwanzai* populations and sequences of parasitoid release on the number of eggs parasitised for different numbers of egg batches exposed in caged experiments.

	BATCH2		BATCH4		BATCH6		BATCH8		BATCH10	
SEQUENCES GROUPS	n	Means	n	Means	n	Means	n	Means	n	Means
SEQ1	15	13.5 A	15	22.67 A	14	34.07 A	15	40.73 A	13	43.00 A
SEQ2	15	8.7 A	15	26.67 A	15	36.20 A	14	41.86 A	15	41.60 A
SEQ3	15	21.2 A	15	40.53 A	15	47.87 A	15	27.80 A	14	66.29 A
TRICHO LEVELS										
0	9	0.00 C	9	0.00 B	8	0.00 B	9	0.00 C	8	0.00 A
6	9	3.67 CB	9	9.22 B	9	7.89 B	9	13.11 CB	8	11.25 AB
12	9	11.00 CBA	9	13.67 B	9	24.56 B	9	27.89 CB	9	22.00 AB
24	9	26.22 BA	9	76.33 A	9	83.22 A	9	90.89 A	9	106.22 CB
48	9	31.44 A	9	50.56 A	9	77.44 A	8	53.38 AB	8	108.37 C

Means with the same letter, on the same column, within a particular group, are not significantly different at $p < 0.05$

Appendix 4: ANOVA fop Trichogramma populations and the number of egg batches exposed on the number of egg batches and eggs parasitised, and the number of black heads formed in caged experiments

	BPAR			BH			EPAR		
SOURCE	DEF	MS	PROB>F	DEF	MS	PROB>F	DEF	MS	PROB>F
MODEL	24	22.9068	0.0001	24	90234.788	0.0001	24	11248.025	0.0001
TRICHO	4	96.2617	0.0001	4	41757.702	0.0001	4	51682.909	0.0001
BATCH	4	22.9739	0.0001	4	487431.62	0.0001	4	7344.1259	0.0008
TRICHO X BATCH	16	4.8728	0.0002	16	3223.394	0.1238	16	2197.8901	0.1072
ERROR	197	1.6221		191	2227.858		195	1477.4150	
Contrast of single degree of freedom components									
TRICHO									
LINEAR	1	318.136	0.0001	1	163906.1	0.0001	1	165871.46	0.0001
QUADRATIC	1	2.244	o.2409	1	198.796	0.7655	1	32.5051	0.8822
CUBIC	1	42.005	0.0001	1	359.594	0.6883	1	22152.781	0.0001
QUARTIC	1	19.820	0.0006	1	2503.772	0.2904	1	16187.593	0.0011
BATCH									
LINEAR	1	85.412	0.0001	1	1948561.	0.0001	1	26044.297	0.0001
QUADRATIC	1	1.397	0.3543	1	2092.921	0.3336	1	816.7395	0.4581
CUBIC	1	2.556	0.2109	1	740.049	0.5651	1	1933.3787	0.2540
QUARTIC	1	2.537	0.2126	1	288.62	0.7193	1	485.0176	0.5673

Appendix 5: Models relating field data of the climate to the weather conditions in the cages when the thermohygrograph was protected with s Stevenson's screen.

DEPENDENT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDENT VARIABLES							
	INTERCEPT	X1	X2	X3	X4	CV	100_R2	SSE
Y1	10.737086	0.579479	--	--	--	3.21004	70.74**	0.82
Y2	5.927495	--	0.813442	--	--	2.75672	71.30**	0.55
Y3	47.298639	--	--	0.506110	--	3.84565	61.73**	3.36
Y4	30.508688	--	--	--	0.695765	6.74712	72.66**	4.07

Note: ** = P < 0.01; X1, X2, X3, and X4 are maximum Temp.,minimum Temp., maximum Rh and minimum Rh in the field respectively, while Y1, Y2, Y3, and Y4 are Temp. and Rh from a thermohygrometer protected by a stevenson's screen in the caged experiment.

Appendix 6 : Pearson correlation coefficients for (a) *Trichogramma* population levels, (b) number of egg batches exposed, (c) sequence of parasitoid release, (d) Temp. and Rh, on the levels of parasitism for (1) eggs, (2) batches, (3) number of black heads formed, under field conditions.

	BH	EPAR	BPAR
TRICHO	0.05555	0.21629	0.283881*
BATCH	0.88135**	0.22913	0.31868*
CHILO	0.92285	0.23261	0.32018*
SEQ	-0.10085	-0.04415	-0.02781
XTMP1	0.17999	-0.05922	-0.12456
MTMP1	-0.11404	0.12602	0.21062
XTMP2	-0.17118	-0.21406	-0.28388*
MTMP2	-0.03193	-0.20774	-0.30268*
XTMP3	-0.05825	-0.21499	-0.30813*
MTMP3	0.07163	0.21776	0.30955*
XRH1	0.17999	-0.05922	-0.12426
MRH1	0.03821	0.20968	0.30429*
XRH2	-0.22611	-0.01411	0.02478
MRH2	0.12294	0.22202	0.30549*
XRH3	-0.11404	0.12602	0.21062
MRH3	-0.24655	-0.08004	-0.06919

note: * = $p < 0.05$ and ** = $p < 0.01$.

Appendix 7 : ANOVA for *Trichogramma* sp. nr. *nwanzai* populations and sequence of parasitoid release on the number of egg batches parasitised for different batch numbers in caged experiments.

	BATCH2			BATCH4			BATCH6			BATCH8			BATCH10	
SOURCE	df	ms	P>F	df	ms	P>F	df	ms	P>F	df	ms	P>F	df	ms	P>F
MODEL	14	0.927	0.0563	14	4.975	0.0001	14	9.545	0.0001	14	7.851	0.0057	14	13.767	0.0002
SEQ	2	0.289	0.5452		1.689	0.2086		0.197	0.9034		1.422	0.5870		1.090	0.680
TRICHO	4	2.078	0.0061		12.411	0.0001		28.369	0.0001		24.811	0.0001		45.359	0.0001
SEQ*TRICHO	8	0.511	0.3935		2.078	0.0764		2.338	0.3274		0.978	0.9267		0.668	0.980
ERROR	30	0.467		30	1.022		30	1.931		30	2.622		28	2.786	

x 8 : Duncan's multiple range test for *Trichogramma* sp. nr. *nvanzai* populations and sequences of parasitoid release on the number of egg batches parasitised for different batch numbers in caged experiments.

	BATCH2		BATCH4		BATCH6		BATCH8		BATCH10	
ences groups	n	Means	n	Means	n	Means	n	Means	n	Means
	15	0.5 A	15	0.933 A	14	1.929 A	15	2.000 A	13	2.231 A
	15	0.5 A	15	1.200 A	15	1.800 A	15	2.000 A	15	2.400 A
	15	0.5 A	15	1.600 A	15	2.000 A	15	1.467 A	15	2.800 A
HO LEVELS										
	9	0.0 B	9	0.000 B	8	0.000 C	9	0.000 C	8	0.000 C
	9	0.222 B	9	0.556 B	9	0.333 BC	9	0.778 C	9	0.667 CB
	9	0.556 AB	9	0.778 B	9	1.556 B	9	1.444 BC	9	1.889 B
	9	1.000 A	9	2.889 A	9	4.111 A	9	4.222 A	9	4.889 A
	9	1.000 A	9	2.000 A	9	3.333 A	9	2.667 AB	8	5.000 A

; with the same letter, on the same column, within a particular group, are not significantly different at $p < 0.05$

ppendix 9 : ANOVA for Trichogramma sp. nr. nvanzai populations and sequences of parasitoid release on the number of black heads formed for different number of egg batches exposed in caged experiments.

	BATCH2			BATCH4			BATCH6			BATCH8			BATCH10	
SOURCE	df	MS	P>F	df	MS	P>F	df	MS	P>F	df	MS	P>F	df	MS	P>F
MODEL	14	650.022	0.5903	14	2522.341	0.1160	14	4921.536	0.52	14	4318.607	0.2423	14	10094.755	0.2423
SEQ	2	672.356	0.4150	2	741.23	0.6143	2	96.095	0.9606	2	8744.813	0.0826	2	2294.273	0.5528
TRICHO	4	1257.300	0.1774	4	6200.76	0.0092	4	10872.13	0.0061	4	6986.445	0.097	4	28171.180	0.0004
SEQ*TRICHO	8	340.800	0.8748	8	1245.436	0.5813	8	3099.538	0.2891	8	1799.24	0.7997	8	2943.821	0.6258
ERROR	30	742.289		28	1494.708		28	2485.232		28	3203.024		27	3786.29	

Appendix 10 : Duncan's multiple range test for Trichogramma sp. nr. nvanzai population size and sequence of parasitoid release, on the number of black heads formed for different number of egg batches exposed in caged experiments.

	BATCH2		BATCH4		BATCH6		BATCH8		BATCH10	
	n	Means	n	Means	n	Means	n	Means	n	Means
SEQ1	15	52.7 A	14	122.93 A	13	176.69 A	15	232.80 B	13	339.23 A
SEQ2	15	66.00A	14	111.00 A	15	184.27 A	14	260.29 BA	15	327.33 A
SEQ3	15	58.7A	15	118.86 A	15	184.33 A	14	280.07 A	14	307.93 A
TRICHO LEVELS										
0	9	73.33 A	9	145.22 A	8	228.87 A	8	303.87 A	8	390.37 A
6	9	59.78 AB	8	133.75 A	9	208.67 A	9	257.78 AB	8	356.00 AB
12	9	66.33 AB	8	131.37 A	8	174.87 CB	9	260.22 AB	9	342.56 AB
24	9	52.44 AB	9	90.44 B	9	162.11 CB	9	235.89 B	9	297.22 CD
48	9	43.00 B	9	89.78 B	9	139.89 C	8	230.12 B	8	237.75 C

Means with the same letter, on the same column, within a particular group, are not significantly different at $p < 0.05$

APPENDIX 11

MODELS RELATING PROPORTION OF EGGS PARASITISED AS FUNCTION OF TRICHOGRAMMA POPULATION LEVEL, MAXIMUM TEMP. AND RH OF THE DAY OF THE RELEASE OF THE PARASITOIDS FOR DIFFERENT EGG BATCHES AND SEQUENCES OF RELEASE IN THE CAGE.

DEPENDENT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDENT VARIABLES						
LNPEPAR	INTERCEPT	TRICHO	LTRICHO	XRH1	XTMP1	100_{R^2}	SSE
BATCH2 SEQ1	1.822550	-0.017793	--	-0.032302	0.049689	27.82	0.70
" " 1	1.893704	--	-0.064702	-0.033655	0.043416	13.68	0.77
" " 2	0.819002	0.009663	--	-0.001485	-0.027034	11.91	0.53
" " 2	0.970987	--	0.052936	-0.000909	-0.031494	6.65	0.54
" " 3	-1.328653	-0.038308	--	-0.024839	0.143677	36.57	1.08
" " 3	-1.897389	--	-0.206700	-0.027151	0.159964	21.64	1.20
BATCH4 SEQ1	0.911339	-0.0110527	--	-0.015605	0.020064	21.03	0.49
" " 1	0.5605262	--	-0.058097	-0.016842	0.033689	13.17	0.51
" " 2	-0.418238	-0.000846	--	-0.007121	0.043358	8.49	0.39
" " 2	-0.445080	--	-0.005898	-0.007160	0.044308	8.47	0.39
" " 3	1.649448	-0.014930	--	-0.028071	0.042796	31.15	0.53
" " 3	1.481256	--	-0.044994	-0.025420	0.032204	12.13	0.60
BATCH6 SEQ1	-0.698897	0.003552	--	-0.016461	0.082036	30.57	0.41
" " 1	-0.855012	--	-0.029099	-0.019168	0.102630	30.24	0.41
" " 2	4.147192	-0.010317	--	-0.034433	-0.022815	20.83	0.64
" " 2	5.116465	--	0.049123	-0.035990	-0.064748	16.09	0.66
" " 3	1.272880	-0.004969	--	-0.038784	0.093630	27.74	0.61
" " 3	1.436810	--	-0.004619	-0.039282	0.085933	25.86	0.62
BATCH8 SEQ1	1.800078	0.006962	--	-0.039021	0.072251	33.31	0.55
" " 1	2.045040	--	0.050786	-0.038718	0.063448	33.23	0.55
" " 2	1.025980	-0.005896	--	-0.025962	0.067315	29.83	0.44
" " 2	1.402795	--	0.043956	-0.025973	0.046904	30.99	0.43
" " 3	0.876028	-0.001207	--	0.006556	-0.040631	4.75	0.57
" " 3	1.626503	--	0.070642	0.005229	-0.71024	13.38	0.54
BATCH10 SEQ1	4.309715	-0.002522	--	-0.027178	-0.062628	20.37	0.47
" " 1	4.422045	--	0.082670	-0.021940	-0.086905	34.76	0.43
" " 2	-1.433407	0.000043	--	0.000210	0.071695	6.27	0.67
" " 2	-0.686379	--	0.069919	-0.000828	0.040876	13.75	0.64
" " 3	-2.147043	-0.003631	--	-0.004744	0.114798	22.99	0.48
" " 3	-1.176469	--	0.027152	-0.008384	0.085307	23.28	0.48

Note: none of the above model was significant.

APPENDIX 12
: MODELS RELATING PROPORTION OF EGG BATCHES PARASITISED AS FUNCTION OF TRICHOGRAMMA POPULATION LEVELS NUMBER OF CHILO EGG BATCHES AND THE MAXIMUM TEMP. AND RH ON THE DAY PARASITOIDS WERE RELEASED IN THE CAGES. (2^e adjustement)

DEPENDENT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDENT VARIABLES							
	INTERCEPT	LTRICHO	TRICHO	BATCH	XRH1	XTMP1	100_R2	SSE
LNPEPAR	6.2916436	--	-0.064386**	--	-0.135700**	0.266016 *	32.00**	2.11
"	5.470035	--	-0.064303**	0.130645**	-0.135628**	0.267342 *	34.10**	2.09
"	6.604320	-0.536393**	--	--	-0.168851**	0.355297**	38.75**	2.01
"	5.711415	-0.537802**	--	0.135743**	-0.168603**	0.357752**	41.02**	1.97

Note: * = 0.05 > P > 0.01
** = P < 0.01

APPENDIX 13

: MODELS RELATING THE PROPORTION OF BATCH PARASITISED AS A FUNCTION OF TRICHOGRAMMA POPULATION LEVELS, DAY1 MAX TEMP. AND RH, AND THE SEQUENCES OF RELEASE, FOR DIFFERENT EGG BATCHES NUMBER IN THE CAGE (2^e adjustement)

DEPENDENT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDENT VARIABLES							
LNPBPAR	INTERCEPT	TRICHO	LTRICHO	XRH1	XTMP1	SEQ	100_R2	SSE
BATCH 2	28.761492	-0.070520*	--	-0.329005**	0.093490	-0.723558	37.99**	2.97
BATCH 2	27.622557	--	-0651411**	-0.359273**	0.231220	-0.723558	45.73**	2.78
BATCH 4	-9.530878	-0.099053**	-	-0.074970	0.738607*	-0.782663	45.06**	2.48
BATCH 4	-7.264037	--	-0.719414**	-0.131032	0.816778*	-0.782663	47.12**	2.43
BATCH 6	5.205938	-C.065602**	--	-0.138702	0.302761	0.170730	38.54**	2.00
BATCH 6	6.062493	--	-0.573176**	-0.176271*	0.392473	0.115815	47.66**	1.85
BATCH 8	7.001526	-0.032930**	--	-0.095603*	0.088560	0.181090	47.33**	0.90
BATCH 8	5.810196	--	-0.337534**	0.107426**	0.172537	0.181090	71.14**	0.67
BATCH 10	1.786825	-0.051994	--	-0.036679	0.124650	-0.126458	64.14**	0.73
BATCH 10	2.564673	--	-0.391753**	-0.64772	0.184323	-0.189320	71.32**	0.65

Note:
* = 0.05 > P > 0.01
** = P < 0.01

APPENDIX 14

: MODELS RELATING PROPORTION OF BATCH PARASITISED AS FUNCTION OF TRICHOGRAMMA POPULATION LEVEL, MAXIMUM TEMP. AND RH OF THE DAY OF THE RELEASE OF THE PARASITOIDS FOR DIFFERENT EGG BATCHES AND SEQUENCES OF RELEASE IN TE CAGE. (2^e adjustment)

DEPENDENT VARIABLE	PARAMETER ESTIMATES FOR INDEPENDENT VARIABLES						
LNPBPAR	INTERCEPT	TRICHO	LTRICHO	XRH1	XTMP1	100_R2	SSE
BATCH2 SEQ1	25.141164	-0.069715	--	-0.256306	-0.256306	30.95	3.09
" " 1	26.498014	--	-0.518401	-0.294927	0.007768	32.61	3.06
" " 2	56.442835	-0.033027	--	-0.397988[6]	-0.786343	53.55*	1.95
" " 2	55.695954	--	-0.315877	-0.411416**	-0.715474	57.74*	1.86
" " 3	0.359126	-0.108819*	--	-0.332720	1.121179	54.33*	3.52
" " 3	-3.667647	--	-1.119956**	-0.371477	1.401367*	72.74**	2.72
BATCH4 SEQ1	-2.988014	0.102692**	--	-0.052603	0.385013	53.02*	2.02
" " 1	3.872086	--	-0.517752	-0.126525	0.331591	32.06	2.43
" " 2	22.478853	-0.015402	--	-0.376078	0.403116	45.15	2.75
" " 2	13.249828	--	-0.596457*	-0.351227*	0.700946	63.63	2.24
" " 3	-52.779451	-0.179064**	--	0.203771	1.427692**	79.28**	1.85
" " 3	-43.610003	--	-1.044032**	0.084656	1.417799*	58.01*	2.64
BATCH6 SEQ1	23.502612	-0.044554	--	-0.353787	0.314080	44.4[illegible]	2.84
" " 1	22.222890	--	-0.751044*	-0.387336*	0.499865	62.81*	2.32
" " 2	-12.211173	-0.104435**	--	0.021279	0.473196	58.17*	1.76
" " 2	-6.703146	--	-0.600809*	-0.048753	0.462651	40.96	2.09
" " 3	5.620988	-0.048458*	--	-0.085237	0.117033	56.01*	1.02
" " 3	4.904227	--	-0.444284?*	-0.106267	0.209710	81.48**	0.66
BATCH8 SEQ1	4.919661	-0.040203*	--	-0.091785	0.169663	55.79*	0.95
" " 1	3.833764	--	-0.393441**	-0.107511*	0.261198	82.77**	0.59
" " 2	-1.841639	-0.0374175	--	-0.033109	0.228713	35.80	1.09
" " 2	-3.326932	--	-0.362885**	-0.044508	0.323286	65.40*	0.80
" " 3	19.013093	-0.024412	--	-0.161913*	0.132694	61.60*	0.78
" " 3	18.010297	--	-0.256276**	-0.170259**	-0.066873	78.28**	0.59
BATCH10 SEQ1	-4.141253	-0.052576**	--	-0.016622	0.279316	75.15**	0.64
" " 1	-4.221702	--	-0.401239**	-0.043488	0.366664*	81.56**	0.55
" " 2	2.381486	-0.059914**	--	-0.044316	0.125374	70.75**	0.80
" " 2	4.572100	--	-0.393705**	-0.081097	0.148224	63.95**	0.89
" " 3	5.669362	-0.041887*	--	-0.045802	-0.016111	52.50*	0.85
" " 3	5.269943	--	-0.372907	-0.064752	0.057435	78.12**	0.58

Note: * = 0.05 > P >0.01 and ** = P < 0.01

Appendix 15: SAS program for model validation.

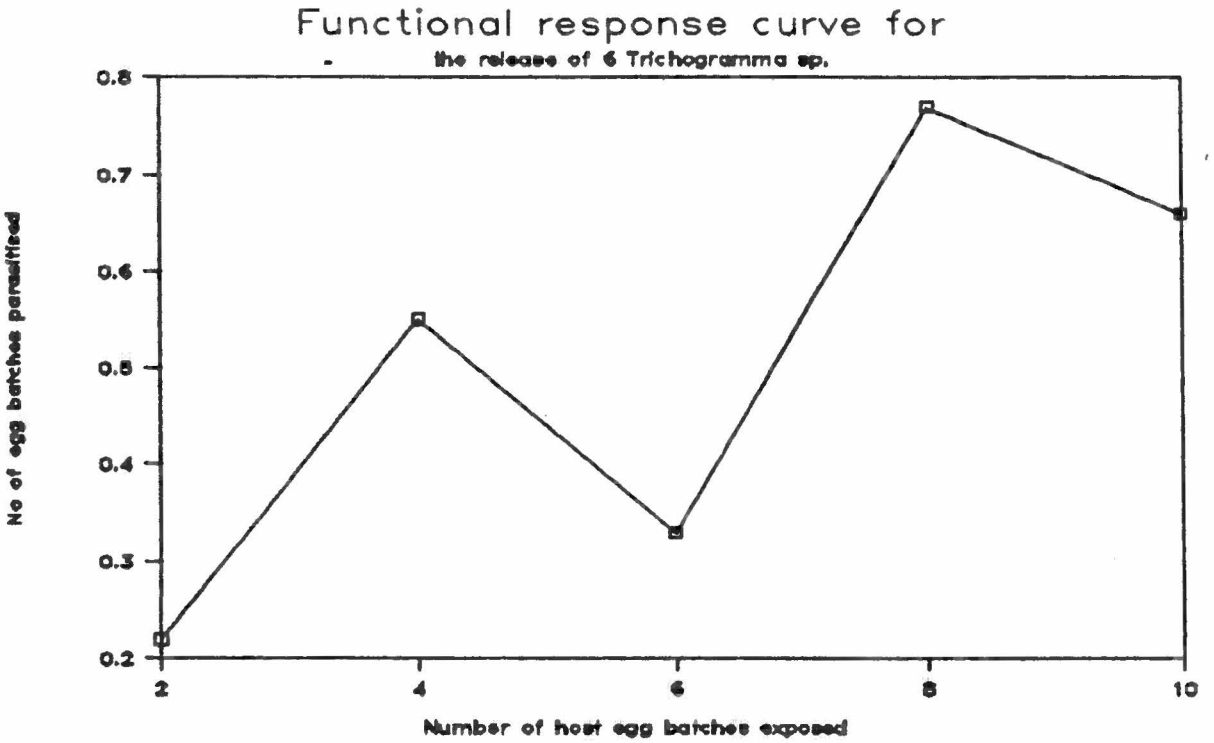
```
TITLE'TESTING REGRESSION MODEL OF PARASITISM';
OPTIONS LS=78 PS=21 NODATE NONUMBER;
DATA CHERRI;
INFILE'A:JAPHIE.PRN';
INPUT REP TRT $ SEQ BATCH CHILO TRICHO BH EPAR BPAR XRH1 MRH1 XRH2 MRH2
      XRH3 MRH3 XTMP1 MTMP1 XTMP2 MTMP2 XTMP3 MTMP3;

DATA NEW1;
SET CHERRI;
IF SEQ = 2;
INTERCEP = 3.082504;          * STDERR = 5.20244874 *;
ABATCH = 0.060892;            * STDERR = 0.08669046 *;
BTRICHO = -0.060228;          * STDERR = 0.01440294 *;
CXRH1 = -0.079245;            * STDERR = 0.04135952 *;
DXTMP1 = 0.193824;            * STDERR = 0.12345165 *;
PBPAR=(BPAR/BATCH);

IF PBPAR=0 THEN LNPBPARO=LOG(-LOG(PBPAR +.0005)); ELSE
LNPBPARO=LOG(-LOG(PBPAR -.0005));

LNPBPARE =ABS(INTERCEP + ABATCH*BATCH + BTRICHO*TRICHO + CXRH1*XRH1 +
          DXTMP1*XTMP1);

CELLCHI = ((LNPBPARO - LNPBPARE)**2)/LNPBPARE;
SUMCHI + CELLCHI;

PROC PRINT DATA=NEW1;
  VAR LNPBPARO LNPBPARE CELLCHI SUMCHI;
RUN;
```

Appendix 16 : Observation on the handling time of *T.* sp. nr. *mwanzai* in the laboratory.

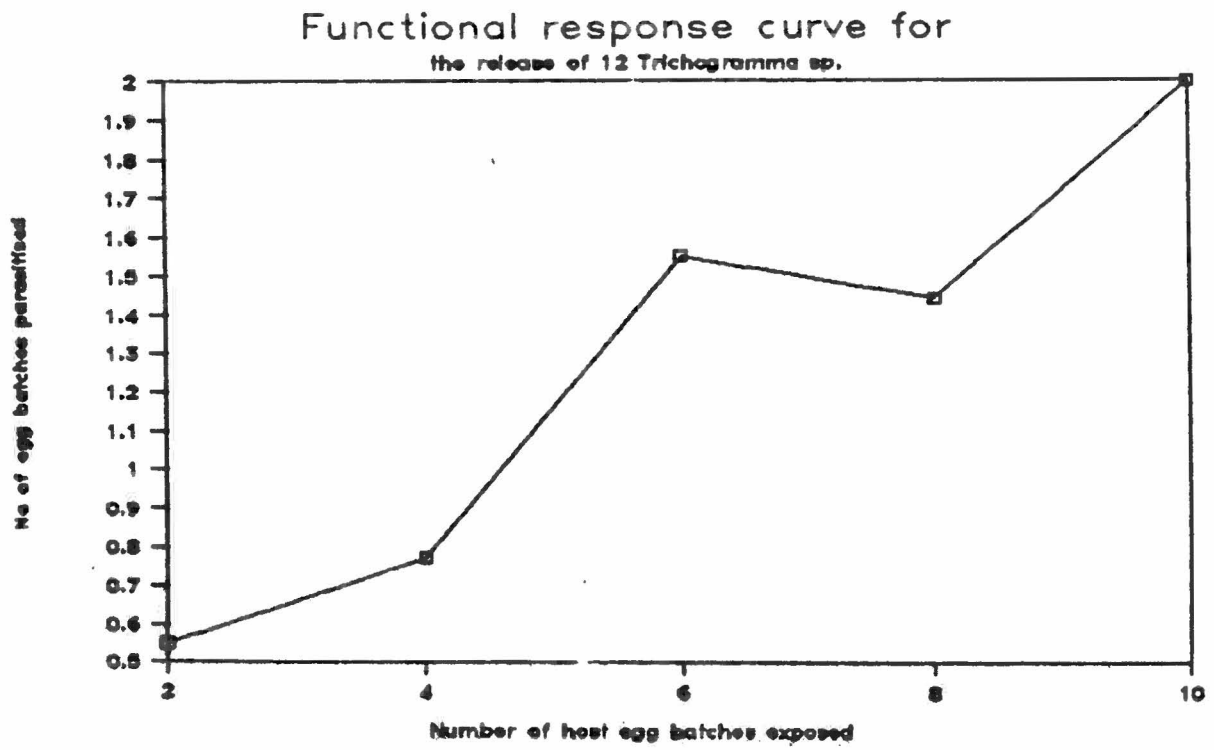
Replicate	Time spent on eggs(mns)	Host location time (mns)
I	1.95	1.88
II	2.38	1.61
III	2.00	2.04
IV	1.77	1.31
V	1.42	2.22
VI	1.73	2.02
Mean	1.88	1.85
S.E.	0.30	0.30

Total time spent on egg = T_h = 1.88 + 1.85 = 3.73 mins

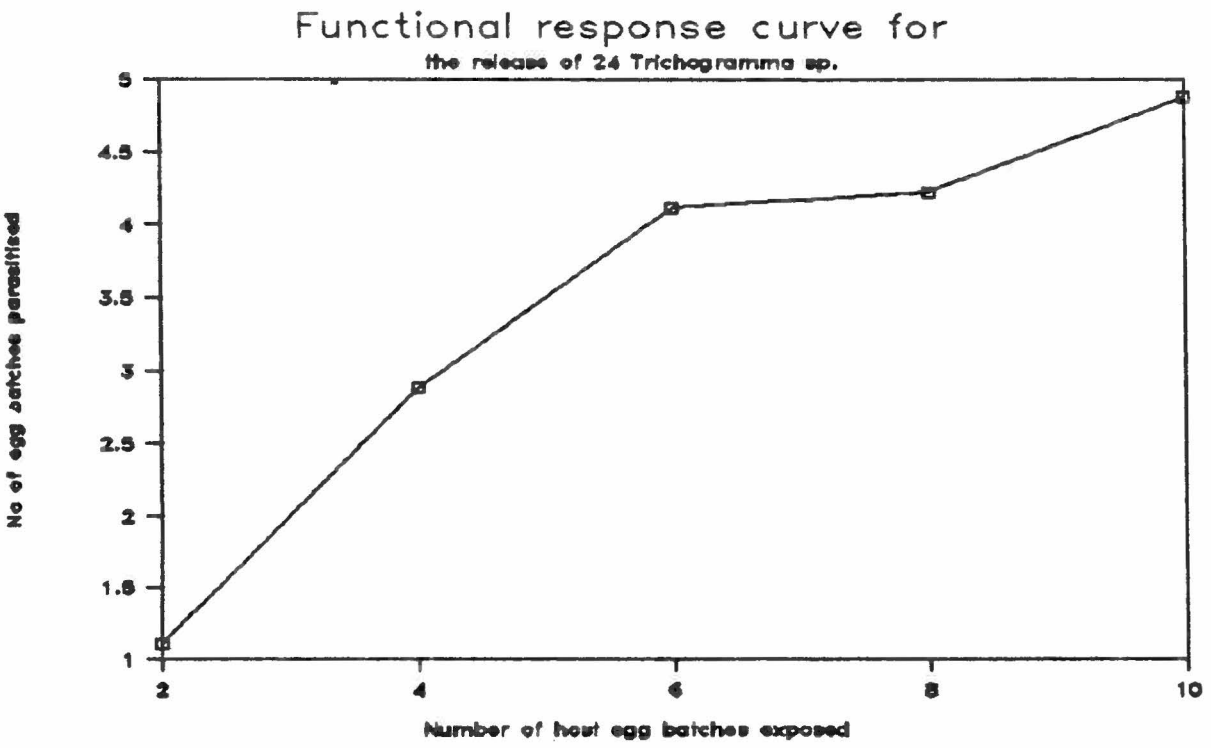
Appendix 17



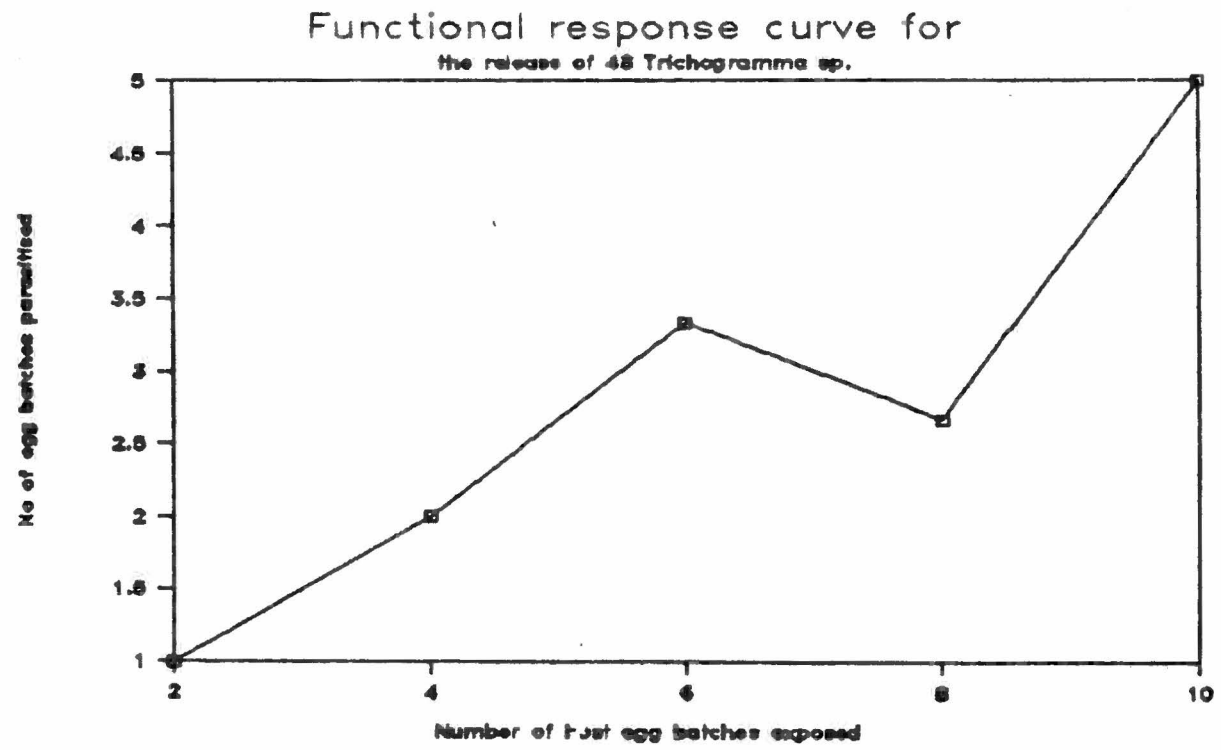
Appendix 18



Appendix 19



Appendix 20



Appendix 21: Average temperature and relative humidity of Day 1, 2, and 3 in cages (first adjustement).

N Obs	Variable	N	Mean	Std Dev	Std Error	CV
225	XRH1	225	88.5066667	5.8066464	0.3871098	6.5606882
	MRH1	210	58.5428571	9.8141862	0.6772432	16.7641052
	XRH2	210	89.7285714	5.0048439	0.3453670	5.5777594
	MRH2	195	56.2000000	10.7731051	0.7714781	19.1692262
	XRH3	225	88.5733333	2.6871387	0.1791426	3.0338010
	MRH3	225	57.8866667	12.3792128	0.8252809	21.3852577
	XTMP1	210	25.9785714	2.0654987	0.1425330	7.9507787
	MTMP1	210	19.3714286	1.5986366	0.1103164	8.2525490
	XTMP2	210	26.2428571	1.2038898	0.0830763	4.5874952
	MTMP2	210	20.0500000	1.3329196	0.0919802	6.6479780
	XTMP3	225	25.6800000	2.0051941	0.1336796	7.8083884
	MTMP3	225	20.0266667	0.9355098	0.0623673	4.6713205

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
225	XRH1	225	80.0000000	97.0000000	88.5066667	5.8066464
	MRH1	210	28.0000000	70.0000000	58.5428571	9.8141862
	XRH2	210	74.6000000	95.0000000	89.7285714	5.0048439
	MRH2	195	24.0000000	68.0000000	56.2000000	10.7731051
	XRH3	225	82.6000000	93.0000000	88.5733333	2.6871387
	MRH3	225	20.0000000	68.0000000	57.8866667	12.3792128
	XTMP1	210	22.4000000	29.4000000	25.9785714	2.0654987
	MTMP1	210	16.5000000	22.0000000	19.3714286	1.5986366
	XTMP2	210	24.0000000	28.4000000	26.2428571	1.2038898
	MTMP2	210	17.5000000	22.5000000	20.0500000	1.3329196
	XTMP3	225	22.4000000	31.4000000	25.6800000	2.0051941
	MTMP3	225	18.5000000	21.5000000	20.0266667	0.9355098

Appendix 22: Average temperatures and relative humidities of Day 1, 2, and 3 in cages (second adjustement).

N Obs	Variable	N	Mean	Std Dev	Std Error	CV
225	XRH1	225	87.2400000	4.6636608	0.3109107	5.3457827
	MRH1	225	58.7066667	6.1342641	0.4089509	10.4490077
	XRH2	225	88.7800000	4.0539663	0.2702644	4.5663058
	MRH2	225	57.9466667	5.4019920	0.3601328	9.3223516
	XRH3	225	88.3066667	2.3990698	0.1599380	2.7167482
	MRH3	225	59.6000000	6.7316218	0.4487748	11.2946675
	XTMP1	225	26.1200000	1.3796350	0.0919757	5.2819106
	MTMP1	225	19.8200000	1.4730617	0.0982041	7.4321982
	XTMP2	225	26.2333333	0.9434928	0.0628995	3.5965416
	MTMP2	225	20.2666667	1.1206264	0.0747084	5.5294067
	XTMP3	225	26.0266667	1.2255465	0.0817031	4.7088109
	MTMP3	225	20.0800000	0.8135570	0.0542371	4.0515787

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
225	XRH1	225	80.0000000	97.0000000	87.2400000	4.6636608
	MRH1	225	47.2000000	68.8000000	58.7066667	6.1342641
	XRH2	225	80.2000000	95.0000000	88.7800000	4.0539663
	MRH2	225	44.4000000	68.0000000	57.9466667	5.4019920
	XRH3	225	83.7000000	93.0000000	88.3066667	2.3990698
	MRH3	225	39.6000000	68.0000000	59.6000000	6.7316218
	XTMP1	225	23.5000000	28.7000000	26.1200000	1.3796350
	MTMP1	225	17.3000000	22.0000000	19.8200000	1.4730617
	XTMP2	225	24.0000000	27.8000000	26.2333333	0.9434928
	MTMP2	225	17.7000000	22.2000000	20.2666667	1.1206264
	XTMP3	225	24.5000000	29.3000000	26.0266667	1.2255465
	MTMP3	225	18.9000000	21.4000000	20.0800000	0.8135570

Appendix 23: Average temperatures and relative humidities of Day 1, 2, and 3 in the field experiment.

N Obs	Variable	N	Mean	Std Dev	Std Error	CV
54	XRH1	54	96.0000000	1.4274929	0.1942572	1.4869717
	MRH1	54	55.0000000	5.0131901	0.6822088	9.1148912
	XRH2	54	96.6666667	1.2589304	0.1713187	1.3023418
	MRH2	54	56.0000000	2.9715633	0.4043786	5.3063631
	XRH3	54	93.6666667	1.2589304	0.1713187	1.3440538
	MRH3	54	52.3333333	2.0740990	0.2822491	3.9632466
	XTMP1	54	26.3333333	0.4758310	0.0647524	1.8069530
	MTMP1	54	17.8333333	0.6294652	0.0856594	3.5297113
	XTMP2	54	26.1666667	0.6294652	0.0856594	2.4055994
	MTMP2	54	17.0000000	1.0902657	0.1483664	6.4133275
	XTMP3	54	26.3333333	0.2379155	0.0323762	0.9034765
	MTMP3	54	18.1666667	0.2379155	0.0323762	1.3096265

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
54	XRH1	54	95.0000000	98.0000000	96.0000000	1.4274929
	MRH1	54	51.0000000	62.0000000	55.0000000	5.0131901
	XRH2	54	95.0000000	98.0000000	96.6666667	1.2589304
	MRH2	54	53.0000000	60.0000000	56.0000000	2.9715633
	XRH3	54	92.0000000	95.0000000	93.6666667	1.2589304
	MRH3	54	50.0000000	55.0000000	52.3333333	2.0740990
	XTMP1	54	26.0000000	27.0000000	26.3333333	0.4758310
	MTMP1	54	17.0000000	18.5000000	17.8333333	0.6294652
	XTMP2	54	25.5000000	27.0000000	26.1666667	0.6294652
	MTMP2	54	15.5000000	18.0000000	17.0000000	1.0902657
	XTMP3	54	26.0000000	26.5000000	26.3333333	0.2379155
	MTMP3	54	18.0000000	18.5000000	18.1666667	0.2379155

Appendix 24: General level of eggs and egg batches parasitism in the cages.

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
180	PE	174	0	98.8888889	17.7321112	21.6740911
	PB	179	0	100.0000000	34.2364991	33.0186305

Symbols: PE = percentage of eggs parasitised; PB = percentage of egg batches parasitised.

Appendix 25: General level of eggs and egg batches parasitism in the field experiment.

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
36	PE	36	0	51.5021459	7.3372211	10.4040244
	PB	36	0	66.6666667	16.3887608	16.8031856

Appendix 26: Percentage parasitism in caged experiments for different number of egg batches exposed.

BATCH=2

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
36	PE	36	0	98.8888889	20.2345701	28.1511813
	PB	36	0	100.0000000	36.1111111	40.7275111

BATCH=4

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
36	PE	34	0	80.1282051	22.3537293	24.7389517
	PB	36	0	100.0000000	38.8888889	38.4728311

BATCH=6

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
36	PE	35	0	75.5555556	18.5508665	21.5224415
	PB	36	0	100.0000000	37.0370370	32.3941772

BATCH=8

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
36	PE	35	0	68.2656827	13.3091718	15.1660893
	PB	36	0	87.5000000	28.4722222	25.9826713

BATCH=10

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
36	PE	34	0	54.2253521	14.1710204	15.2507063
	PB	35	0	90.0000000	30.5714286	24.8457426

Appendix 27: Percentage parasitism in caged experiments for different parasitoid densities and different number of egg batches exposed.

TRICHO=6 BATCH=2

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	0	26.3736264	4.1068735	9.0545652
	PB	9	0	50.0000000	11.1111111	22.0479276

TRICHO=6 BATCH=4

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	8	0	27.8688525	5.1785218	10.3232847
	PB	9	0	75.0000000	13.8888889	25.3448439

TRICHO=6 BATCH=6

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	0	12.7906977	3.0618922	4.8684113
	PB	9	0	16.6666667	5.5555556	8.3333333

TRICHO=6 BATCH=8

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	0	14.4781145	4.1804775	5.2251749
	PB	9	0	37.5000000	9.7222222	12.1478164

TRICHO=6 BATCH=10

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	8	0	11.6173121	2.5028106	4.7131484
	PB	9	0	30.0000000	6.6666667	11.1803399

TRICHO=12 BATCH=2

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	0	54.8780488	13.1450568	19.8464158
	PB	9	0	100.0000000	27.7777778	36.3241579

TRICHO=12 BATCH=4

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	8	0	30.0000000	9.2431696	12.3653446
	PB	9	0	75.0000000	19.4444444	27.3226605

TRICHO=12 BATCH=6

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	8	0	37.2384937	10.5275550	12.9465065
	PB	9	0	66.6666667	25.9259259	22.2222222

TRICHO=12 BATCH=8

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	0	25.2336449	8.5505019	9.5731673
	PB	9	0	37.5000000	18.0555556	14.1298541

TRICHO=12 BATCH=10

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	0	13.2678133	5.2706332	4.3145288
	PB	9	0	30.0000000	18.8888889	9.2796073

TRICHO=24 BATCH=2

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	0	66.6666667	29.3951577	29.6470277
	PB	9	0	100.0000000	55.5555556	52.7046277

TRICHO=24 BATCH=4

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	14.7651007	62.1301775	41.0766094	18.8836640
	PB	9	50.0000000	100.0000000	72.2222222	23.1990182

TRICHO=24 BATCH=6

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	7.0671378	55.0607287	29.9826191	20.3429039
	PB	9	33.3333333	100.0000000	68.5185185	24.2161052

TRICHO=24 BATCH=8

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	6.2500000	68.2656827	26.4068545	20.5326616
	PB	9	25.0000000	87.5000000	52.7777778	23.1990182

TRICHO=24 BATCH=10

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	5.8111380	52.2504892	22.5886736	15.0436697
	PB	9	20.0000000	80.0000000	48.8888889	20.8832735

TRICHO=48 BATCH=2

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	0	98.8888889	34.2911925	38.0325570
	PB	9	0	100.0000000	50.0000000	35.3553391

TRICHO=48 BATCH=4

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	0	80.1282051	30.5515311	31.6873898
	PB	9	0	100.0000000	50.0000000	45.0693909

TRICHO=48 BATCH=6

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	9	0	75.5555556	29.7399205	27.6104119
	PB	9	0	100.0000000	48.1481481	30.5555556

TRICHO=48 BATCH=8

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	8	0	34.1991342	14.1975636	11.9042854
	PB	9	0	87.5000000	33.3333333	29.3150985

TRICHO=48 BATCH=10

N Obs	Variable	N	Minimum	Maximum	Mean	Std Dev
9	PE	8	6.4066852	54.2253521	26.3823060	16.5942969
	PB	8	20.0000000	90.0000000	50.0000000	22.0389266