BIOLOGY AND BIOCONTROL POTENTIAL OF PEDIOBIUS FURVUS (GAH.) FOR THE MANAGEMENT OF CEREAL STEM-BORERS IN KENYA

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Abstract

Pediobius furvus (Gah.) (Hymenoptera:Eulophidae) is a gregarious endoparasitoid of graminaceous stem-borers in east Africa.

An extensive survey on the incidence and abundance of the parasitoid in different agroecological localities in Kenya shows that *P. furvus* parasitoid is more abundant in the drier localities such as Mombasa where over 46 % natural parasitism on *B. fusca* pupae was recorded. Similarly, more progeny per host pupa was recorded on *B. fusca* than on *C. partellus*. This low incidence of the parasitoid on its host pupae *C. partellus* is partially due to the fact that both the parasitoid and the host *B. fusca* are indigenous to Africa.

Studies on parasitism by *P. furvus* under netted field conditions and its attraction to two cultivars of maize in the field showed that more *C. partellus* pupae were recovered from the maize cultivar INB-A (Susceptible) than on ICZ-2 (Resistance) and hence more parasitized *C. partellus* pupae on INB-A than on ICZ-2. However, the parasitoid did not show any significant preference on internode levels of the maize plant for oviposition.

Investigations on the nature of trophic interactions between the plant, host insect and the parasitoid showed

that no one stimulant alone performed the service of guiding *P. furvus* females to their proper host habitat, and the host location is achieved by a complex of array of stimuli working in harmony.

Studies in the laboratory show that changes in temperatures and relative humidities affects the rate of reproduction and development of the parasitoid and modify the behaviour of the adult female in its response to pupae of stem-borers, *C. partellus* and *B. fusca*. The optimum temperature and relative humidity levels for the parasitoid's reproductive rate was found to be 25 ±1°C and 30 ±1.5°C under relative humidity levels of 60 % to 70 %. However, low temperature resulted in longer developmental period, less progeny production and more male progeny per host pupa parasitized.

Host's age as well as the parasitoid's age, independent of size, were found to be one of the most important factors influencing the acceptability and suitability of both *C. partellus* and *B. fusca* pupae. Percentage of parasitoid larvae which complete their development and their sex determinations was found to be affected by the host's age.

Five days or older female parasitoids failed to parasitize at any age of the host pupae *C. partellus* and *B. fusca*. Optimum host acceptability remained between 0-2-day -old for *C. partellus* and 0-4-day -old for *B. fusca*.

Sucrose and / honey concentrations as food for the adult parasitoid played an important role in prolonging

the longevity of the adult parasitoid but did not affect it's fecundity. Studies on the oviposition and dissection of the parasitoid reveal that it is proovigenic. The adult female emerges after development of immature stages with a full complement of ripe eggs and does not develop further eggs during its life.

It has been observed that when superparasitism occurs in *P. furvus*, the maximum number that can develop to adult stage on a fully developed pupa of *C. partellus* is 133, even though more can start development in *C. partellus* host pupa. It was also found that superparasitism in this parasitoid is accompanied by a reduction in size of the adult parasitoid and a preponderance of males which reduce the efficacy of the parasitoid.

When superparasitism occurs in *P. furvus*, the competition among the developing parasitoids for the available food in the host is the factor that inhibits normal development.

The rate of multiplication of *P. furvus* in one generation was found to be 335 and the mean length of the parasitoid generation recorded was 21 days. The species has a finite rate of increase as 1.31, which means the population would multiply 1.31 times per day at 25 ±1°C under relative humidity levels of 65 ±5 %.

DECLARATION

I, ALI-NUR HUSSEIN DUALE, do hereby declare to the Senate of River State University of Science and Technology, Port Harcourt, that the work presented in this dissertation was carried out by me and has not been submitted in full or in part for a similar degree in any other University.

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CERTIFICATION

This thesis has been submitted with our approval as supervisors.

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DEDICATION

I dedicate this work with pleasure to my father, Hussein Duale, and my brothers and sisters who endeavored to educate me,in the hope that we may have a better future.

List of abbreviations used in the text

Anova.	Analysis of Variance
A.R.P.P.I.S.	African Regional Postgraduate Programme in Insect Science
Cm	centimeter
C.P.R.P.	Crop Pest Research Programme
Conc.	Concentration
°C.	Degrees centigrade
D.M.R.T.	Duncan's Multiple Range Test
F.A.O.	Food and Agricultural Organization
Fig.	Figure
G.	Gram
Ha	Hectare
Hr.	Hour
I.C.I.P.E.	International centre of insect physiology and ecology
Kg	Kilogram
Lat.	Latitude
L.R.S.	Long rainy season
M	meter
Mg.	Milligram
M.P.F.S.	Mbita Point Field Station
mm.	Millimeter
N.C.America	North Central America

Reps.	Replications
R.H.	Relative humidity
S.E.	Standard error
S.A.S.	Statistical Analysis System
S.R.S.	Short rainy season

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CHAPTER ONE

1.0 INTRODUCTION

Millions of people in Africa and Asia depend on maize and sorghum as a staple food. The stalk and stover of the crops serve as fodder to millions of dairy and beef livestock which provide protein requirements for man (Duale, 1988).

The world production of maize in 1990 was about 475,429 metric tones. N.C.America produced the greatest proportion (226,510 tones) followed by U.S.A. (201,509 tones) and Africa (33,794 tones) (FAO, 1990). In Africa, there was an overall decrease in maize production, thus, total African production of maize decreased by 87.74%. Maize production in Africa is led by South Africa, which contributes up to 27.94 %, Egypt 13.02%, and Kenya , 7.98%, being the other leading maize producers (FAO,1990). In East Africa, however,in 1990 Kenya, Tanzania and Somalia contributed 7.98%, 7.23 % and 0.93 % respectively to African maize production (Appendix 1). Grain yield of maize in Africa is about 1616 kg/ha compared with 6023 kg/ha in N.C.America (FAO,1990). In Eastern Africa, it ranges from 700 kg/ha in Sudan to 1800 kg/ha in Kenya (Appendix 1). There are many constraints in the production of maize, and the maximum yield potential

has never been realized on-farm, (Seshu Reddy,1983). The most significant factor that contributes to low yields and decrease in overall production in the tropics is drought stress.

But the perennial problems caused by insect pests and other biotic factors cannot be ruled out (Duale,1988).

It is generally agreed that a host of lepidopterous stem-borers constitutes the most widely distributed and economically important group of insect pests of maize in different agroecosystems in various geographical areas (Srivastava, 1985). Of the several stem-borer pests, *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae), *Busseola fusca* (Full.), (Lepidoptera:Noctuidae), *Sesamia calamistis* (Hamps.) (Lepidoptera:Noctuidae), and *Eldana saccharina* (Walk.) (Lepidoptera:Pyralidae) are the most serious and destructive borers attacking maize in East Africa.(Seshu Reddy,1983).

The extent of crop losses of maize due to stem-borers has been reported by numerous workers in Africa (Usua,1968; Conley,1969; and Seshu Reddy,1985). In East Africa, up to 50% yield losses due to insect attack on this crop have been estimated (Singh,1983). Conley (1969) reported an estimated loss in yield of 18% and 27% due to stem-borers in Kenya and Tanzania respectively. Seshu Reddy (1989) reported that infestations of borer complexes of *C. partellus*, *B. fusca*.,

S. calamistis, and *E. saccharina* ranged from 95 to 100%.in Western Kenya. Singh (1983) reported up to 40-50% yield losses of maize in Kenya caused by *B. fusca*. Ingram (1958) reported grain yield losses of up to 50% due to *C. partellus*. in Uganda. In Nigeria, Usua (1968) reported that one or more *B. fusca* larvae per maize plant reduced the yield by as much as 25 %.

Maize is protected to some extent from these insect pests mainly by the use of insecticides, and through cultural practices, and insect resistant varieties in that order. Biological control in the form of man-manipulated use of parasitoids, predators, and pathogens is little practised currently. Other control practices such as the use of light traps, pheromone traps, and the release of sterile males are currently not used in maize.

Cultural control of stem-borers is most frequently aimed at the destruction of the diapausing larvae which normally serve as the initial source of crop infestation in the field. Field sanitation and adjustment of planting dates are some cultural methods which have been considered by different workers (Trehan and Butani,1949; Jepson,1954; Nye,1960; Roome,1976; Sarup *et al.*,1978; Brader,1979, Seshu Reddy;1982, Kumar,1984).

The possibilities for chemical control are restricted

by the nature of the typical stem-borer life cycle, which only permits direct application of insecticides to the larvae during the limited period before they enter the stems. Other limitations to chemical pesticides are apparent: first, the cost of pesticides and their applications has risen considerably, and is beyond the means of the farmer; second, great losses due to pests occur despite the advances in modern chemical control (Pimental,1978); and third, potentially of even more concern, significant groups of pests have developed strains that are genetically resistant to chemical pesticides. These call for the adoption of economic and environmentally sound approach towards insect pest management.

Host plant resistant appears to hold a greater promise than pesticides for stem-borer control in the Semi-Arid-Tropics especially when combined with other control measures (Seshu Reddy,1982).

Unless upset by pesticides or gross environmental changes, classical biological control, once established, characteristically remains effective. This is to say, coevolution appears to ensure that pests seldom develop resistance to biological control agents (Kamath,1982). In this respect, biological control seems to have an advantage over the use of resistant cultivars.

At the International Centre of Insect Physiology and Ecology (ICIPE), as part of an effort to improve maize yields, research has been geared towards developing cost effective and environmentally sound integrated pest management systems. To this end, the IPM strategies being developed are non-pesticidal as farmers can neither afford nor handle pesticides which pose hazards (Anon, 1985).

Under this scheme, use of biological control agents has been one of the foremost strategies at the ICIPE. Biocontrol utilizes natural enemies such as parasitoids, predators and pathogenes which require a relatively minimal financial input for their development. To this end, emphasis has been put towards utilizing parasitoids of stem borers with some degree of success (Anon, 1985).

A number of natural enemies of stem-borers have been reported (Appert and Ranaivosoa, 1970; Mohyuddin and Greathead,1970; van Rensburg and van Humburg, 1975; Teetes *et al*.,1979). In East Africa,the role of natural enemies (parasitoids, predators and pathogens) as a cause of population fluctuations in stem-borers of sorghum and maize has been investigated by several workers (Jepson,1954; Ingram,1958; Mohyuddin,1970; Schmutterer,1968; Mathez,1972; Seshu Reddy,1989). In Kenya, five egg parasitoids(two Scelionids and three Trichogrammatids) caused mortalities up to 92% in *Chilo spp*.and 97% in *S. calamistis* (Mathez,1972).

Parasitism of larvae and pupae is below 10% (Mathez,1972).

Parasitoids make up at least 14% of the more than one million insect species known (Askew,1971) and are an important group in determining the population dynamics of their host insects. This is because the mortality resulting from their action is frequently the main biotic factor limiting the density of host insect populations and this contribution is economically important in control programmes. Among the major parasitoids attacking cereal stem-borers, *Pediobius furvus* (Gah.) (Hymenoptera.: Eulophidae) is an important gregarious pupal parasitoid of several graminaceous stem-borers in East Africa. It is indigenous to Africa and is distributed roughly between latitude 17°N and 17°S.(Mohyuddin,1970).

Studies on its biology and principal hosts (graminaceous stem-borers) have been reported by some workers (Mohyuddin,1970, Mohyuddin and Greathead,1970, Overholt and Smith,1989), but there is a paucity of information on the effect of host age on the parasitoid's development, progeny production and sex-ratio and other aspects in literature. Information is also very sparse on the effect of some abiotic factors such as temperature and relative humidity on some biological characters (e.g.developmental period, progeny production, sex-ratio, fecundity, adult longevity etc.) of *P. furvus*. Mohyuddin

(1970) mentioned that in most areas *P. furvus* competes with *Dentichasmias busseolae* (Heinrich.) (Hymenoptera :Ichneumonidae), for pyralid stem-borers.

However, this conclusion remains tentative since no further studies on their host discrimination and competition in different ecological zones were conducted. Field evaluation of parasitization by *P. furvus* was undertaken by Overholt and Smith (1989). However, they did not investigate whether larval frass and/or stems damaged by the host borer or the host plant itself play any important role in attracting the parasitoid to host insect for oviposition.

Laboratory studies reported by Mohyuddin (1970) has shown that adult *P. furvus* lived longer on sucrose in solid or in liquid form than on water. The study did not differentiate between sexes, nor did it comment on the effect of varying sucrose concentrations and/or of honey solutions on adult longevity and fecundity. It is evident that for possible mass production and subsequent periodic release of this parasitoid against graminaceous stem-borers these outstanding questions should be answered.

The present study (principally laboratory investigations) was therefore undertaken with the following objectives to provide information on the salient points mentioned in the previous paragraphs:

It is expected that observations on the biology and biocontrol potential will provide a basis for understanding the interactions between *P. furvus* and its hosts. The information obtained from this study would therefore, provide a rational basis for the development of biological control as a component of an Integrated Pest Management (IPM) programme that is appropriate for the resource poor farmer in the Tropics.

Objectives of the study

1. Seasonal survey for the incidence of *P. furvus* (Gah.) in maize fields in different agroecological localities in Kenya.

2. *P. furvus* : Parasitization of *C. partellus* pupae and its attraction to two cultivars of maize in the field

3. To investigate the nature of the trophic interactions between the plant, host insect and the parasitoid.

4. To study the effect of temperature and humidity levels on *P. furvus* parasitism.

5. To study the effect of age on the parasitoid biology.

6. To determine the effect of diet on the parasitoid's

longevity and fecundity.

7. To investigate the effect of superparasitism on the biology of the parasitoid.

8. To study the intrinsic rate of natural increase of *P. furvus* on *C. partellus* pupae.

CHAPTER TWO

2.0. LITERATURE REVIEW

2.1. Geographical Distribution of the Genus Pediobius (Gahan.) (Hymenoptera: Eulophidae)

The genus *Pediobius* is distributed throughout the world, with both primary and secondary modes of parasitism among the species (Patric-Parkman *et al*, 1983). Several species in the genus have been used in classical biological control programmes against certain Coleoptera, Lepidoptera, and Hymenoptera (Sawflies) (Clausen, 1978; Greathead, 1971). It is a gregarious pupal endoparasitoid of a wide range of insect groups (Lepidoptera, Coleoptera etc.).

A study in India by Lall (1961) indicated that *P. foveolatus* has a sufficiently short life cycle (10-30 days depending on temperature) so that it can pass through several generations during a season and has the potential of attaining high levels of parasitism in a single season. *P. facialis* is a Palaer tic insect and in Europe is a primary parasitoid of certain Ichneumonidae and Braconidae (Boucek and Askew ,1968). A study by Milner (1967) reported *P. furvus* as a hyperparasite of *Apanteles sesamiae* (Cam.), Glyptomorpha sp (Braconidae) and *Sturmiopsis parasitica*

(Curr.) (Tachinidae). However, later studies by Mohyuddin (1970) to demonstrate *P.furvus* as a hyperparasite has verified that records of *P. furvus* as a hyperparasite were most probably due to misidentification and that this species is quite safe for introduction in to other countries.

Pediobius foveolatus (Crawford) (Hymenoptera: Eulophidae), from India is released annually in the United States for control of the Mexican bean beetle, *Epilachna varivestis* Mulsant, in soybean (Boucek and Askew, 1968).

Pediobius furvus (= *Pleurotropis furvum* (Gah.), is indigenous to Africa and according to Mohyuddin (1970), the parasitoid is widely distributed from the moist forest zone of Seirra Leone, and Uganda to the sub-desert steppe of the Sudan. The parasitoid occurs also in the woodlands and Savanas in East and West Africa with a tropical summer-rain climate (Mohyuddin and Greathead,1970). *Pediobius furvus* has been recorded from all the major graminaceous crops in Africa especially in the drier areas of Nigeria (Jarath, 1968); Sierra Leone (Jordan, 1966); Cameroun (Descamps, 1956); Ghana (Forsyth 1966); Mali, Senegal and Ivory Coast (Risbec,1958); and East Africa (Mohyuddin, 1970) . According to Overholt and Smith (1989), *P. furvus* may have potential in an inundative or inoculative approach to biological control of stem-borers.

2.2. Investigation on the nature of the Trophic interactions between the plant, host insect and the parasitoid

In recent years, considerable interest has been evoked all over the world in the application of biological control methods against crop pests. Three of the major reasons for this have been, according to Kamath (1982): (1) the rapid development of resistance to chemicals by a number of insect pests; (2) the hazards that many of the recently developed, most potent, powerful organophosphorous and other toxic compounds pose to human health,domestic animals and wild life; and (3) the accumulation of chlorinated hydrocarbons or their degradation products in food chains, and the more general dangers of destroying the pollinators and useful,and often essential, natural enemies which are keeping other pests in check.

The rationale of biocontrol is to reestablish equilibria in ditrophic interactions between the prey and predator or host and parasitoid, mimicking the action of natural systems. Most insect and mite pest species remain permanently below any economic injury level, partially due to suppressive activities of natural enemies. In contrast to natural biocontrol, applied biological control involves active intervention with biotic agents of agricultural and urban ecosystems.

The suppressive action of parasitoids/predators, of phytophagous organisms and pathogens in maintaining another organism (pest in this case),at a lower average density than it would attain in their absence can be subjected to man's manipulations. The spectacular success in the control of the cottony cushion scale *Icerya purchasi* in 1888 using the predatory coccinellid beetle *Rodolia cordinalis* led to great enthusiasm for the use of natural enemies.

Parasitoids make up at least 14% of the more than one million of known insect species (Askew,1971) and are an important group in determining the population dynamics of their host insects. Inundative release programmes with the parasitoid *Pediobius foveolatus* have been particularly successful (Stevens *et al.* 1975; Clausen, 1976; Barrow and Hooker 1981), in the U.S.A and the parasitoid is the primary factor around which several pest management programmes for the Mexican Bean beetle (MBB), *Epilachna varivestis* Mulsant (Coleoptera: Chrysomelidae) have been structured (Clausen,1976; Schroder 1981).

Success in biocontrol programmes have been attributed partly to the high searching efficiency of the natural enemy for it's host or prey. Natural enemies are trophically associated with the host plant of their hosts or prey, and to evaluate their potential as agents for pest suppression

it is important to understand the host- or prey-finding mechanism employed by them. Doutt (1964) analyzed the host/prey selection process as a hierarchy of events (plant stimuli-insect/mite responses) succeeding each other in time and space. Five major phases are defined in the selection process: (1) host habitat location, (2) host location, (3) host recognition , (4) host acceptance, and (5) host suitability (Doutt,1964). By following this sequence of events, a natural enemy successfully narrows its search to areas most likely to contain a host/prey and thus avoid wasting time and energy in an undirected search throughout the environment.

2.2.1. Host habitat finding

Parasitoids (also predators) use protective chemical products (volatile and non-volatile) produced by plants before phytophagous attack (constitutive products) or synthesized by plants when there is a herbivore damage (inductive products) to narrow their search and to guide them to their hosts (or prey) habitat. Dispersing parasitoids arrive at the general habitat by responding to plant stimuli (usually olfactory, but also visual). These plant chemicals may have the potential to attract or 'verdict' and 'sustain' parasitoids. Some parasitoids may be attracted by the odor of the host plant alone (Read *et al.*,1970; Elzen *et al.*,1983; Herrebout and van der

Veer,1969), regardless of the presence or absence of hosts. Other parasitoids search preferentially among plants which emit cues of infestation by the host, such as odors released from plant tissues which have been damaged by the host (Monteith,1958; 1964; Bragg,1974; Nadel and Van Alphen, 1987). Damaged plant tissue may also be attractive to some parasitoids even when it is not caused by the host organism, probably because artificially damaged plants emit large amounts of chemical volatiles (Dicke and Sabelis, 1988; Dicke *et al.*, 1990).

A parasitoid initially and fundamentally seeks a certain environment, irrespective of the presence of hosts. Laing (1937) reported that when some parasitoids are ready to oviposit, they do not immediately look for the host itself, but first search for a special kind of situation. However, this is not in agreement with the view expressed by Edwards (1954) and Wylie (1958).

In species with a preoviposition period, the attraction to a particular habitat is associated with the ovarian development, as has been shown by a study carried out by Nishida (1956) who found that *Opius fletcheri* (Silv.) (Hymenoptera: Braconidae), was attracted to a medium irrespective of the presence of the larvae of its host, the melon fly, but because there was a pre-oviposition period of three days, only those female *Opius* that were four to five

days old responded to the attraction. The phenomenon of insect parasitoids being more strongly attracted by the food plant of the host than by the host itself has been discussed by several authors (Picard and Rabaud 1914; Cushman 1926, Salt 1935; Laing 1937; Monteith 1958)

2.2.2. Host finding

According to Huffaker (1971), the ability of a parasitoid to reduce the size of its host population and maintain it below an economic injury level depends, to a large extent, on the searching ability of the female parasitoid. Ullyett (1953) noted that a parasitoid tends to search in the parts of its environment most likely to contain its host and that is caused by a combination of pre-adaptation to habitats and a specific attraction exerted by the portion of the environment concerned.

Long-range sensorial mechanisms (visual and/or olfactory) bring parasitoids into close contact with a host. Once in the locality of the host, short-range tactile and olfactory sensorial inputs arrest further movement, causing the parasitoid to remain in the vicinity. Tarsal and antennal chemoreceptors of the parasitoid play a major role in prey finding (Read *et al.*,1970). The chemical cues involved in the host habitat and host finding phases may be derived from the host plant, the host, or a combination of

food and host factors. These cues elicit a series of responses which restrict the searching process until the host is located (Lewis *et al*, 1976; Vinson, 1976).

Work by many authors (Thorpe and Caudle, 1938; Richards, 1940; Monteith, 1955; Nishida 1956; Read *et al.*, 1970) showed that odor from the host's food plant or food medium may not be the only cue employed by parasitoids in finding their hosts, but it may be the most important one in some.

2.2.3. Host acceptance

This step is truly host selection and clearly a matter of innate behavior of the parasitic species. It encompasses the category designated by Salt (1935) as the physiological selection of host. The marked change in behavior which characterized this step can be seen in a description by Edwards (1954) of the activities of a female *Nasonia vitripennis* (Walk.) (Hymenoptera: Pteromalidae) when placed in a petri-dish with puparia of *Musca domestica* L.(Diptera: Muscidae). He found that initially there was an aimless wandering, and a fly puparium had no marked attraction until it is within 2 to 3 mm. Edwards (1954) made a general analysis of this behavior pattern and showed that although the female might follow alternative paths at some points, there were other parts where the behavior was

invariable.

Motion of the host has been reported as a necessary stimulus for oviposition in some parasitoids (Doutt,1959). Lathrop and Newton (1933) found that the stimulus to oviposition in *Opius mellius* (Gah.),a parasitoid of the blueberry maggot, is the vibration produced by the movements of the host larvae within the plant tissue. Bryden and Bishop (1945) reported the same phenomenon in a study of *Perilitus coccinellae* (Schrank).

Obviously, host movement is not always a stimulus for attack since many hosts are sessile, and the criteria for accepting a host in such cases include host odor,size location, and shape (Salt, 1934; Edwards,1954). A report of such criteria by Edwards (1954), in his studies of *Nasonia vitripennis* showed that the host's size, shape and physiological condition, were requisites for attack.

Different chemicals (also volatile and non-volatile surface chemicals) may evoke behavioral and physiological responses in parasitoids, mainly females. Such responses in female parasitoids are exhibited through the quest to oviposit. The adult Ceccidomyid fly, *Aphidoletes aphidimyza* responds to tryptophan, a compound found in the honeydew of aphids and this stimulates oviposition (Fortmann, 1985). Lewis *et al.*,(1975) demonstrated that the scales of adult

Heliothis zea (Boddie) contain kairomones that stimulate the feeding of the larval *Chrysopa carnea* on eggs of *H. zea*. There is the assumption that the search stimulant has a primer effect that is necessary before a parasitoid becomes responsive to the acceptance component since neither the search stimulant nor the efficiency in the field would orient females towards plants or plant parts on which stem-borers are present. However, care must be exercised in extrapolating laboratory results to field conditions, as positive responses in an olfactometer do not imply longer-range attraction (Kennedy, 1965).

2.2.4. Host Suitability

Having found the potential host in its habitat and selected it for attack, the host-parasitoid relationship may not succeed if the potential host individual is immune or otherwise, unsuiTable (Muldrew, 1953).

According to Bess (1939), the oviposition by a parasitoid is not necessarily an index to host suitability. A study by Muldrew (1953) showed that in larch sawfly, *Pristiphora erichsonii* (Htg.) the embryonic development of the parasitoid *Mesoleius tenthredinis* (Morley.) was inhibited. It should also be mentioned that in some cases an otherwise normal host can be rendered unsuiTable by the host plant on which it grows (Smith, 1957; Flanders, 1963). An

outline of the factors which may cause a host to be unsuiTable is given by Salt (1938).

The nutritional value of a host and the absence of toxic compounds finally determine the adequacy of the food to sustain the various physiological processes related to growth and development of the larvae and the longevity and fecundity of the adult parasitoids. There is little sensorial involvement during this phase, with which host acceptance is of key importance to the mechanisms of dynamics of the parasitoid's population. The predatory flower bugs of the genus *Anthocoris* are disturbed in their larval development and survival when fed on the pea aphid *Aphis faba* (Scopoli) (Dwumfour, 1987; Ruth and Dwumfour, 1989). In most cases, the host finding activities of entomophagous insects begin with the selection of a suiTable habitat (Laing, 1937; and Doutt, 1959). The female parasitoid perceives an environment in which its hosts occur either by a chemical, or a visual stimulus.

Olfactometers have been used to investigate qualitative and quantitative aspects of insect response to odors. Most consist of wind tunnels in which the insect is exposed to odor-treated air-screams, while some systems rely on diffusion gradients of particular odors in a given environment. They have been used with Orthoptera (Anderson and Fisher, 1960; Mustaparta, 1975), Diptera (Kasoyannos *et*

al, 1980, Nettles, 1980), Hymenoptera (Ferreira *et al*; 1979; Brewer, 1983; Vet *et al*; 1983), Lepidopteran adults (Guerra, 1968; Kasoyannos *et al* 1980), and Lepidopterous larvae (Khatter and Saxena, 1978; Sutherland, 1972).

Olfaction is an important mechanism involved in host-habitat location and host location by insect parasitoids (Vinson, 1981; Weseloh, 1981). Olfactometer studies have shown that parasitoids can be attracted by odors produced by the food plant or their host, thus, partly explaining the choice of a particular habitat by a searching parasitoid (Read *et al*; 1970; Schuster and Starks, 1974; Powel and Zhang, 1983).

Plants produce protective chemicals (volatile and non-volatile) in tissues even in the absence of herbivore attack or synthesize these only when phytophage damage is experienced. Plant body odors may affect an impact on the plant-herbivore-natural enemy interaction, attracting or "reruiting" and "sustaining" members of the third trophic level. Many parasitoids locate their host via kairomones associated with frass or body scales or host mandibular and labial secretions (such as salivary enzymes). Infochemicals (Dicke and Sabelis, 1988) inducing attraction may be emitted above by the herbivore or the odor may be produced when compounds by the host (or prey) react with plant chemicals after host (or prey) damage.

Odor from the host frass may not be the only cue employed by parasitoids in finding their hosts, but it may be the most important one for some (Thorpe and Caudle, 1938; Richards, 1940; Monteith, 1955; Nishida, 1956; Read *et al*; 1970). For such parasitoids, habitat odor becomes a major component in host specificity.

A study by Fortmann (1985) shows that the physiology of finding suiTable hosts and responding to them appropriately can be as varied and intricate as the insects themselves. A parasitoid may rely on physical and/or chemical stimuli (short and long range chemoreception) to locate its host. But also, Deithier (1947) remarks that "we recognize the fact that no one attractant alone performs the service of guiding an organism to it's proper habitat, or mate or food. The desired end is achieved by a complex array of stimuli working in harmony."

Tests with olfactometer provide much stronger evidence that parasitic insects are attracted from a distance and olfactometers have been used to demonstrate that volatile chemicals from the host's food plant or from the habitat of the host are attractive to tachinids (Montieth, 1964) and to hymenopteran parasitoids (Arthur, 1981). Hoskins and Craig (1934) demonstrated that five criteria were important in the design of successful insect olfactometer viz, 1. the

environment should be nearly normal, 2. a large fraction of the insects should respond, 3. the results should be attribuTable only to the specific chemical stimulus ; 4. the results should be obtainable within a short time; 5. the results should be obtainable with either a homogenous or heterogeneous population. Cole (1932) and Stafford *et al;* (1984) used a T-tube arrangement to give beetles a choice of 2 air currents. Lethman (1932) and Kleiforth *et al;* (1964) used an arrangement which passed air through holes in the floor of a chamber to carry the attracting odors upwards. Lilly and Mc Ginnis (1965) used a rectangular olfactometer with a current of air passing through it. Test chemicals were spotted on filter paper lining the floor of the chamber.

Vet *et al;* (1983) and Bouchad and Cloutier (1984) used an olfactometer which consisted of a four arm star-shaped test chamber, each arm being connected to a series of two 50 ml glass flasks. Kudon and Berisford (1980) used an "H" olfactometer designed to be used specifically for bark beetle parasitoid-attractant and host-preference studies.

2.3. Effect of temperature and relative humidity levels on the biology of parasitoids

The numerical relationship between a host and its associated parasitoids is influenced by the rate of turnover

of successive parasitoid generations relative to those of the host. In insects and other poikilothermic animals, the speed of the development varies with the temperature (Andrewartha and Birch 1954). Considerable differences exist in the temperature requirements between populations of any one species from different geographic areas (Campbell *et al.* 1974). Anderson and Paschke (1970) showed that comparative biological data on five European cultures of *Anaphes flavipes* (Forster.) (Hymenoptera.: Mymaridae), an egg parasitoid of *Oulema melanopus* (L.) (Coleoptera.: Chrysomalidae), indicated differences in developmental rates as those individuals representing cultures from the southern most latitudes develop most slowly at 21°C, while those from the northernmost latitudes develop fastest at this temperature.

Killian and Nielson (1971) and Siddiqui *et al.* (1973) have reported on the speed of development of different pea aphid biotypes, *Acrthosiphon pisum* (Harris.) (Homoptera.: Aphididae), whereas Wiackowski (1962) examined the development of a Californian strain of the pea aphid parasitoid *Aphidius smithi* (Hymenoptera.: Aphididae) under various temperature and relative humidity regimes. Many workers have reported the effect of temperature and relative humidities on various organisms. The majority of these papers deals with the rate of development of either the whole organism or the organism in its separate developmental

stages (Wiggleseworth 1950; Howe, 1967).

Temperature and relative humidity regimes have been accepted as major or limiting factors to the geographic range and distribution of insects (Uvarov, 1931; and Messenger, 1959). These factors directly or indirectly govern the abundance of insect species in their occupied habitats (Uvarov, 1931; Birch, 1948; 1957; Klomp, 1962; and Huffakar and Messenger, 1964).

Temperature and relative humidities have a simple effect on many chemical reactions. The rate of development of an insect species may change with climatic trends caused by latitude or altitude (Varley *et.al*, 1973). Bursell (1974) has summarized the extensive literature on the relationship between temperature and insect development. The developmental physiology of the local climates. For example, more rapid development at a given temperature has been observed in Northern Hemisphere populations of lepidopterous species (Danileviskii, 1965), aphids (Campbell *et al*. 1974), mites (Beck 1968).

Additionally, in both aphids (Campbell *et al*.1974), and lacewings (Tauber and Tauber, 1976) the threshold for development is lower in Northern than in Southern Hemisphere populations of the same species. According to Wellington and Trimble (1984) the more rapid rate of development and lower

development threshold are adaptations to a cooler climate which serve to synchronize the growth , development and reproduction of insects with local phenological events. Campbell *et al*, (1974), reported that the temperature requirements of several parasitoids of aphids were narrower than those of their hosts. Rearing the host at a high or low temperature may result in the death of the parasitoid but not the host (Kaya and Tanada, 1969; Williams and Floyd, 1971).

A direct demonstration that temperature and humidity affect reproductive rate of an insect is provided by the work of Buxton and Lewis (1934) on the tsetse-fly *Glossina tachinoides* in West Africa. They found that temperature and humidity in the field were often far from the optimum for the species and indeed approached close to the lethal limits; In one series of one hour's exposure and for one day's exposure. In another experiment at a constant temperature of 30°C and at different relative humidity levels of between 11% and 88% R.H, the flies were kept in small jars and given a chance to feed once a day on human blood.

Results from this study showed that in favorable conditions the female flies, which are viviparous, gave birth to a fully grown lava every few days.

According to Campbell and Vargas-Piqueras (1985). The form of reproduction in *Tetrastichas cordubenis* is influenced by temperature and that this species, though uniparental at 20°C, can produce both sexes and sexual mosaics if the rearing temperature is increased to 29°C. Kfir (1982) found in his studies that laboratory colonies of *T. brasiliensis* (Ashmead) gave rise from time to time a small proportion (less than 40 %) of males, the overcrowding of the cultures apparently being the cause of the phenomenon. Bowen and Stern (1966) demonstrated that uniparental strain of *Tetrastichas semifumatum* produced males and sexual Mosaics when the cultures were exposed to heat (78-90°f), but found that the emerged males were sterile. A study by Jardak *et.al* (1979) showed the existence of males and enter sexes in a thelytokous species, *Tetrastichas oleae*, pointing out that as temperature increased the percentage of male progeny increased.

In a study on Knapweed gall-fly, Varley (1947) found a very different relationship between weather condition and the reproductive activities of the insect. At constant temperature and humidity, optimum conditions for egg laying occurred between a temperature of 30-35°C and a relative humidity of 50-70 %. Through the temperature range of 15-30°C, the reproductive potential of *Harogenes chrysostictos* was highest when individuals were reared at 25°C (Fisher,1959) . Baker and Jones (1934) reported that

Exeristes roborator (F.) (Hymenoptera: Ichneumonidae) was found to be more fecund when reared from over-wintering host, and Flanders (1978) suggested that this effect was due to increased nutrition obtained by developing larvae. Females derived from slowly developing over-wintering larvae retain food in their midgut longer because the midgut-hindgut connection is delayed, thus allowing time for absorption of more nutrients (Flanders,1978).

In some cases temperature affects sex-ratio. Wilson and Woolcock (1960) showed that 29.5°C was the critical, sex-determining temperature for *Ooencyrtus submetalicus*. Lower temperatures produced females, but 29.5°C and higher produced males. A uniparental strain of *Trichogramma semifumatum*, very rarely produced males below 25.5°C., but at that temperature and above, males were produced with 30 % gynandromorphs (Bowen and stern,1966).

2.4. Influence of age on the parasitoid's biology

The association that exists between a parasitoid and its host is complex, and the prime prerequisites for its existence are synchronic between host and parasitoids in time and space (Schoonhoven, 1962; Danileviskii, 1965; Saunders, 1962), acceptance of the host (Salt, 1935;) and nutritional and immunological suitability (Gilmore, 1938;

Lange and Bronskill, 1964; Price, 1970).

Host's age is one of the most important factors influencing the ethological and physiological aspects of parasitoid-host relations (Reznik and Umarova, 1990). Detailed investigations of reactions of entomophagous insects of various host ages have been summarized (Vinson, 1976; 1985; Vinson and Iwantsh,1980). The majority of these studies have been carried out with entomophagous insects used in biological control of pests, often with *Trichogramma*. Usually, the number of parasitized hosts, percentage of parasitoid larvae which complete their development, and fecundity of emerging females decrease with the development of host's embryo (Reznik and Umarova, 1990).

In a number of studies the ethological and physiological components of the parasitoids reaction to host age were analyzed in more detail. In particular, some authors (Heihata *et al.*, 1976) revealed a behavioral reaction: the refusal to oviposit before or after inserting the ovipositor in the older hosts; other authors (Lewis and Redlinger, 1969; Marston and Ertle, 1969) concluded that a physiological mechanism is responsible i.e. the decrease of availability or a combination of both components. However, under natural conditions females come across hosts of various ages.

Therefore, the problem of host selectivity is not only of theoretical, but also of practical value. Salt (1941) discussed many effect that the host can have upon the parasitoids that attack them, but the hosts age variation remained without mention. Several workers have demonstrated the effect of different host species on the fecundity and longevity of a parasitoid (Ohghushi,1959; Smith and Pimental,1969), sex-ratio and size (Salt,1941).

Acceptability and suitability of a host may vary according to host age (Puttler and Van den Bosch,1959; Puttler,1961, 1967; Guitierrez,1970; Gerling and Bar,1971; Schmidt,1974).

Longitudinal studies that can compare the breeding success of the same individual at different ages have an important advantage over the usual practice of survival of comparing the reproductive performance of survival of separate samples of animals observed (or collected) at different ages; since individual differences in reproductive rate are often correlated with longevity (Bryant,1979; Bell,1980; Smith,1981; Clutton-Brock,1983).

Lewis and redlinger (1969), found that host eggs of various ages were accepTable to *Trichogramma*, although suitability was reduced in eggs in which the head capsule of the host was evident. Various workers (Lewis,1970; Hays and

Vinson,1971; Smilowitz,1974) have shown that as a host reaches the pharate stage, it becomes unaccepTable. Such changes in acceptance have been related to hormones or to alteration in the factors necessary for acceptance (Smilowitz, 1974). Thus, the importance of age in most studies must remain in question until the chemicals involved in host age selection have been determined for the various ages and stages not attacked.

Changes in the frequency of superior or inferior phenotypes in samples of insects at successive age may generate or obscure relationships between breeding success may be caused by progressive elimination of inferior phenotypes from the population. Similarly, individuals with superior reproductive success may appear to decline with age in situations where age has no affect on reproduction .

Conversely, where individual with superior phenotypes show high reproductive performance and live longer than average, cross-sectional samples may fail to reveal the effects of increasing age. Where longitudinal date are available, it is possible to avoid problems of this kind by comparing the reproductive success of the same individuals at different ages.

2.5. Effect of Diet on adult parasitoid longevity and fecundity

Activities which are particularly well known in terms of the influence of the nutritive quality of food are egg production and other development of immature stages to adulthood (Folsom and Wardle,1934), longevity, and size may be determined to a large extent by the quality of available food.

As a group, insects are essentially omnivorous. As individual species, however, they exhibit much variation, some being extremely selective and perhaps feeding on only one or few kinds of food (including host plants and prey/host) and others taking advantage of many kinds (Romoser,1973). Whatever the particular habits of a given species may be abundance and quality of food may play an important role in its survival, longevity, distribution, reproduction, speed of development, and so on.

According to reports by Hagen (1953), the female parasitoids that are synovigenic require a source of protein for the continuous production of eggs throughout their effective adult life. The protein needs in some species may be supplied by feeding on honeydew or plant nectaries, both of which have been shown to contain free amino acids. A work by Hagen (1953) has clearly indicated the essential role of

honeydew in the longevity and fecundity of insect species. In a number of species, it is quite evident that the location of the food sources of the adults has a strong influence on the distribution and effectiveness of these parasitoids (Allen and Smith, 1958), studying *Apanteles medicaginis* (Mues), found that certain areas contain many sources of food for adult *Apanteles* and thus favour increased longevity and fecundity. They found that in these areas there was genetically a higher degree of parasitism of the lepidopterous host *Colias philodice eurytheme* (Bdvl.), than in localities where there was not an abundant source of plant nectaries and aphid honeydews.

Townes (1958) emphasized the great importance of direct moisture source to species of Ichneumonidae, and notes that the great majority of species, and individuals occur only where and when rain or dew are generally available. Kugler (1955) reported that in the field, adults of hymenoterous parasitoids find a rich supply of different food that varies greatly in content, not only between sources but also within the same source. According to Leius (1960), adults are usually guided to the vicinity of their natural foods by the visual senses, and when an insect in flight enters an area of odor stimulation it will land if attracted but will continue flight if not. When attracted by odor the insect will taste the food and if it is accepTable, feeding will follow.

Insects vary greatly with respect to amounts of food needed, some like the meal worm, *Tenebrio molifor*, (L.) (Coleoptera: Tenebriodae) can survive and reproduce on essentially dry food. Others, for example, honey bees and muscid flies, require large amounts of water for survival and reproduction (Romoser, 1973).

According to Hagen *et al.*, (1984), insect growth, development and reproduction directly depend on the quantity and quality of food ingested. Moreover, they found that ingestion of food depends upon its being found and accepted. Richards (1953) reported that the quality of ingested food in some instances influence the outcome of development. The best example the author gave is the difference between worker and queen honey bees. The difference between these two castes depend entirely on the diet that each receives during its period of larval development, notwithstanding the fact that each caste is reared in a cell unique to that caste. It is known that many adult hymenopterous parasitoids feed on flowers, aphid honeydew, and other substances (Jackson, 1937; Thorpe and Caudle, 1938; Gyorfi, 1945).

Results reported by Flanders (1935) have shown that the host body fluid, or haemolymph, is an important food for many, but not all, female adults of hymenopterous

parasitoids. He found that males do not feed on this food and thus suggested that this type of feeding is essential for egg production. The manner by which the female parasitoids feed on the host body fluids is of considerable interest. Flanders (1935; 1951) reported that most hymenopterous parasitoids feed on the fluid which exuded from the oviposition wound. This habit has also been noted on other species by several workers (Fulton, 1933; Simmonds, 1956).

Mohyuddin (1970) reported that the *Pediobius furvus* adults live longer when provided with sucrose in solid or liquid form compared with those provided with nothing or only water. He reported that 90% of the females died in 8.75 - 9.75 days when provided with sucrose as compared to 3.75 - 4 days when provided with nothing or water. Gyorfi (1945) reported catching many species of Inchneumonids, branconids, Pteromalids, Eulophids, and Chalcids on honeydew, especially species that parasitize aphids, scale insects, syrphid and coccinellid larvae.

Because of the difficulty of collecting and storing natural food for the laboratory maintenance of hymenopterous parasitoids, entomologists have been forced to use semi-natural, or even artificial food that more or less resemble the natural food in content. Semi-natural foods, such as diluted or undiluted honey, sugar solutions, molasses, fruit

marmalade, soaked raisins and brewer's yeast, are well known sources of carbohydrates, proteins of vegeTable origin and vitamins (Gyorfi, 1945).

2.6. Effect of superparasitism on the biology of the parasitoids

Superparasitism as used in this study, refer to a super-abundance of individuals on a given host. This usage of the term, involving individuals of only one parasitoid species, was first recommended by Smith (1916) and was adapted by Salt (1934) and other investigators. Many factors may influence the levels of parasitism, some of these, independent of the host, primarily reflect environmental effects (e.g. adult nutrition and its effects on longevity and fecundity; overwintering mortality out side the host). Others affect population numbers from generation to generation (e.g. host and parasitoid density, which in turn may influence such factors as fertility). There are also the effects of parasitoid size, or number of parasitoids per host in the previous generation (Elsey and Rabb, 1970; Delobel, 1970; Adams and Watson, 1971; Danks, 1975).

Superparasitism was thought to be an error by the parasitoid that resulted in egg wastage (Van Lenteren, 1981). More recently, several workers (Charnov and Skinner, 1985; Mackaur,1990) have suggested that superparasitism can

be adoptive when hosts are rare and when the probability of a younger inhabitant surviving is greater than zero.

Most endophagous insect parasitoids require the entire host for their development. In case of solitary parasitoid species, only one parasitoid emerges from a super or multi-parasitized host (Fisher, 1971).

Although many mature female parasitoids have the ability to discriminate between parasitized and unparasitized hosts because of the marking of the host by the ovipositing female (Fisher, 1971; Beegle and Oatman, 1976; Van Lenteren, 1976; Vinson, 1976). Some parasitoids reportedly parasitized their own species (Mohyuddin, 1970; Griffths, 1961; Lewis and Snow, 1971; Varma and Bindra, 1973), or by other species Hokyo *et al*., 1966; Mclead, 1972).

Also, ovipositional restraint may break down in some situations (Chacko, 1969). Furthermore, oviposition and marking of aggressive host must occur rapidly, and the possibility exists that one or the other of these behaviors may not occur. The result is that oviposition may occur in some hosts with out marking and some hosts may be marked without oviposition (Sato, 1977). Thus, a degree of superparasitism of hosts may maximize host utilization particularly for those hosts capable of evasive or defensive

action (Vinson, 1972; Vinson and Guillot, 1972). Mohyuddin (1970) reported that *Pediobius furvus* oviposits in an already parasitized pupa and therefore had no discriminatory ability between parasitized and nonparasitized hosts.

It has been reported by Vinson and Srok (1979) that increasing superparasitism by a solitary species decreased the total number of hosts yielding parasitoids because all competitors in the superparasitized hosts often died, although as many as two hundred and twenty progeny of *P. furvus* could emerge from one *Chilo partellus* pupa. Earlier, Anderson and Paschke (1969) reported that eight progeny of *Anaphes flavipes* (Forster.) (Hymenoptera. : Mymaridae) could emerge from one *Oulema melanopus* (L.) (Coleoptera. : Chrysomalidae) egg but with increasing superparasitism no parasitoids were produced.

Supernumerary parasitoids may be eliminated in two primary ways : physical attack, where an early instar parasitoid uses its mandibles to attack or by toxin, anoxia, or nutritional deprivation (Fisher, 1971). Elimination of competitors by physical attack appears to be a common phenomenon in the mandibulate hymenoptera Fisher (1971) and Vinson (1972), and has been observed in the major families of parasitic hymenoptera: Ichneumonidae (Fiihrer and Kilincer, 1972; Vinson,1972; Schröder,1974), Braconidae

(Lawrence *et al.*, 1976; Schröder,1974; Vinson,1972), Eulophidae (Beaver,1966), Chalcididae (Dowden,1935), and Enartidae (Bartlett and Ball,1964).

Each of the several mechanisms that have been identified (or hypothesized in the literature) as being involved in the elimination of potential competitors appears to be specific and generally occurs early during the first-instar stage, whereas, physiological suppression is thought to occur either after the eclosion of the oldest embryo to the first instar, by a toxic secretion or late during larval development by starvation or asphyxiation (Makauer,1990). Vinson and Barras (1970) reported that the attack of competing *Camdiochiles nigriceps* in *Heliothis virescens* (Fabr) (Lepidoptera:Noctuidae) was similar to that described by Fisher (1971) in the manner that, the newly hatched larvae actively move about the host haemocoel; using their mandibles, they attack other parasitoid larvae that they may have encourted. The victim ceases to feed and is eventually encapsulated by the host's phagocytic blood cells while the vector resumes feeding and growth. A similar phenomenon involving physical attack exists in some parasitic Diptera. Mellini and Baronio (1971), reported that the first instar planidia of *Macquartia chalconota* used their buccal hook to injure competitors.

Developmental suppression of competing parasitoids my occur during embryonic development. this has been observed in Braconidae (Tremblay,1966; Walloff, 1967), ichneumonidae (Fisher,1961; Vinson,1972), Mymaridae (Jacson,1966), Eulophidae (Beaver,1966), Spalangidae (Gerling and Legner,1968), and Cynipidae (Guttierrez,1970). Although many examples are cited in the literature, the mechanism involved is unknown. Anoxid has been suggested as a mean of physiological suppression (Lewis 1960; Richards, 1940) and was supported by observations that the preimaginal development of the survivor was prolonged (simmonds,1943) and suppressed larvae recovered when they were transferred to un parasitized hosts (Simmonds,1943; Fisher,1961). Latter, Fisher (1963), provided evidence that low oxygen content of host haemolyph was the cause of physiological suppression.

Selection starvation has also been suggested as a means of physiological suppression for several species of tachinids (Pschorn-Walcher,1971) and *Trichogramma embryophagum* (Harting) (Hymenoptera:Trichogrammatidae) (Klomp and Terrink,1978). Chacko (1964, 1969) attributed changes in fecundity and longevity of *T. minutum*, when the host egg was superparasitized, to larval nutritional deficiency and a change in sex-ratio to more rapid food absorption by the male, which left the female little food. Wylie (1965) noted that superparasitism reduced survival,

size, and sex-ratio of *Nasonia vitripennes* and he suggested the effect were due to food shortage. However, changes in the physiology of the host brought about venoms or virus-like particles injected by the ovipositing female (Fisher and Ganesalingam,1970; Guillot and Vinson,1972; Dhalman and Vinson,1975; Sroka and Vinson,1978) may result in an environment unsuiTable for the younger competing parasitoids. in fact, Vinson (1972) provided evidence that *Campoletis sonorensis* competed by physical attack during the first instar and by physiological suppression in the later instars.

2.7. Intrinsic rate of natural increase of parasitoids

The intrinsic rate of increase is a basic parameter which an ecologist may wish to establish for an insect population. Messenger (1964) defined it as an index of rate of population growth in a particular environment and potential effectiveness of a natural enemy. But earlier, Chapman (1931) referred to it as biotic potential; and although he does state in one place that biotic potential should in some way combine fecundity rate, sex ratio and survival rate, he never precisely defined this expression. Work by Stanley (1946) discussed a some what similar concept which he called the relative suitability of different environments, but it does not give the actual rate of increase of the insect under these different conditions.

Birch (1945) attempted to provide this as an index combining the total number of eggs laid, the survival rate of immature stages, the rate of development and the sex ratio.

The first determination of the intrinsic rate of increase of an animal other than man was made by Leslie and Ranson (1940). They calculated the true rate of natural increase, of the vole, *Microtus agrestis* , from age specific rates of fecundity and mortality determined under laboratory conditions. Lotka (1945) has dropped the use of true rate of natural increase for the more precise intrinsic rate of natural increase.

A different analysis of the problem was carried out by Lewontin (1965) who considered the effect on r of changes in the age of first, maximum, and last reproduction. He concluded that a 10 % increase in developmental time generally had the same effect on r as a 100 % increase in net fecundity. However, Mac Arthur and Wilson (1967) later showed Lewontin's results were not general because they could not be extrapolated to low net fecundities. Later Meats (1971) had extended Lewontin's approach by partitioning net fecundity into mortality and natality parameters. Green and Painter (1975) took an analytical approach to this problem and showed that the effect on r

changes in developmental time increased as net fecundity increased, with results similar to those obtained independently by Lewontin (1965) and by Meats (1971).

CHAPTER THREE

3.0. Materials and Methods

3.1. Location of the study.

The study was carried out at the Mbita Point Field Station (MPFS) of the International Centre of Insect Physiology and Ecology (ICIPE) on the shores of lake Victoria, Kenya.

The field station is located at about 500 km South of Nairobi (Latitude $0^{\circ}25'- 0^{\circ}28'$ south and 34° 11'- 34° 17' east at an altitude of 1170m. above sea level). Mbita is a hot dry area. Temperatures range from 21° to 30°C in the long rainy season and may rise to 35°C during the un reliable short rainy season with a mean annual temperature of 22°C. This is followed by the dry and fairly cold month of July. The short rains begin in October and end in December.

Records on the annual average rainfall show inconsistencies varying from year to year. The mean annual rainfall varies from 760 to 1015mm (30" to 40") (Anon., 1970). Due to the un reliability of rainfall levels, experimental plots were irrigated by overhead sprinkelers to supplement the scanty rain.

Both Field and Laboratory studies were conducted during the years of 1990-1991. All experiments in the laboratory were carried out at a temperature of 25-27°C under relative humidity level of 60-70% unless otherwise mentioned.

3.2. The Insects:

Three species of insects, that is *Chilo partellus* (Swinhoe.), *Busseola fusca* (Fuller.) and *Pediobius furvus* (Gah.) a gregarious endoparasitoid (Plate 1) were used during this studies. *P. furvus* was used as the model test in most aspects of the work. The insects were supplied by the Insect and Animal Breeding Unit (IABU) of Mbita Point Field Station. The insects were reared following a standard method developed by Ochieng *et al.*, (1985).

3.3. Seasonal survey for the incidence of P.furvus (Gah.) in Maize fields in different Agroecological localities in Kenya.

The survey was carried out for three seasons during the maize harvest time to determine the parasitoid's distribution and incidence. Fields in Busia, Kakamega, Kisumu, Mbita, Mombasa and Siaya (10 fields / location) were chosen at random for the survey. The four corners and the middle of the fields were sampled. One hundred plants were examined per field by dissecting the stalks lengthwise and making counts of *C. partellus* and *B. fusca* pupae. The pupae

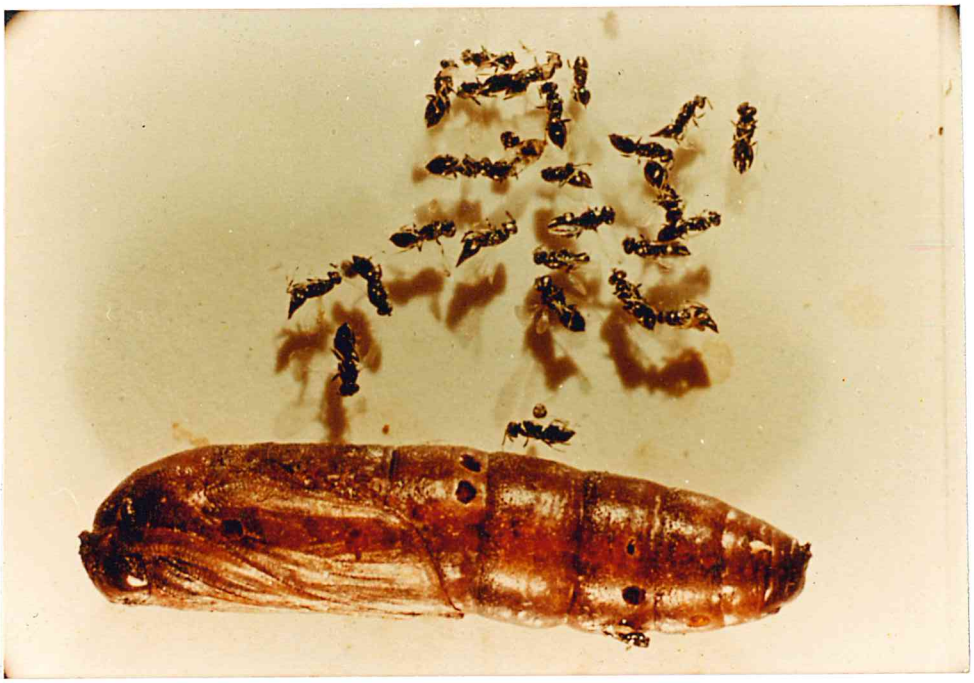

Plate No. 1

P. furvus: a gregarious endoparasitoid of graminaceus stem-bores.

were maintained in the laboratory and the following data were recorded.

Seasonal parasitism per location. The number and species of pupae collected per location. The number of pupae parasitized by *P. furvus*, progeny production per host pupa and their sex ratio.

Distribution and incidence of *P. furvus* in the different agroecological locations in Kenya.

Pupae from upper, middle and lower internodes were sorted out and reared separately to find out whether the female parasitoid had any preference for any part of the host plant.

3.4. P. furvus: parasitization of C. partellus pupae and its attraction to two cultivars of maize in the field.

The experiment was conducted to study the field parasitization by *P. furvus* of *C. partellus* pupae artificially infested on two maize cultivars (ICZ-2 and INB-A). The maize cultivars were planted in a Randomized complete Block Design (RCBD) where each plot was covered with a fine mosquito net (Plate 2). Plot spacing was 70cm and 15 cm between and within rows respectively, each treatment involved four replicates. In all there were 4 plots, with 7 plants per row and four rows per plot. Three

Plate No. 2

Artificial infestation demostrated in a plot enclosed in a mosquito type netting to exclude non experimental insects.

seeds were planted in each hole and later thinned to one seedling per hole one week after plant emergence.

Compound DAP fertilizer was applied at the rate of 40 kg / ha at the time of sowing. Three weeks after plant emergence (W.A.P.E.) each maize plant was artificially infested with twenty first instar *C. partellus* larvae using a fine camel hair brush (Plate 2) During the long rainy season of 1990 parasitoids from a field collected host pupae were used for the release, while during the short rainy season of 1990 and the following long rainy season of 1991, parasitoids from a laboratory reared host pupae on artificial diet were used.

Four to five weeks after plant infestation, when pupation commenced, a cohort of 100 one-day- old gravid females and 20 males of *P. furvus* was released between 17.00 and 17:30 hrs. in each field cage. Another release of 100 females and 20 males per field cage followed five days after the first release.

Ten days after the first release, all the plants in each plot were dissected and the pupae from each plant collected and kept singly in labelled 4-ml vials until the emergence of the moths or parasitoids. The internode (upper, middle or lower) in which the pupae were found was

noted to see if the parasitoid has any preference for any part of the host plant.

The seasonal percent parasitism on each cultivar under the netted experiments, the number of pupae recovered, progeny production per host pupa and their sex ratio were also recorded. The experiment was repeated during three seasons between March, 1990 and July, 1991.

3.5. Investigation on the nature of the trophic interactions between the plant, host insect and the parasitoid.

The experiment was conducted in order to investigate the interaction between the host, the host-plant and the parasitoid, with respect to *P. furvus* response to chemical cues emanating from host habitat and / or host itself.

The experiment was carried out in an air-conditioned room, using a still-air cylindrical glass olfactometer supplied by Prof. Saxena, Programme leader, Crop Pest Research Programme, ICIPE, MPFS (Plate 3). The cylindrical glass olfactometer measuring 20 x 20 x 20 cm was placed 3cm above an overhead projector. Light from the projector was passed through the glass box and through a prism where the image was reflected from a mirror to the surface of a Table.

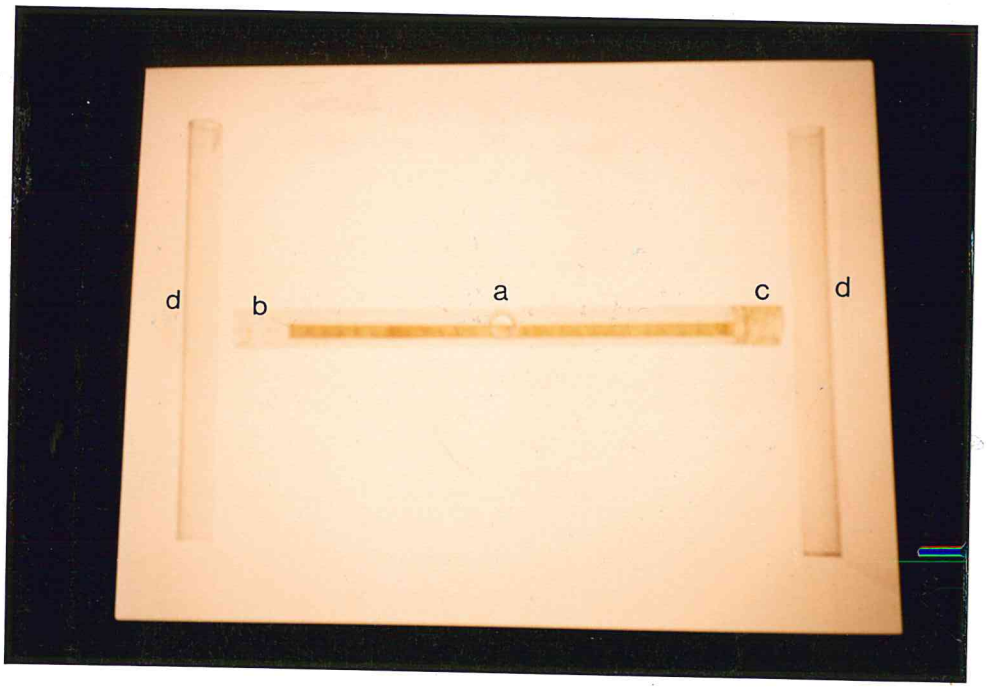

Plate No. 3

Olfactory instrument used for olfaction study.

a. hole (1cm) for introducing the parasitoid.

b. Cylindrical glass olfactometer with graph paper bottom.

c. Opening for introduction of test material.

d. tube containing test material.

The apparatus used was two cylindrical glass tubes of 20 x 1.8 cm and a third ruled cylindrical glass tube of 20 cm x 2 cm that had an outflow port of 2 cm x 1.2 cm (Plate 3).

From the image reproduced on the Table, a tracing was made of the parasitoid's movements without disturbing the insect. A voltage regulator was used to lessen the intensity of the projected light so as not to disturb the parasitoid being tested (Plate 3).

The presence of an observer near the apparatus did not seem to disturb the insects. The system relays on diffusion gradients of particular odors in a given environment. Parasitoids to be tested were introduced individually in the chamber through the out flow port on the floor, and allowed a maximum of 30 min to make a final choice between the two air fields.

As in previous experiments, in order to avoid any possible error due to the incidence of any slight bias in the apparatus, the position of the pupae and frasses to be tested was alternated from one arm to the other at frequent intervals during each set of experiments. Thus in one half of each series the main stimulus would be on the right links and in the other half on the left. In this way any errors due to imperfection of the apparatus cancelled out. Between

which was applied on the inner wall of the 4-ml vial lids.

To study the effect of temperature and relative humidity on the parasitoid development, four replications, each with 10 pairs of parasitoids and 10 host pupae were maintained. The relative humidities were maintained using concentrated sulphuric acid and distilled water (Solomon, 1951), in different desiccators placed in an incubator (Plate 4) at different temperature regimes.

The effect of temperature and relative humidity on parasitoid oviposition for 24 hours was studied by keeping the parasitoids at 15, 20, 25, 30 and 35 degrees centigrades under different relative humidities of 30, 40, 50, 60, 70 and 80% . Parasitoid development was also studied at the above temperature levels and relative humidities after allowing oviposition to occur at 25-27°C and 60-70% R.H.

Only parasitized host pupae based on colour changes in four to five days, were considered for the analysis (Plate 4). Exposed pupae which failed to produce parasitoids or moths were dissected to determine parasitoid mortality, if any.

Plate No. 4

Dessicators to maintain relative humidity levels under fixed temperature in the laboratory.

3.7. Influence of age on the parasitoid's biology.

3.7.1 Influence of host age on parasitism

In order to determine the influence of age of host (*C. partellus* and *B. fusca*) on the parasitoid's developmental period, progeny production, and sex-ratio, 50 synchronously developing pupae of *C. partellus* pupae. were randomly selected and placed separately in an oviposition container. Ten pupae were used for each replication.

Similarly, 20 *B. fusca* pupae were also used for the experiment. The hosts used were zero to eight-day-old *B. fusca* and zero to five-day-old for *C. partellus*, and 24hr for female parasitoids. The exposed host pupae and the gravid female parasitoids used were changed daily by keeping the female parasitoid age one-day old. The exposure time was 24hrs.

Parasitism was considered successful if the developing parasitoids reached pupal stage and the ovipositional rate was based on the number of eggs deposited per host in less than 24 hours. before they were dissected and the remaining pupae taken out and kept separately until the moth or parasitoid emerged.

3.8.2. Influence of P. furvus female age on parasitism

Sixty pairs of *P. furvus* upon eclusion were placed in vials (4-ml) each pair in a vial and provided with 20 % sucrose solutions. The sixty pairs were divided in to six treatments, each treatment consisting of ten pairs. Ten host pupae (1-2-day-old) were introduced into the first treatment upon eclosion, the second after 24 hrs, and continued until the sixth treatment on fifth day . A new male was introduced if the first one died. Exposed pupae which failed to produce parasitiods or moths were dissected to determine parasitoid mortality.

The extent of successful parasitism was determined from the proportions of parasitoid emergence to host adults recovered. Dead host pupae and parasitoids failing to complete development were not included in the computations.

3.7.3. Influence of withholding oviposition on the fecundity of the parasitoid:

One hundred pairs of *P. furvus* upon eclusion were kept in a cage and fed with 20% sucrose solution. Dissections of ten females were made daily to investigate the number of eggs in their ovaries.

3.8. Effect of Diet on P. furvus adult longevity and fecundity

Studies were conducted to determine the effect of various concentrations of sucrose and honey (5, 10, 20, 30, and 40%), distilled water and no food on longevity, number of eggs per female parasitoid, and the ovipositional period of *P. furvus*. Parasitized *C. partellus* pupae were obtained from a culture in the laboratory, and upon eclosion, twelve pairs of parasitoids were selected for each experiment, and each pair introduced into a 4-ml vial. Each experiment was replicated five times. The parasitoids were fed by applying the appropriate diet on the inner wall of the vials using a fine camel hair brush.

The following observations were taken during the experimental period;

(a) Number of days males and females survived.

(b) The effect on fecundity by dissecting the adult and counting the number of eggs in the ovaries.

(c) The effect of the diet on the female's ovipositional period.

The diet was changed daily until the death of the parasitoids. In the control, test parasitoids were given no food or distilled water. Two-day-old host pupae (*C. partellus*) were used in each experiment.

3.9. Effect of Superparasitism on the biology of the parasitoid

Superparasitism as used in this study, refers to a superabundance of individuals on a given host. Female parasitoids for the experiment were cultured in the laboratory with periodic infusion of field-collected materials and were confined with males and fed with 20% sucrose for the entire duration of the experiment. Effects of the density of immature *P. furvus* in an individual host on parasitoid survival and on the number of parasitized host producing mature parasitoids were investigated as follows:

1. Low parasitoid egg densities were obtained by exposing each *Chilo* pupa (host) to one female parasitoid for only 12 hours. A total of 48 host pupae in four replications were used for the experiment. Five hosts from each replication were then dissected to determine the number of eggs laid and the rest reared until the parasitoid had matured and their survival could be calculated.

2. Higher parasitoid egg densities in hosts were obtained by using two arbitrary host densities(1 and 2)and three arbitrary parasitoid densities(1, 2, and 5) under two different exposure times (12 and 24 hours). In each density combination there were 12 host pupae replicated five times in a completely random design and each host pupa was kept separately in a specimen tube .

Five hosts from each density combination were dissected and the remainder reared except 1:2 host-parasitoid combination experiment for the 24hr.exposure. Three host pupae exposed singly to five female parasitoids for 24hrs, were dissected from one to six days later, and the number of living and dead parasitoids in each when dissected was recorded.

Dissections were carried out to investigate:

(a) If larvae hatched from all of the eggs of *P. furvus* at all egg population densities.

(b) Method by which supernumeraries were eliminated (Combat, starvation, suffocation, etc.).

The developmental stage at which supernumerary parasitoids were eliminated, and the method of elimination, were determined as follows;

Effects of superparasitism on size, rate of development, progeny production, sex-ratio, percentage parasitism and their ability to emerge were determined.

C. partellus pupae confined singly for either 12 or 24hrs, with the three parasitoid densities were reared, parasitoid emergence recorded, and the number of unemerged parasitoids (adults or larvae) determined by dissection of host pupae. The remainder of the hosts were dissected 16 days after parasitism, when most of the parasitoids were in pupal stage, and the number of mature parasitoids counted, sexed and their size measured . Those parasitized pupae were only considered for the analysis and were separated from the unparasitized hosts by the colour changes. The host pupa turns blackish four to five days after parasitization depending upon the age of the host at exposure time (Plate 5). Since the development of 120 or 140 specimens of *P. furvus* on a single full grown pupa of *C. partellus* is normal (Mohyuddin,1968) the development of more than 140 individuals on a host is considered to be superparasitism.

3.10. Intrinsic rate of natural increase of P. furvus on C. partellus pupae

Single-generation life Table of *P. furvus* based on the females only, were constructed under laboratory conditions.

Intrinsic rate of natural increase can be estimated from the equation: [e-rm x. lx.mx=1] where x is the pivotal age in days. Finite rate of increase is the number of female

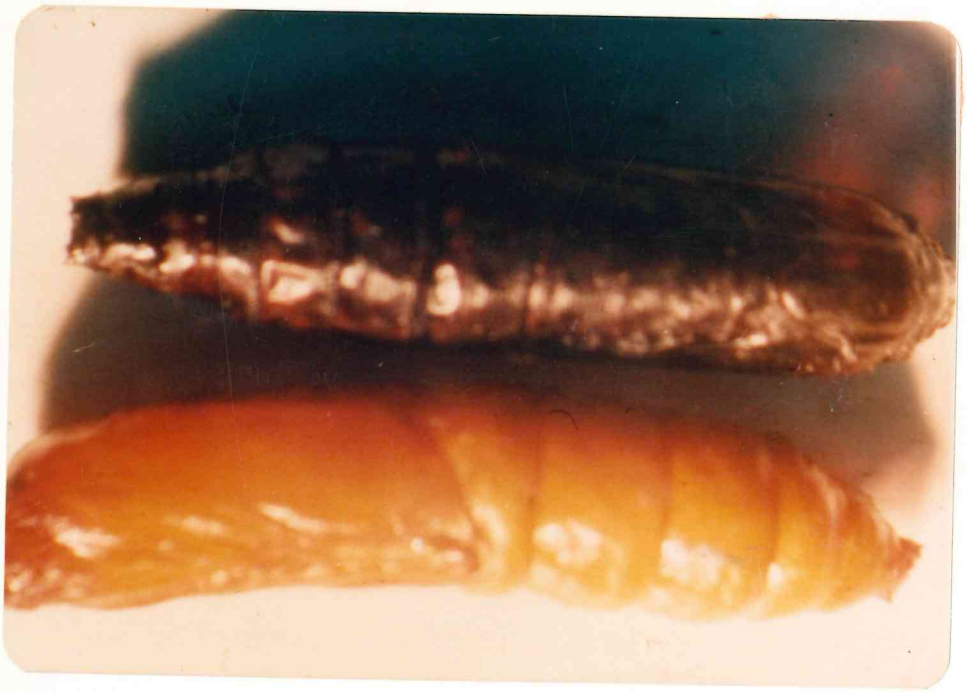

Plate No. 5

Colour differences between parasitized (black) and non-parasitized (yellow) host pupae of *C. partellus*.

progeny per female per day and can be estimated from the natural antilogarithm of rm. Net generation time was estimated from the quotient of the logarithm of Ro divided by rm.

As for the parasitoid experiment, the test host (*C. partellus*) pupae were obtained from a laboratory colony maintained on artificial diet. Two-day-old pupae were used during the entire period of the experiment by replacing the host pupae on daily basis. The test parasitiods were also obtained from a laboratory colony maintained on *C. partellus* pupae. Upon eclosion 20 randomly selected pairs of parasitoids were used which formed a cohort and the observations started as soon as the adult females started ovipositing and ended with the death of the last female parasitoid. Each parasitized host pupa was maintained and labelled in a separate 4-ml vial in the laboratory until the progeny emerged from the host pupae.

Experimental data recorded:

The calculation of r for the parasitoid is based on the female populations:

The primary data required were as follows;

(1) The female life Table giving the probability at birth of being alive at age X. This is usually designated Lx (Lo=1).

(2) The age specific fecundity Table giving the mean number of female offspring produced in a unit of time by the female parasitoid aged X. This is designated mx.(mx= (proportion of females) X (age specific oviposition).

In the calculation of the sTable age distribution the age specific survival rates (or the proportion of females alive at age X) (Lx) of both the immature stages and the reproductive stages are required. For the calculation of r the life Table of the adult and only the total survival of the immature stages (irrespective of age) are needed. The age-specific survival (Lx) and age-specific fecundity (mx) at each pivotal age (X) were worked out daily for the entire reproductive period, to prepare the fertility Table as per the method outlined by Verma and Makhmoor (1988).The method of Graham (1967) was used assuming that there was no immature mortality and the population on the first day of adult life was based on 100 % survival (lx= 1.00) The net reproductive rate (Ro), approximate generation time (TC) and capacity for increase (rc) were estimated according to the methods of Andrewatha and Birch (1954), Krebs (1978) and Southwood (1978).The true generation time (T) and finite

rate of increase were further calculated. Also, time taken (in days) to double the population (DT) was calculated by the formula:

$$DT = \frac{\log_e 2}{rm} .$$

In the present study, fecundity of the parasitoid was simply based on the number of eggs recorded from the parasitized host.

female parasitoids were dissected and examined to confirm whether the female wasps have oviposited. Twenty (1-2 day old) host pupae were used for each time interval. The experiment was carried out under the laboratory conditions stated above.

3.11. Analysis of Data:

All data were analyzed using the statistical Analysis System (SAS^R) programme (Anon., 1987) and an IBMR computer. percentages were transformed into arcsine where there were great variations in the data before being subjected to statistical tests. In all cases, levels of significance were determined by " F " values. means were compared using Duncan's multiple range test (DMRT) or least significant

difference (LSD). Graphs were traced from sketches drawn by computer employing Lotus^{R} 123 programme.

CHAPTER FOUR

RESULTS

4.1. Seasonal survey for the incidence of P.furvus in different agroecological localities in Kenya.

Detailed observations on surveys for the incidence of *P. furvus* in different agroecological locations in Kenya are presented below.

For three seasons, study was carried out on the distribution and incidence of *P. furvus* in different locations and the result showed that the average number of pupae of *C. partellus* and *B. fusca* collected varied significantly ($P \leq 0.05$) with season (Fig. 1, Appendix 2). The long rainy season (March-june 1990) had less number of borers collected, the mean values for this parameter were : 20.75, 22.29, 14.83, for *C. partellus* and 2.21, 4.21, and 2.54 for *B. fusca* pupae (Fig.1).

As regards the average number of *C. partellus* and *B. fusca* pupae seasonally parasitized, the results show that there is no significant difference in the case of *B. fusca*, However, significant differences ($P \leq 0.05$) in terms of *C. partellus* pupae parasitized were recorded over the seasons (Fig 2).

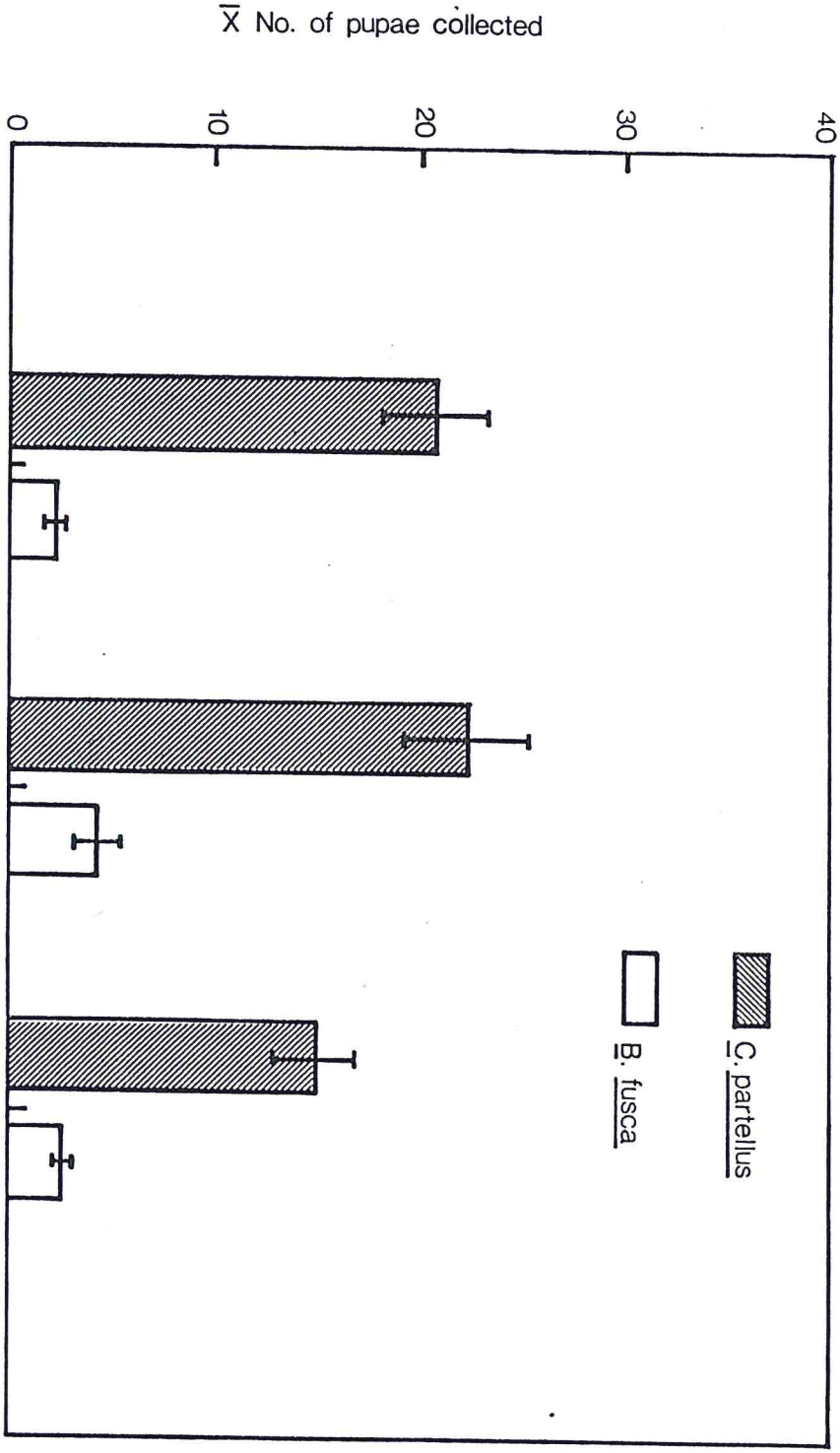

Fig:1 Seasonal No. of parasitized pupae collected in different agroecological locations In Kenya

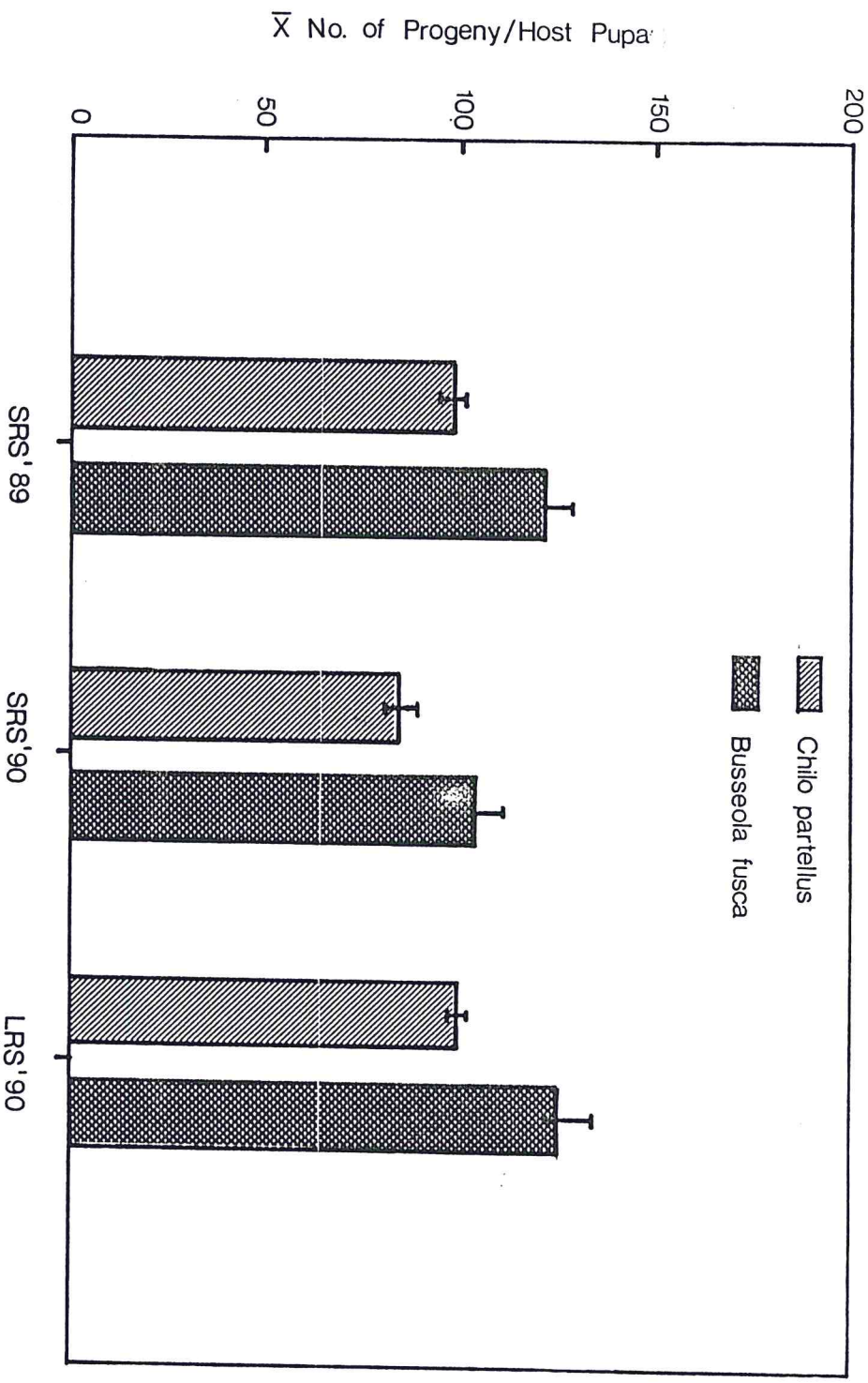

Fig: 2 Seasonal Progeny Production of P. furvus in different agroecological locations in Kenya

Comparing the total number of *C. partellus* and *B. fusca* pupae collected in relation to different agroecological locations in Kenya, it was found that Mombassa location had the highest (32.75 and 46.50) mean number of *C. partellus* and *B. fusca* pupae respectively (Table 1).

However, average number of *B. fusca* collected varied significantly with locations and the least is recorded in Kakamega. The percentage parasitism of the pupae collected from these agroecological locations also varied significantly ($P \leq 0.05$) and the highest percentage parasitism of *C. partellus* pupae collected was recorded from Mombassa location (Table 1). Kakamega and Kisumu locations had the lowest percentage parasitism of *C. partellus* and *B. fusca*. The mean values for this biological parameter were : 8.22, and 6.72 % for *C. partellus* pupae and 3.75, and 7.90 % for *B. fusca* pupae (Table 1). There was no significant difference in terms of percentage parasitism among locations of Busia, Mbita, and Siaya for *C. partellus* pupae as well as for *B. fusca* pupae.

Table 2 shows comparison of progeny production of *P. furvus* per host pupa of *C. partellus* and *B. fusca* and their sex ratio by locations in different agroecological localities in Kenya. The highest mean values of *P. furvus*

Table 1

Distribution and Incidence of P. furvus in different Agroecological lacations in Kenya

Localities	TOTAL NO.PUPAE collected (±SE)		% PARASITISM	
	C.partellus	B.fusca	C.partellus	B.fusca
BUSIA	21.00 ±1.48 b	12.15 ±1.39 b	21.00 b	12.15 b
KAKAMEGA	8.22 ±1.04 c	3.75 ±1.11 c	8.22 c	3.75 c
KISUMU	6.72 ±1.97 c	7.90 ±1.57 bc	6.72 c	7.90 bc
MBITA	16.12 ±1.94 bc	12.75 ±1.49 b	16.12 bc	12.75 b
MOMBASA	32.75 ±8.90 a	46.50 ±4.66 a	32.57 a	46.50 a
SIAYA	13.57 ±1.91 bc	13.62 ±0.55 b	13.57 bc	13.62 b

Means in the same column followed by different letter are significantly different at 5 % level by DMRT.

Table 2

Comparison of progeny production and Sex-ratio of P. furvus by locations in different agroecological locations in Kenya.

Location	C. partellus		B. fusca	
	Progeny/host pupa (±SE)	% male progeny per host pupa (±SE)	Progeny/host pupa (±SE)	% male progeny per host pupa (±SE)
Busia	101.25 ±17.99 ab	44.50 ±4.01 a	99.25 ±14.27 b	38.25 ±5.45 a
Kakamega	72.25 ±12.45 b	34.50 ±2.10 ab	88.50 ±9.07 b	34.00 ±2.48 a
Kisumu	81.75 ±12.00 b	35.75 ±3.25 b	72.50 ±11.97 b	38.25 ±2.68 a
Mbita	102.00 ±10.00 ab	34.00 ±1.35 b	150.75 ±29.95 ab	34.75 ±3.35 a
Mombasa	142.50 ±26.49 a	34.50 ±3.79 b	195.25 ±49.79 a	25.07 ±1.49 a
Siaya	86.50 ±14.20 b	32.25 ±1.49 b	85.50 ±16.07 b	32.25 ±2.04 a

Means in the same column followed by different letters are significantly different at 5 % level by DMRT

progeny production per host pupa of *C. partellus* and *B. fusca* were recorded in Mombassa with an average mean values of 142.50 and 195.25 for *C. partellus* and *B. fusca* respectively (Table 2, Appendix 3). The mean values of progeny production per host pupa of *C. partellus* in locations of Busia, Kakamega, Kisumu, Mbita and Siaya are : 101.25, 72.25, 81.75, 102.00 and 86.50 respectively (Table 2). Similarly, *P. furvus* progeny production per host pupa of *B. fusca* have shown no significant difference in relation to different agroecological locations in Kenya, with the exception of 195.25 progeny production per host pupa in Mombassa. The percentage of male progeny per host pupa of *C. partellus* varied significantly from a lower mean value of 32.25 % in Siaya to a higher mean value of 44.50 % in Busia location (Table 2, Appendix 4). The mean values of this parameter in locations of Kakamega, Kisumu, Mbita and Mombassa were : 34.50, 35.75, 34.00, and 34.50 % respectively (Table 2). Interestingly, there was no significant differences in terms of percentage male progeny per host pupa of *B. fusca* in all localities surveyed, and the mean values ranged from 25.07 % in Mombassa to a higher mean value of 38.25 % in Busia and Kisumu locations (Table 2, Appendix 4).

4.2. P. furvus: Parasitization of C. partellus pupae and its attraction to two cultivars of maize in the field.

Seasonal parasitization by *P. furvus* under fine mosquito net field conditions carried out at MPFS between 1990 and 1991 is shown in Tables.3-6.

More *Chilo partellus* pupae were recovered from INB-A in all seasons than on ICZ-2. The highest mean number of pupae recovered was obtained in the long rainy season of 1990 and the values for this parameter were: 235 and 196 pupae from INB-A and ICZ-2, respectively (Table 3 and appendices 5,6,7). Looking into the number of *C. partellus* pupae parasitized out of the number recovered, there was a significant difference between the two cultivars tested, INB-A showing more parasitized pupae than ICZ-2.

The results show that the number of pupae recovered from INB-A and ICZ-2 was lower in the short rainy season of 1990. Table 4 shows the number of *C. partellus* pupae recovered in respect of different seasons and cultivars; it is clear from the date collected that more pupae were recorded from the lower internodes of the maize cultivars and hence significantly more pupae were parasitized in that portion compared to upper and middle internodes of the maize plant (Table 4, Appendices 8, 9).

Table 3

Seasonal parasitization of P. furvus under netted field conditions at MPFS.

Season	Characters	Cultivars	
		INB-A	ICZ-2
LRS.90	No.pupae recovered	235.25±1.49 a	195.75±1.92 b
	No.pupae parasitized	96.19±0.56 a+	70.82±0.69 b
SRS 90	No.pupae recovered	182.25±4.96 a	126.50±2.24 b
	No.pupae parasitized	65.93±1.79 a	46.44±0.78 b
LRS.91	No.pupae recovered	212.25±2.73 a	145.00±4.34 b
	No.pupae parasitized	79.56±0.75 a	56.18±1.81 b

Means in the same row followed by different letters are significantly different at 5 % level by DMRT.

Key.
LRS = Long Rainy Season.
SRS = Short Rainy Season.

Table 4

Seasonal Percentage parasitism of P. furvus under netted experiments at MPFS

Cultivar	Season	No. pupae recovered	No. of pupae parasitized			Percent parasitism
			Upper	Middle	Lower	
ICZ-2	LRS90	195.75 ±3.68bc	8.31 ±2.66c	29.86 ±0.56cd	62.98 ±1.21b	70.82 ±1.33c
ICZ-2	SRS90	126.50 ±4.29e	28.00 ±0.96a	35.34 ±0.98ab	44.80 ±2.41e	46.45 ±1.50e
ICZ-2	LRS91	145.00 ±8.31d	13.92 ±1.23b	38.65 ±2.64a	56.32 ±3.06c	56.18 ±3.48d
INB-A	LRS90	235.25 ±2.86a	13.89 ±0.82b	15.72 ±0.60e	74.08 ±1.24a	96.19 1.08a
INB-a	SRS90	182.25 ±9.50c	28.33 ±1.77a	31.26 ±1.94bc	51.70 ±2.69cd	65.93 ±3.43c
INB-a	LRS91	212.25 ±5.23b	29.76 ±1.15a	25.05 ±1.54d	46.84 ±1.74de	79.56 ±1.44b

Means in the same column followed by different letters are significantly different at 5 % level by DMRT

The highest mean percentage parasitism was recorded in the long rainy season of 1991 followed by the long rainy season of 1990 and the mean values of this biological parameter is 79.56 % and 70.82 % for INB-A and ICZ-2 respectively (Table 4).

Overall number of pupae collected during the study period (1990-1991) showed a significant difference ($P \leq 0.05$) between the two cultivars tested, and more pupae were collected from INB-A with a mean value of 231.25 ± 28.78 and 171.00 ± 27.05 for ICZ-2 (Table 5). Similarly, the number of *C. partellus* pupae collected in respect of different levels of the maize plant remained more or less constant for both cultivars with the exception of the lower internode position.

However, overall parasitism was found significantly higher on INB-A compared to that of ICZ-2.and the mean values for this biological parameter were : 85.00 ± 10.35 and 65.00 ± 11.13 for INB-A and ICZ-2 respectively (Table 5).

Table 6 shows the average number of male and female progenies per *C. partellus* pupa parasitized. The result in this study shows no significant different of the sex ratio in relation to the two maize cultivars tested. Similarly, the results in Table 6 shows no significant difference

Table 5.

C. partellus parasitism and internode preference under netted field conditions at MPFS.

Treatment	Cultivar	
	INB-A	ICZ-2
No.pupae collected	231.25±28.78 a	171.00±27.05 b
Internode position		
Upper	51.50±10.52 a	29.25±6.91 a
Middle	55.25±10.62 a	50.25±4.00 a
Lower	126.75±21.32 a	91.50±18.43 b
% parasitism	85.00±10.35 a	65.00±11.13 b

Means in the same row followed by different letters are significantly different at 5 % level by DMRT.

Table 6

Influence of maize cultivars on P. furvus sex ratio and mortality without progeny

Progeny production	maize cultivar	
	ICZ-2	INB-A
No. males/host pupa	20.16 ±0.28 a	19.94 ±0.24 a
No. females/host pupa	68.18 ±0.30 b	72.09 ±0.55 a
% mortality	11.06 ±0.09 a	12.76 ±0.63 a

Means in the same row followed by same letters are not significantly different at 5 % level by DMRT.

($P \leq 0.05$) in the per centage mortality without progeny production between the cultivars tested. The mean values for this parameter were : 11.02 % and 12.25 % for ICZ-2 and INB-A respectively (Table 6, Appendix 10).

4.3. Investigation on the nature of the Trophic interactions between the plant, host insect and the parasitoid

The test using cylindrical tubes indicated that no detecTable bias was present in the system since the mean time spent per field did not differ significantly between each of the four fields ($P \leq 0.05$). In experiments involving test materials, a positive response in terms of a greater percentage of parasitoids choosing test fields over controls was always confirmed by a significantly longer time spent walking in test fields (Table 7). *P. furvus* female parasitoids showed a significant attraction to a combination of hosts and host frasses (Table 7). The mean values for this biological parameters were : 40.0, 47.5, 42.5 and 40.0 for the test fields of a_1, a_2, b_1, and b_2, respectively (Table 7, Appendix 11).

In all of the 4 trails the number of *P. furvus* females responding to the combination of host pupae with frasses was about twice -as much as those responding to either frass or pupae alone.

Table 7

Results of testing various materials as odour sources to P. furvus in a cylindrical olfactometer.

Test	Treatment	% choosing test fields (±SE)	Time spent in the test field (±SE)
1	*C. partellus* frass	40.0 ±0.41 b	2.11 ±0.05 c
2	*B. fusca* frass	47.5±0.47 b	2.09±0.10 c
3	*B. fusca* pupae	42.5±0.41 b	1.55±0.27 b
4	*C. partellus pupae*	40.0 ±0.57 b	1.19 ±0.29 b
5	*B. fusca* pupae and it's larval frass	80.0 ±0.41 a	0.31 ±0.05 a
6	*C. partellus* pupae and it's larval frass	75.0 ±0.64 a	0.21 ±0.02 a
7	*B. fusca* frass and *C. partellus* pupae	72.5 ±0.47 a	0.16 ±0.05 a
8	*C. partellus* frass and *B. fusca* pupae	70.0 ±0.41 a	0.20 ±0.02 a

Means in the same column followed by different letters are significantly different at 5% level test (DMRT).

4.4.Effect of Temperature and Relative humidity levels on P. furvus parasitism

The biology of the endopupal parasitoid *P. furvus* reared on *C. partellus* was studied under different temperature and relative humidity levels, and the results are given in Tables 8-13. Combined effects of temperatures and relative humidity levels tested were found to affect significantly the reproduction of the parasitoid by modifying the behaviour of the adult female parasitoids in their ability to parasitize host pupae of *C. partellus* . Less than 8 % of the host pupae were parasitized at 20 ± 1.5°C under all relative humidity levels tested (Table 8, Appendix 12). The highest (84) mean number of host pupae parasitized was recorded from 25 ±1.5°C under relative humidity level of 60 % (Table 8).

It was found that the number of parasitized host pupae of *C. partellus* performed better with temperatures of 25 ± 1.5 °C and 30 ± 1.5° C (Table 9, Appendix 15).

The percentage of host pupae parasitized was influenced by the relative humidity levels tested and the lowest (2.75%) was recorded at 40 % rh. while 80 % rh. gave the highest (80%) mean value for this parameter (Table 8).

TABLE 8.

Influence of temperature and relative humidity on P. furvus parasitism. (% Number of host pupae parasitized ±SE)

Tempr. (°C)	Relative humidity levels (%)				
	40	50	60	70	80
15	0.00 ±0.00 a	0.00 ±0.00 a	0.00 ±0.00 a	0.00 ±0.00 a	0.00 ±0.00 a
20	2.75 ±0.44 b	4.00 ±1.06 ab	6.00 ±2.03 ab	7.75 ±1.57 a	1.75 ±0.42 b
25	31.25 ±3.28 d	53.75 ±6.67 c	83.75 ±9.50 a	73.75 ±6.86 ab	60.00 ±2.59 bc
30	27.75 ±1.93 c	61.25 ±2.39 a	44.50 ±3.12 b	42.00 ±2.73 b	31.50 ±1.84 c
35	0.00 ±0.00 a	0.00 ±0.00 a	0.00 ±0.00 a	0.00 ±0.00 a	0.00 ±0.00 a

* Means in the same row followed by different letters are significantly different at 5% level (DMRT).

Table 9

Effect of temperature on *P. furvus* development progeny/host and sex-ratio.

Temperature C°	No.host pupae exposed	No. host pupae parasitized +SE	Developmental period (days) (+SE) (+ SE)	Progeny production per host pupa +SE	% male progeny per host +SE
15	60	0.00+0.00 d	0.00+0.00 c	0.00+0.00 d	0.00+0.00 c
20	30	7.67+2.00 c	36.85+0.88 a	64.21+3.60 c	50.39+2.52 a
25	30	16.25+1.75 b	19.54+0.21 b	93.79+2.59 a	25.80+0.56 b
30	60	54.87+4.96 a	20.15+0.26 b	76.28+4.17 b	27.78+1.06 b
35	60	0.00+0.00 d	0.00+0.00 c	0.00+0.00 d	0.00+0.00 c

* Means in the same column followed by different letters are significantly at 5% level (DMRT).

Looking at the results in Table 9, it is clear that the female parasitoids failed to parasitize any host pupae offered at the two extreme temperatures tested - 15^{o}_{c} and 35^{o}_{c}.

Table 9, presents also the duration of development of *P. furvus* at different temperature regimes tested and shows the trend for a longer duration of development at lower temperatures. At 20 ± 1.5°C the mean values of this biological parameter were : 36.85, 19.54 and 20.15 days under temperature regimes of 20 ±1.5 °C, 25 ± 1.5 °C and 30 ± 1.5°C (Table 9). The longest mean duration for development (37 days) was observed at 20 ± 1.5°C and the shortest (19 days) mean value at 30 ± 1.5°C. However, the study showed that there was no development of the immatures at 15 ± 1.5 °C and 35 ±1.5 °C.

As regards the progeny production, *P. furvus* reacted sharply to a change in rearing temperature between 15 ± 1.5°C and 35 ± 1.5°C. The average progeny production varied from a high mean value of 93.79 at 25 ± 1.5°C to a lower mean value of 64 at 20 ± 1.5°C (Table 9). Sex ratio was found to be highly influenced by temperature regimes tested and almost a ratio of 1:1 was observed at 20 ±1.5°C, while at 25 and 30 ±1.5°C the ratio came to 1:4 in favour of females. The mean values for this parameter were : 50.39, 25.80 and 27.78 % under temperature regimes of 20 ±1.5°C, 25 ±1.5°C and 30 ±1.5°C respectively (Table 9, Appendix 15).

Similarly, developmental period of the immatures and progeny production was found to vary significantly under different relative humidity levels tested (Table 10). The results showed no significant different in development under relative humidity levels of 60 %, 70 %, and 80 %.

Progeny production of *P. furvus* per host pupa remained more or less constant between relative humidity levels of 60 %, 70 % and 80 % with a mean value of 82.27, 85.86 and 82.81, respectively (Table 10, Appendix 14). Similarly, the relative humidity levels tested affected significantly *P. furvus* sex ratio , and at 40 % and 50 % the ratio of male to female become 1:3.5 and 1:3.5 . However, a ratio of 1:2.80 in favour of females was observed at 60 % relative humidity level (Table 10).

The average time for development of *P. furvus* from oviposition to adult emergence was found to vary greatly with combined effects of temperature and relative humidity levels tested. The results show that the developmental periods were longest at 20 ±1.5°C and their mean values were : 36.18, 36.56 and 37.81 days under relative humidity levels of 60 %, 70 % and 80 % rh.,respectively (Table 11, Appendix 13).

Table 10

Effect of relative humidity on P. furvus development, progeny production and sex-ratio.

Relative humidity (%)	% host pupae parasitized	Developmental period (days) (±SE)	Progeny/ hostpupa (±SE)	Sex-ratio* (±SE) (%male/ progeny)
30	0.00 ±0.00 d	0.00 ±0.00 c	0.00 0.00 d	0.00 ±0.00 d
40	27.75 ±1.97 c	20.30 ±0.59 b	74.65 ±7.32 ab	28.66 ±1.66 b
50	61.25 ±2.39 a	20.50 ±0.28 b	70.42 ±5.73 b	28.91 ±1.47 b
60	44.50 ±3.12 b	25.01 ±2.49 a	82.27 ±5.80 a	35.69 ±4.87 a
70	42.00 ±2.73 b	25.18 ±2.44 a	85.86 ±5.44 a	32.11 ±2.78 ab
80	31.50 ±1.84 c	25.64 ±2.63 a	82.81 ±4.95 a	33.51 ±3.67 ab

* Means in the same column followed by different letters are significantly different at 5% level (DMRT).

Table 11

Effect of combined temperature and relative humidity on P. furvus development (days) ±SE

Relative humidity (%)	Temperature regimes (C°)		
	20	25	30
30	0.00 ±0.00 c	0.00 ±0.00 c	0.00 ±0.00 c
40	0.00 ±0.00 b	19.03 ±0.34 b	21.58 ±0.67 b
50	0.00 ±0.00 b	20.75 ±0.47 b	20.25 ±0.32 b
60	36.18 ±2.37 a	19.20 ±0.31 b	19.65 ±0.56 b
70	36.56 ±0.83 a	19.35 ±0.39 b	19.62 ±0.23 b
80	37.81 ±1.33 a	19.37 ±0.47 b	19.62 ±0.55 b

* Means followed by different letters are significantly different at 5% level (DMRT)

Looking at the results in Table 12, the progeny production of *P. furvus* varied significantly in relation to combined effects of temperature and relative humidity levels tested. Less progeny production was observed at 20 ±1.5°C under relative humidity levels of 60 %, 70 % and 80 %. It would be worth while to note here that the developing parasitoids could not survive and as such, there was no adult emergence when the rearing temperature was lowered to 15 ±1.5°C or raised to 35 ±1.5°C under all relative humidity levels tested. In general more parasitoids emerged as the rearing temperatures were raised from 20 to 30 ±1.5°C (Table 12, Appendix 13). The mean values of this biological parameter in a single host were : 93.12, 81.85, 104.75, 94.58 and 94.67 at 25 ±1.5°C under relative humidity levels of 40 to 80 %, respectively. However, some times as many as 120 *P. furvus* could emerge from a single host at that temperature.

Table 13, presents the sex ratio (percent male progeny per host pupa parasitized) which is significantly influenced by varying temperature regimes and relative humidity levels tested. As regards with the temperature regime of 20 ±1.5°C under relative humidity levels of 60 % , 70 % and 80 % only 1.5-to-2-fold increase of females were recorded, while at 25 ± 1.5°C 4-fold increase in female production was observed under humidity levels of 40-80% (Table 13).

Table 12

Effect of combined temperature and relative humidity on P. furvus progeny production/host. (±SE).

Relative humidity (%)	Temperature levels (C°)		
	20	25	30
40	0.00 ±0.00 f	93.12 ±3.56 ab	56.18 ±3.25 e
50	0.00 ±0.00 f	81.85 ±8.12 bc	59.00 ±0.40 de
60	68.10 ±9.43 cde	104.75 ±3.35 a	73.95 ±3.42 cd
70	62.65 ±5.48 de	94.58 ±2.52 ab	100.37 ±3.69 a
80	61.87 ±3.96 de	94.67 ±5.34 ab	91.90 ±2.15 ab

* Means followed by different letters are significantly different at 5% level (DMRT).

Table 13.

Effect of combined temperature and relative humidity on *P.* furvus sex-ratio (% male progeny / host (±SE)

Relative humidity (%)	Temperature regimes (°C) 20	25	30
40	0.00 ±0.00 f	24.04 ±1.07 e	33.41 ±1.02 c
50	0.00 ±0.00 f	25.08 ±1.65 e	32.00 ±1.68 dc
60	62.63 ±2.33 a	25.00 ±2.19 e	24.45 ±2.59 e
70	46.58 ±2.95 b	26.75 ±1.49 de	25.50 ±1.19 e
80	49.49 ±4.46 b	26.57 ±0.25 de	24.50 ±0.86 e

* Means followed by different letters are significantly different at 5% level (DMRT)

The highest (63 %) mean value of male progeny per host pupa was recorded at
20 ±1.5°C under 60 % relative humidity level (Table 13).

4.5. Influence of age on the parasitoid's biology

4.5.1. Influence of host age on parasitism

C. partellus and *B. fusca* pupal ages did affect host acceptability and suitability. *P. furvus* is polyphagous, parasitizing numerous species of cereal stem-borers which exhibit a great range of pupal ages. Therefore, it would be advantageous for the parasitoid to be able to attack equally well pupae of a wide range of ages.

Both *C. partellus* and *B. fusca* pupal ages did affect the number of *P. furvus* progeny production per host pupa with progeny production decreasing as hosts grow older (Table 14-29).

Pupal ages of *C. partellus* and *B. fusca* were also found to affect developmental period of the parasitoids and their sex determination (Table 14-29). The results shows also that percent successful parasitism and host mortality was affected by host pupal ages (Tables 14 and 15) and therefore, host acceptability and suitability (Tables 14-29).

TABLE 14

Effect of host age (*B. fusca*) on *P. furvus* parasitism. (+SE)

Host age (days)	No.eggs/ host pupae	No.host * pupae parasitized ± S.E	No host pupae produced mature parasitoids	% successful parasitism (suitability)
0	124.55 +3.95 a	11.00 (55%) +1.04 a	9.00 +1.08 a	81.81 a
1	128.55 +4.16 a	11.00 (55%) +1.08 a	8.60 +1.20 a	78.18 a
2	128.30 +5.26 a	10.40 (52%) +1.24 b	8.60 +1.12 a	82.69 a
3	125.25 +4.90 a	8.00 (40%) +0.76 bc	5.80 +0.88 b	72.50 b
4	118.25 +4.55 ab	8.20 (41%) +0.84 bc	5.20B +0.92 b	63.41 b
5	112.60 +3.97 b	7.80 (39%) +1.00 c	4.60BC +0.83 bc	58.97B c
6	108.50 +4.09 b	7.00 (35%) +0.78 cd	4.40 +0.68 bc	62.86 bc
7	89.65 +2.19 c	6.00 (30%) +0.84 cd	2.40 +0.60 c	40.00 c
8	83.40 +3.21 c	5.20 (26%) +0.84 d	2.20 +0.52 c	42.31 c

Means in the same column followed by different letters are significantly ($P \leq 0.05$)

* numbers in brackets are % acceptability

** number of pupae exposed= 20

TABLE 15

Influence of host age (*C. partellus*) on *P. furvus* parasitism.

Host age (days)	No.eggs laid/host pupa (+SE)	No.host pupae parasitized (+SE) *	No.host pupae producing mature parasitoids (+SE)	% Successful parasitism (% suitability)
0	133.87 +5.04 a	46.75 (93.5) +1.65 a	33.18 +1.87 a	70.97 a
1	134.31 +3.99 a	45.50 (91.0) +2.84 a	35.00 +1.63 a	76.92 a
2	135.06 +4.86 a	36.50 (73.0) +3.42 b	31.81 +1.76 ab	87.15 ab
3	129.12 +7.05	30.75 (61.5) +2.28 bc	21.42 +1.58 b	69.65 b
4	112.00 +5.17 b	27.00 (54) +2.27 c	17.00 +1.55 c	62.96 c
5	98.81 +3.74 b	20.50 (41) +1.71 d	10.68 +0.08 d	52.09 d

Means in the same column followed by different letters are significantly different (P<by DMRT.
* numbers in brackets are % acceptability
** NO of pupae exposed = 50.

Parasitism was 78.18 % and 76.92 % for one day old *B. fusca* and *C. partellus* pupae, respectively (Table 14 and Table 15), and 87.15 % for two day old pupae of *C. partellus*, after which there was a steady decrease to a level of 52 % for five day old pupae (Table 15). Parasitism was 72.50 % in three day old pupae of *B. fusca* after which parasitism decreased rapidly, becoming 42 % for eight day old *B. fusca* pupae (Table 14).

Both *C. partellus* and *B. fusca* pupal mortality (host mortality with out parasitoid progeny production) also varied with age, generally decreasing with host age. The number of host pupae parasitized was highest in the zero-to-two day old pupae of *C. partellus* (Table 15).

Acceptability of *C. partellus* pupae to female *P. furvus* remained relatively high from day zero to two day old reaching to 61 % and decreased markedly from day three to fifth (Table 15).

For *B. fusca* pupae, the acceptability remained more or less high from day zero to two day old pupae ranging from 52 % to 55 % and decreased sharply from day three to eight. Host suitability for parasitism for both *C. partellus* and *B. fusca* also varied with host pupal ages (Tables 14 and 15).

The number of eggs laid / host *B. fusca* was found to

vary significantly as the host age increases, the number of eggs laid / host pupa remained more or less the same from 0 t0 4 day old *B. fusca* pupae and there was a sharp decline as the host grew older than 4 days. The highest mean value of this parameter (128) was recorded at the age of one and two days and the lowest mean value (83) at eight-day-old *B. fusca* (Table 14, Appendix 16).

The results of this study showed that as the host pupae of *B. fusca* ages the ability of the female parasitoid to lay eggs decreases significantly (Table 14). The average number of eggs laid per host pupa *C. partellus* was found to vary significantly as the host age increases (Table 15, Appendix 17). The study showed a preponderance of males as the host *C. partellus* and *B. fusca* pupae grew older. The highest percentage of males per host pupa of *B. fusca* (40 %) was found at eight day old pupae and the lowest (25.80%) at zero day old *B. fusca* (Table 16, Appendix 18).

The effect of the age of *C. partellus* pupae on parasitoids sex-ratio is clearly evident in Table 17. The results show an increase in male progeny production per host pupa as the host *C. partellus* grew older. The highest percentage male progeny (58 %) was obtained from four day old *C. partellus* pupae (Table 17). However, male production remained more or less constant when *C. partellus* host pupae

TABLE 16

Effect of host age (B. fusca) on the Parasitoids Progeny Production, Developmental Period and Sex-ratio.

Host Age (Days)±SE	Developmental period(days) ±SE	Progeny Production ±SE	Sex-Ratio (%male/progeny ±SE
0	20.01 ±0.23 b	116.60 ±3.01 a	25.80 ±0.84 a
1	19.83 ±0.22 b	114.11 ±2.30 a	26.80 ±0.24 ab
2	19.87 ±0.24 b	118.51 ±2.48 a	27.20 ±1.12 ab
3	19.57 ±0.14 b	118.50 ±3.42 a	26.70 ±1.08 ab
4	20.14 ±0.21 ab	116.20 ±3.19 a	27.65 ±0.62 b
5	20.00 ±0.14 b	112.30 ±3.27 a	29.85 ±2.32 c
6	20.73 ±0.19 a	93.10 ±2.69 b	32.45 ±1.04 d
7	21.81 ±0.27 a	74.70 ±3.04 c	37.60 ±2.66 e
8	20.81 ±0.24 a	62.95 ±2.69 d	39.90 ±1.75 f

Means in the same column followed by different letters are significantly different. (DMRT).

TABLE 17

Influence of host age (C. partellus) on parasitoids' Development, Progeny Production and sex-ratio

Host age (days)	Developmental period (days) (±SE)	Progeny/host pupa (±SE)	Sex-ratio (% male/host)
0	19.75 ±0.47 a	100.30 ±19.95 a	26.85 ±0.69 c
1	19.95 ±0.46 a	102.95 ±2.90 a	27.70 ±0.90 c
2	20.10 ±0.71 a	101.50 ±5.62 a	28.23 ±1.10 c
3	20.25 ±0.25 a	98.25 ±3.55 a	41.77 ±1.57 b
4	20.35 ±0.27 a	76.55 ±4.78 b	58.14 ±1.80 a
5	22.00 ±0.47 b	26.08 ±3.67 c	12.77 ±5.87 d

Means in the same column followed by different letters are significantly different at 5 % level by DMRT.

were zero to two day old and the mean percentage values for this parameter were 26.85, 27.70 and 28.23 (Table 17, Appendix 19).

4.2. Influence of P. furvus female age on parasitism

Tables 18 and 19 show the effect of the age of the parasitoid on its host acceptability and suitability, the highest percentage of successful parasitism (suitability) was observed in one day old and in zero day old parasitoids (91.43% and 73.3%) for *C. partellus* and *B. fusca*, respectively. Acceptability and suitability both decreased with parasitoid age and the lowest rate of successful parasitism for *C. partellus* and *B. fusca* were found to be 38.46% and 49.78% respectively in four day old female parasitoid. (Tables 18 and 19, Appendices 20, 21). The results show that there was a significant difference on ovipositional rate (number of eggs laid per host pupa) between the parasitoid groups, laying smallest number of eggs as the female parasitoid grew older (Tables 14 and 18).

Parasitoid age did not affect significantly the duration from oviposition to adult emergence of the immatures development in *B. fusca* pupae (except where the female parasitoid is two-day-old), and remained constant throughout (20 days). However, progeny production and sex ratio varied with parasitoid age (Table 20, Appendix 22).

TABLE 18

Effect of parasitoid age (P. furvus)on its parasitism (Host C. partellus)

Parasitoid age (days)	No.eggs laid /host pupa (±SE)	No.host pupae parasitized (acceptability) (±SE)	No.host pupae that produced mature parasitoids	% successful parasitism (suitability)
0	136.58 ±4.47 a	35±1.00 a	31 a	88.57 a
1	134.95 ±4.11 a	35±1.91 a	32 a	91.43 a
2	138.56 ±5.01 a	32.±1.63A b	23 ab	71.87 ab
3	112.08 ±3.72 b	31.±1.91 ab	19 ab	61.29 ab
4	111.88 ±4.98 b	26±2.56 b	10 b	38.46 b

Means in the same column followed by different letters are significantly different by DMRT.

Table 19

Effect of parasitoid age (*P. furvus*) on its parasitism (Host *B. fusca*)

Parasitoid age (days)	No.eggs laid / host pupa (±SE)	No. host pupa parasitized	No.host pupae that produced mature parasitoids (±SE)	% Successful parasitism.
0	124.94 ±4.22 a	9.67 ±1.12 a	7.33 a	73.30 a
1	121.16 ±3.91 a	10.00 ±1.12 a	6.77 ab	70.01 a
2	117.97 ±3.44 a	9.56 ±1.12 a	6.77 ab	70.81 a
3	102.86 ±3.24 b	7.56 ±1.14 b	5.00 b	66.13 b
4	99.19 ±3.31 b	4.68 ±0.40 c	2.33 c	49.78 c

Means in the same column followed by different letters are significantly different by DMRT. ($P<0.05$)

* No. host pupae exposed = 20

TABLE 20

Influence of parasitoid age (P. furvus) on its Development, Progeny Production and Sex-ratio, (HOST. B. fusca)

Parasitoid age (days) ±SE	Development (days) ±SE	Progeny Production ±SE	% male/host pupa (±SE)
0	20.36 ±0.18 a	106.75 ±9.60 a	26.58 ±1.67 d
1	20.27 ±0.17 a	105.66 ±6.05 a	26.94 ±1.65 d
2	19.51 ±0.16 b	110.16 ±8.70 a	34.94 ±3.25 a
3	20.36 ±0.19 a	99.55 ±7.30 b	30.77 ±3.43 c
4	20.47 ±0.19 a	92.64 ±10.20 c	32.97 ±3.51 b

Means in the same column followed by different letters are significantly different at 5% level DMRT.

It was observed that the parasitoid age affected significantly ($P \leq 0.05$) the developmental period of the immatures when reared on *C. partellus* pupae, there was also a preponderance of males per host as the parasitoid female grew older. However, the parasitoid age did not affect the progeny production per host *C. partellus* pupae (Table 21, Appendix 23).

4.3. Influence of with holding oviposition on the fecundity of the parasitoid

The results showed that there was no significant difference ($P \leq 0.05$) in the number of eggs the female parasitoid can lay between zero to four-day-old (Tables 19, 20, Appendix 22). However, there was a significant difference ($P \leq 0.05$) on the parasitoid fecundity when the oviposition was delayed for four days (Fig.3).

The results in this study show that the interaction of host and parasitoid age in relation to number of eggs laid per host pupa varied significantly as they grew older with the exception where the host age remains either zero day or four day old in the case of *C. partellus* host pupae Table 23, Appendix 25).

TABLE 21

Effect of parasitoid age (P.furvus) on its Development, progeny production and sex-ratio (Host C. partellus).

Parasitoid age (days)	Development (days)±SE	Progeny Production /host pupa (±SE)	% male / host pupa (± SE)
0	22.00±0.23 a	112.25 ±4.97 a	28.03 ±3.63 b
1	22.12±0.17 a	113.50 ±4.48 a	28.27 ±3.39 b
2	22.05±0.21 a	109.00 ±4.14 a	39.95 ±3.46 a
3	19.50±0.17 b	108.75 ±7.79 a	33.07 ±4.15 ab
4	19.59±0.28 b	106.50 ±3.43 a	33.56 ±3.87 ab

Means in the same column followed by different letters are significantly different by DMRT.

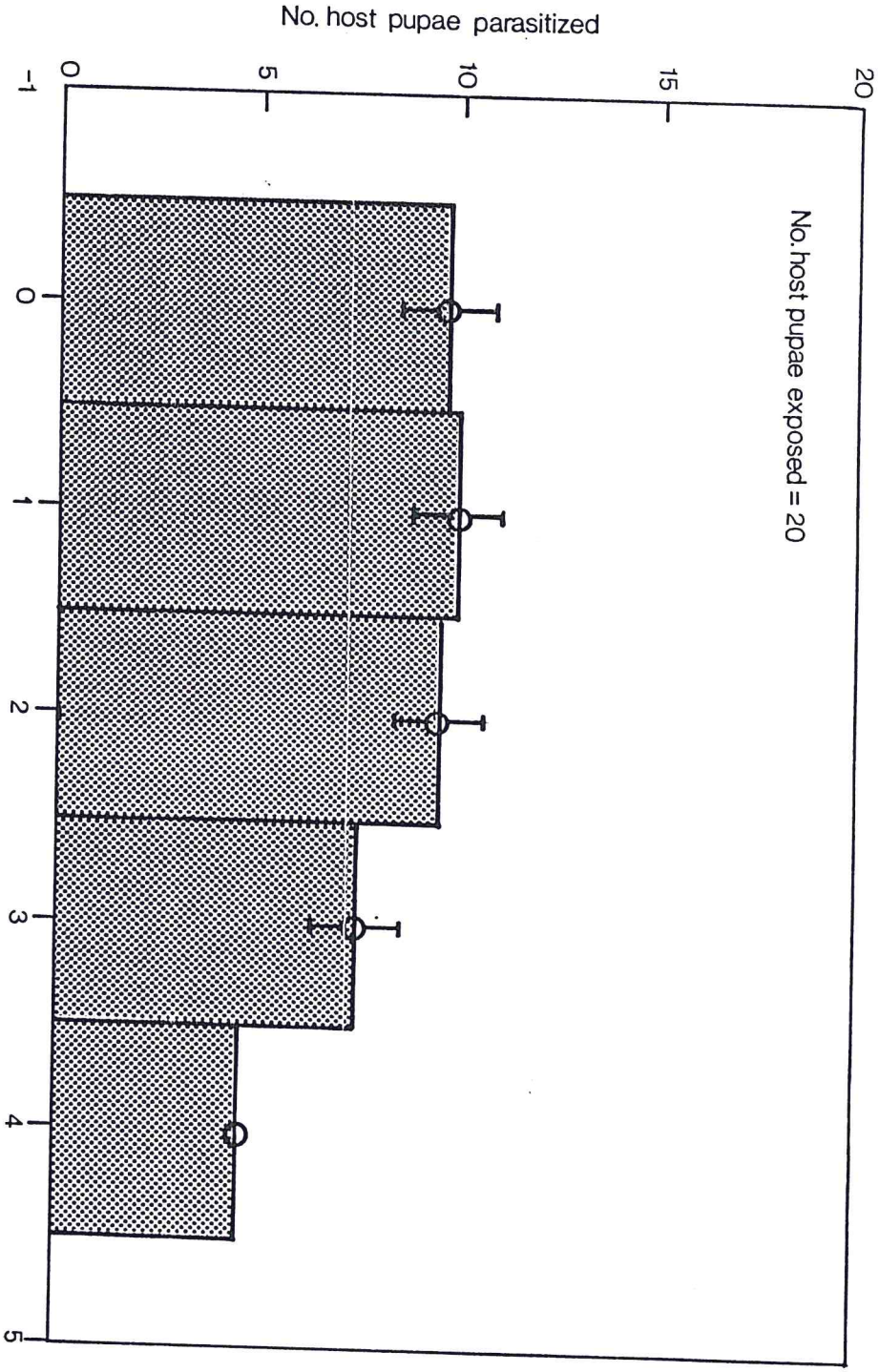

Fig. 3 Effect of female P. furvus age on parasitism

The results show that fifth day old host pupae of *C. partellus* can only be parasitized by the female *P. furvus* when the latter is two days old (Table 23).

Similarly, The results in study shows a significant difference in the number of eggs laid in relation to interactions of host pupae *B. fusca* and parasitoid age except where the host pupal age remains either zero or eight-day-old (Table 22, Appendix 24). Interestingly, females were not able to insert their ovipositors in host pupae that were $\leq$ 6 days old (*C. partellus* and $\leq$ 9 days old *B. fusca*. Host pupae of *C. partellus* and *B. fusca* that were $\cdot$ 6 days old and $\cdot$ 9 days old, respectively escaped parasitism and developed normally (Tables 22 and 23).

Looking in to the interaction of host (*B. fusca*) and parasitoid age in relation to the latter's development, it was found that the developmental period of the immatures did not vary drastically in relation to age eventhough, the difference was significant at 5 % level at four, seven and eight-day-old *B. fusca* pupal age (Table 24, Appendix 25). The longest developmental period was observed when two day old female parasitoids were allowed to attack a four or five-day-old pupae of *C. partellus* (Table 25). Development of parasitoids on 0-day-old *C. partellus* pupae was not significantly affected when parasitoids of the age groups 0,

TABLE 22

Influence of host age B. fusca on P. furvus fecundity (No.eggs laid/host pupae).

Host age (days)	Parasitoid age (days) 0	1	2	3	4
0	135.00 ±9.65 a	118.50 ±13.56 a	123.00 ±5.67 a	131.75 ±6.52 a	114.50 ±6.60 a
1	157.75 ±5.99 a	135.50 ±4.80 ab	129.50 ±8.45 bc	116.75 ±4.66 bc	109.25 ±5.64 c
2	154.25 ±6.07 a	137.00 ±8.53 a	132.25 ±8.43 ab	109.75 ±9.51 b	108.25 ±10.17 b
3	130.25 ±4.82 ab	148.00 ±6.15 a	132.00 ±6.09 ab	110.50 ±11.33 b	105.50 ±11.71 b
4	129.50 ±5.17 a	130.00 ±6.49 a	130.50 ±8.70 a	96.25 ±4.13 b	105.00 ±11.68 b
5	119.50 ±10.27 ab	120.00 ±6.89 ab	123.50 ±9.11 a	100.50 ±6.58 ab	99.50 ±6.50 b
6	126.25 ±4.58 a	124.00 ±4.65 a	101.50 ±5.54 b	105.75 ±7.65 b	85.00 ±3.34 c
7	91.75A ±3.90 ab	92.75 ±4.83 ab	96.75 ±6.00 a	85.25 ±2.92 ab	81.75 ±4.53 b
8	86.25 ±8.07 a	84.75 ±4.42 a	92.75 ±10.37 a	76.75 ±4.34 a	76.50 ±7.28 a

Means in the same row followed by different letters are significantly different at 5% level by DMRT.

TABLE 23

Effect of host age (C. partellus) on P. furvus

Fecundity (No.eggs laid/host).

Host age (days)	Parasitoid age (days) 0	1	2	3	4
0	135.25 ±9.29 a	144.75 ±8.53 a	132.00 ±0.41 a	133.75 ±3.85 a	121.75 ±15.67 a
1	146.00 ±8.50 a	145.50 ±3.57 a	127.00 ±0.41 b	123.50 ±3.96 b	122.25 ±6.57 b
2	152.00 ±2.48 a	145.75 ±3.04 a	145.75 ±0.47 a	124.75 ±2.84 b	117.75 ±13.46 b
3	151.50 ±3.66 a	147.00 ±4.67 a	115.50 ±0.65 b	118.50 ±17.70 b	99.50 ±6.48 b
4	123.25 ±15.12 a	124.25 ±6.62 a	110.25 ±1.31 a	97.75 ±6.3 a	102.75 ±5.77 a
5	0.00 ±0.00 b	0.00 ±0.00 b	86.25 ±2.62 a	0.00 ±0.00 b	0.00 ±0.00 b

Means in the same row followed by different letters are significantly different by DMRT. ($P<0.05$).

Table 24

Effect of host age (B. fusca) on P. furvus developmental period (days)

HOST AGE (days)+SE	PARASITOID AGE 0	1	2	3	4
0	20.00+0.42a	20.00+0.42a	19.26+0.28a	20.37+0.68a	20.43+0.52a
1	19.87+0.58a	19.75+0.57a	19.24+0.22a	20.12+0.36a	20.18+0.35a
2	19.93+0.72a	19.75+0.50a	20.16+0.17a	19.56+0.52a	19.94+0.41a
3	19.56+0.25a	19.25+0.39a	20.17+0.17a	19.25+0.27a	19.50+0.31a
4	20.68+0.57a	20.25+0.27ab	20.41+0.11ab	19.87+0.41ab	19.50+0.31b
5	19.75+0.17a	19.93+0.06a	20.25+0.11a	20.06+0.41a	20.00+0.41a
6	21.00+0.42a	20.68+0.23a	20.42+0.25a	21.06+0.54a	20.50+0.36a
7	21.31+0.56a	21.00+0.51a	18.13+0.12b	21.50+0.51a	22.12+0.68a
8	21.18+0.58a	21.81+0.49a	17.57+0.22b	21.43+0.64a	22.06+0.23a

Means in the same row followed by different letters are significantly different (DMRT).

TABLE 25

Influence of the age of C. partellus pupae on P. furvus developmental period (days).

Host age (days)	Parasitoid age (days) ±SE. 0	1	2	3	4
0	19.75 ±0.47 ab	19.75 ±0.25 ab	21.00 ±0.41 a	19.50 ±0.28 b	19.25 ±0.47 b
1	19.75 ±0.25 a	20.50A ±0.28 a	19.75 ±0.47 a	20.00 ±0.71 a	19.75 ±0.25 a
2	20.50 ±0.64 a	20.25 ±0.25 a	19.75 ±0.25 a	20.00 ±0.41 a	20.00 ±0.41 a
3	20.25 ±0.25 a	20.50 ±0.64 a	19.75 ±0.25 a	20.75 ±0.25 a	20.00 ±0.41 a
4	20.50 ±0.28 a	20.25 ±0.63 a	21.00 ±0.41 a	20.00 ±0.41 a	20.00 ±0.41 a
5	0.00 ±0.00 b	0.00 ±0.00 b	21.25A ±0.47	0.00 ±0.00 b	0.00B ±0.00

Means in the same row followed by different letters are significantly different at 5% level by DMRT.

1, 3 and 4 were used (Table 25, Appendix 27). However, at any other particular host age (1-4), developmental period was not significantly affected by parasitoid age (Table 25). Nevertheless, 5 day old *C. partellus* pupae were parasitized only by 2-day-old female parasitoids, where the parasitoid development took 21 days (Table 25).

The results show that when 0-4-day-old parasitoids were presented with *B. fusca* pupae of varying age (0-8-day-old) there was a significant difference at 5 % level in their progeny production. However, progeny production of different age groups of the female *P. furvus* did not vary significantly when less than a day old host pupae of *B. fusca* were offered (Table 26, Appendix 28). Also, parasitoid age did not affect progeny production significantly when seven day old or eight day host pupae of *B. fusca* were offered.

Table 27 shows that when one day old *C. partellus* pupae were presented with female *P. furvus* of different age groups (0-3-day-old), there was no significant difference in their progeny production. The mean values for this biological parameter were : 103.50, 114.25, 109.25 and 101.50 per host pupa. Similarly, progeny production did not vary significantly when various parasitoid age groups (0-2-day-old) were presented with *C. partellus* pupae of 0-3-day-old (Table 27, Appendix 29).

TABLE 26

Combined effects of host (*B. fusca*) and parasitoid (*P. furvus*) ages on progeny production

Host age (days)	PARASITOID AGE IN DAYS 0	1	2	3	4
0	118.50 +6.03 a	116.75 +8.68 a	120.50 +0.28 a	119.00 +4.49 a	108.25 +4.57 a
1	117.50 +4.17 a	114.00 +4.45 a	119.25 +0.25 a	117.25 +3.84 a	102.50 +2.10 b
2	121.75 +6.98 a	120.50 +4.69 ab	119.50 +0.64 ab	119.75 +1.11 ab	109.25 +4.25 b
3	127.25 +5.34 a	127.75 +5.02 a	125.25 +0.75 a	104.75 +3.70 b	107.50 +3.59 b
4	125.00 +4.37 a	120.50 +6.46 ab	124.25 +0.63 a	106.50 +5.69 b	104.75 +2.95 b
5	120.00 +5.36 a	115.25 +4.97 a	119.50 +0.28 a	112.25 +2.78 a	94.50 +5.39 b
6	100.50 +4.21 a	92.50 +5.67 ab	103.00 +0.91 a	88.75 +3.96 bc	80.75 +3.52 c
7	72.50 +3.42 ab	75.00 +5.73 ab	87.75 +1.03 a	72.75 +7.42 ab	65.50 +8.27 b
8	57.75 +5.58 ab	68.75 +7.98 ab	72.50 +0.86 a	55.00 +3.74 b	60.75 +0.85 ab

Means in the same row followed by different letters are significantly different at 5 % level by DMRT.

TABLE 27

Combined effects of host (C. partellus) and parasitoid (P. furvus) ages on progeny production (±SE).

Host age (days)	Parasitoid age (days)				
	0	1	2	3	4
0	109.25 ±5.28 a	105.50 ±6.78 ab	103.75 ±4.76 ab	92.00 ±2.79 b	91.00 ±3.55 b
1	103.50 ±7.07 a	114.25 ±2.28 a	109.25 ±5.21 a	101.50 ±5.62 a	86.25 ±2.86 b
2	110.00 ±4.71 a	110.25 ±4.98 a	110.50 ±2.17 a	91.75 ±1.79 b	85.00 ±2.27 b
3	102.50 ±2.90 ab	110.75 ±4.95 a	110.25 ±6.53 a	92.00 ±2.04 bc	82.75 ±2.09 c
4	86.00 ±3.63 a	80.25 ±1.11 ab	73.00 ±2.16 b	73.00 ±7.05 b	70.00 ±4.14 b
5	0.00 ±0.00 b	0.00 ±0.00 b	78.25 ±4.78 a	0.00 ±0.00 b	0.00 ±0.00 b

Means in the same row followed by different letters are significantly different at 5% level by DMRT.

When Duncan's Multiple Range Test (DMRT) was done to separate means, it was found that the interaction of host (*C. partellus*) and parasitoid age affected significantly the sex ratio of the parasitoid (Table 28). Table 28 shows that there was a significant difference at 5 % level in the percentage of males per host pupa (*C. partellus*) parasitized due to interaction of host and parasitoid age. Preponderance of males were observed as host and / or parasitoids grow old (Table 28, Appendix 30).

Interestingly, the results show that there was no significant difference in male progeny when two-day-old *C. partellus* pupae were allowed to host female *P. furvus* of various age groups (0-4-day-old) (Table 28). The mean value for this parameter was found to remain more or less constant and were : 26.06, 29.92, 23.96, 29.55 and 31.65 % male progeny per *C. partellus* host pupae (Table 28). The highest mean value for this parameter (65.03 %) was observed when host age was four day old and the female parasitoid three day old (Table 28).

However, it was observed that when a 4-day-old or 7-day-old *B. fusca* pupae were offered to be parasitized by *P. furvus* females of various age groups (0-4-day-old) there was no significant difference in their sex ratio (Table 29). The % mean values of this parameter were : 24.75, 26.00,

TABLE 28

Combined effects of host (C. partellus) and parasitoid (P. furvus) ages on Sex-ratio (% male/progeny)

Host (days)	Parasitoid age (days)				
	0	1	2	3	4
0	25.67 ±1.08 b	25.65 ±0.81 b	24.76 ±1.47 b	27.49 ±0.68 ab	30.69 ±1.84 a
1	24.65 ±1.01 b	25.14 ±1.54 b	26.18 ±1.86 b	30.67 ±1.16 a	31.85 ±1.64 a
2	26.06 ±1.61 a	29.92 ±2.84 a	23.96 ±0.78 a	29.55 ±3.07 a	31.65 ±2.17 a
3	33.83 ±1.30 a	36.41 ±2.25 b	43.80 ±2.29 a	45.68 ±2.54 a	49.16 ±2.06 a
4	58.00 ±4.37 ab	52.53 ±4.70 b	57.16 ±4.27 ab	65.03 ±1.17 a	57.99 ±3.94 ab
5	0.00 0.00 b	0.00 0.00 b	63.85 ±2.10 a	0.00 0.00 b	0.00 0.00 b

Means in the same row followed by different letters are significantly different at 5% level by DMRT.

Table 29

Combined effects of host (B. fusca) and parasitoid (P. furvus) ages on sex-ratio. (% male/progeny)

Host age (days)±SE	Parasitoid age (days) 0	1	2	3	4
0	24.50 ±0.64 b	23.75 ±0.85 b	24.50 ±0.64 b	25.25 ±0.85 b	31.25 ±1.65 a
1	24.00 ±1.08 b	24.50 ±0.64 b	24.75 ±0.47 b	30.25 ±1.25 a	30.50 ±1.55 a
2	25.50 ±0.64 b	23.75 ±0.85 b	25.00 ±0.41 b	29.50 ±0.64 a	32.25 ±1.25 a
3	23.75 ±0.85 b	25.50 ±1.93 ab	23.75 ±1.63 b	29.00 ±1.08 ab	31.50 ±2.90 a
4	24.75 ±0.85 a	26.00 ±2.12 a	28.50 ±0.64 a	28.75 ±1.43 a	30.25 ±2.65 a
5	25.25 ±0.62 c	26.00 ±1.22 bc	34.00 ±0.41 a	31.00 ±0.81 ab	33.00 ±3.02 a
6	26.25 ±0.75 b	27.25 ±1.60 b	44.00 ±0.71 a	31.50 ±0.95 a	33.25 ±2.13 a
7	33.75 ±1.93 a	33.50 ±0.64 a	49.25 ±1.11 a	35.75 ±0.85 a	35.75 ±0.47 a
8	31.50 ±0.95 b	32.25 ±0.47 b	60.75 ±0.47 a	36.00 ±0.41 b	39.00 ±1.22 b

Means in the same row followed by different letters are significantly different (DMRT).

28.50, 28.75 and 30.25 for 4-day-old host pupae and 33.75, 33.50, 49.71, 35.75 and 35.75 % per host progeny for 7-day-old *B. fusca* pupae (Table 29). Generally, the results show a preponderance of males as hosts and parasitoids grew older (Table 29, Appendix 31).

4.6. Effect of Diet on P.furvus adult longevity and fecundity

Activities which are known to be essential in terms of the influence of the nutritive quality of food are egg production. In the present study, it was found that the number of eggs in the ovarioles per female *P. furvus* remained more or less constant in relation to age and different concentrations of sucrose and honey for the adult parasitoids (Table 30). The lowest mean value for this biological parameter was 139 eggs per female, and the highest mean value was found to be 159 eggs per female parasitoid (Table 30, Appendix 32).

The results in this study show that the different honey and sucrose diets tested failed to show any significant difference in the female parasitoid's fecundity, and the number of eggs per female *P. furvus* remained more or less constant from zero to four-days-old (Table 30). The mean values for this parameter remained between 139-158 eggs/female parasitoid (Table 30).

Table 30

Influence of diet on P. furvus fecundity

Parasitoid age (days)	Number of eggs laid / female		
	Unfed	10 % Sucrose	10 % Honey
0	149.90±5.58 a	149.47±7.06 a	150.97±6.20 a
1	146.72±4.37 a	151.21±5.80 a	152.05±7.10 a
2	158.75±7.63 a	150.46±6.53 a	158.83±5.50 a
3	157.75±11.27 a	153.75±3.32 a	149.47±7.25 a
4	139.00±8.43 a	154.13±2.96 a	152.64±4.92 a

Means in the same column followed by the same letters are not significantly different at 5 % level by DMRT

As regards . the influence of diet on ovipositional period of the female *P. furvus*, the results showed that there was no significant ($P \leq 0.05$) differences in this parameter for all diet concentrations tested, and the ovipositional period remained around one-day for all treatments (Table 31, Appendix 33).

Adult longevity of both males and females of *P. furvus* tested with different concentrations of sucrose did not show any significant variations except when fed on 5 % sucrose solutions (Table 32). The mean values for 5 %, 10 %, 30 % and 40 % for this biological parameters were : 2.53; 11.53; 5.20; 4.99 and 4.79 for males and 6.26; 12.39; 6.33; 5.46 and 5.60 for female longevity. 10 % sucrose solutions gave the highest mean value of adult longevity with an average of 11.53 days and 12.39 days for males and females respectively. Even though, the diet could support males for 14 days and females for 16 days in few occasions. With 40 % sucrose solutions, female parasitoids longevity remained 5-6 days with a range of 0-9 days (Table 32).

Interestingly, adult longevity varied significantly ($P \leq 0.05$) in all honey concentrations tested and the females lived longer than the males in each of the treatments (Table 33). With 40 % honey concentration diets, female parasitoids could not live beyond the 11^{th} day after

Table 31

Influence of diet on ovipositional period of the female P. furvus

Concentrations (%)	Ovipositional period (days) (±SE)	
	Sucrose	Honey
5	1.25 ±0.25 a	1.75 ±0.47 a
10	1.25 ±0.25 a	1.75 ±0.47 a
20	1.75 ±0.47 a	1.25 ±0.26 a
30	1.25 ±0.25 a	1.50 ±0.28 a
40	1.00 ±0.00 a	1.00 ±0.00 a
Distilled water	1.00 ±0.00 a	
Un fed	1.25 ±0.25 a	

Means in the same column followed by same letters are not significantly different at 5 % level by DMRT

Table 32.

Adult longevity of P. furvus at different Sucrose Concentrations.

Conc. (%)	Longevity (days) (±SE) Male	(Range)	Female	(Range)
5	2.53 ±0.40 b	(0-4)	6.26 ±0.46 a	(0-11)
10	11.53 ±0.52 a	(0-14)	12.39 ±1.08 a	(0-16)
20	5.20 ±0.44 a	(0-8)	6.33 ±0.79 a	(0-14)
30	4.99+0.21 a	(0-9)	5.46 ±0.29 a	(0-14)
40	4.79 ±0.20 a	(0-8)	5.60 ±0.38 a	(0-9)
Dist. water	1.73 ±0.12 b	(0-3)	2.66 ±0.18 a	(0-4)
Unfed	2.53 ±0.08 b	(0-3)	3.53 ±0.08 a	(0-4)

Means in the same column followed by different letters are significantly different at 5 % level by DMRT.

Table-33

Adult longevity of P. furvus at different honey concentrations

Conc. (%)	Longevity (days) (±SE)			
	Male	(Range)	Female	(Range)
5	7.67 ±0.38 b	(0-9)	11.06 ±0.19 b	(0-14)
10	10.86 ±0.49 a	(0-14)	14.19 ±0.53 a	(0-17
20	4.59 ±0.23 d	(0-7)	9.69 ±0.91 c	(0-18)
30	5.90 ±0.10 c	(0-9)	7.60 ±0.44 d	(0-14)
40	2.10 ±0.23 e	(0-4)	5.80 ±0.39 e	(0-11)
Dist. water	1.73 ±0.12 e	(0-4)	2.66 ±0.18 f	(0-4)
Unfed	2.53 ±0.08 e	(0-3)	3.53 ±0.08 f	(0-4)

Means in the same columns followed by different letters are significantly different at 5 % level by DMRT.

emergence. On the other hand, 20 % honey concentrations supported the parasitoids as long as 18 days (Table 33).

In general, the various honey concentrations tested showed a significant difference in the longevity of male and female parasitoids. The males lived longer with 10 % honey solutions, while males lived only 2 days with 40 % honey solutions (Table 33). Similarly, the longevity of female *P. furvus* varied significantly ($P \leq 0.05$) in the different honey solutions tested. The mean values for this parameter were : 11.06, 14.19, 9.69, 7.60 and 5.80 days for 5, 10, 20, 30 and 40 % honey solutions (Table 33).

Interestingly, 10 % sucrose and 10 % honey solutions gave the highest survival rates for both male and female parasitoids, with a range of longevity of 0-14-days and 0-16-days for males and females respectively (Table 32 and Table 33).

Results in the controls,i.e. distilled water and when starved gave the lowest mean value for both males and females longevity with an average survival of 1.73, 2.53 and 2.66, 3.53 days for males and females respectively (Table 32). The other treatments gave an intermediate range of mean values, they are also significantly different from each other as well as from the controls of distilled water and no food.

The different diet concentrations tested affected significantly *P. furvus* survival rates, and the diet treatment that gave the highest mean value for percentage mortality was distilled water with a mean value of 33.32 % for female parasitoids on their second day after emergence, and the lowest mean values were obtained with 10 % honey and 10 % sucrose solutions on their 14th day after emergence (Fig. 4, Appendices 34, 35). AS regards the percentage mortality for male parasitoids is concerned, the highest mean values were obtained from the controls i.e. the unfed ones with a value of 67 % in their second day after emergence, while the lowest mean value was recorded from 10 % of honey and 10 % sucrose solutions (Fig. 5). With 40 % sucrose solutions, the female parasitoids could not survive beyond the eighth day after emergence, while with 20 % honey diets, female parasitoids could live as long as 19 days. However, with male parasitoids 10 % honey and 10 % sucrose solutions gave the lowest mortality rates and reached 14 days after emergence (Fig. 5, Appendices 34, 35).

4.7. Effect of Superparasitism on the biology of the parasitoid

As expected, the results show that there was a significant difference in the number of eggs laid per host pupa in relation to parasitoid-host densities. The lowest

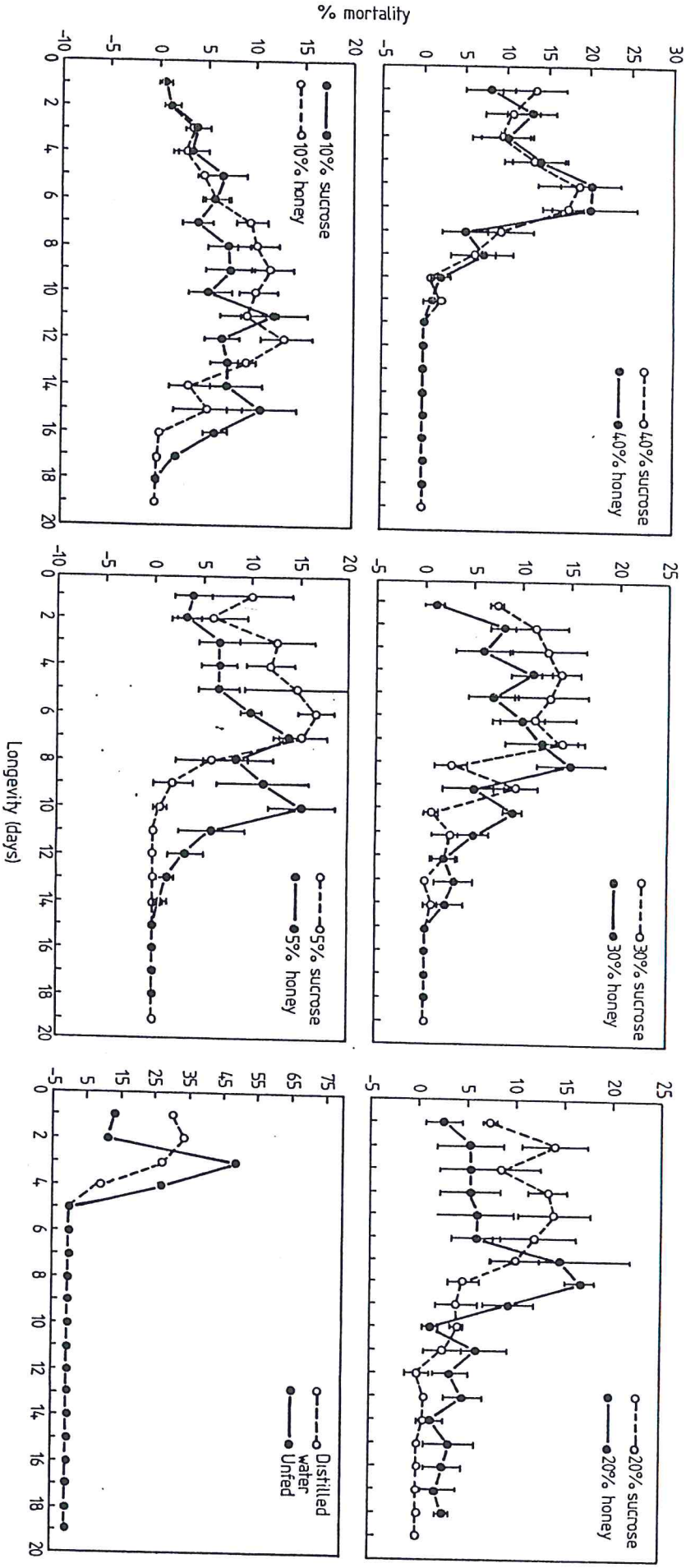

Fig. 4 Effect of diet on *P. furvus* female longivity (days S.E.% mortality)

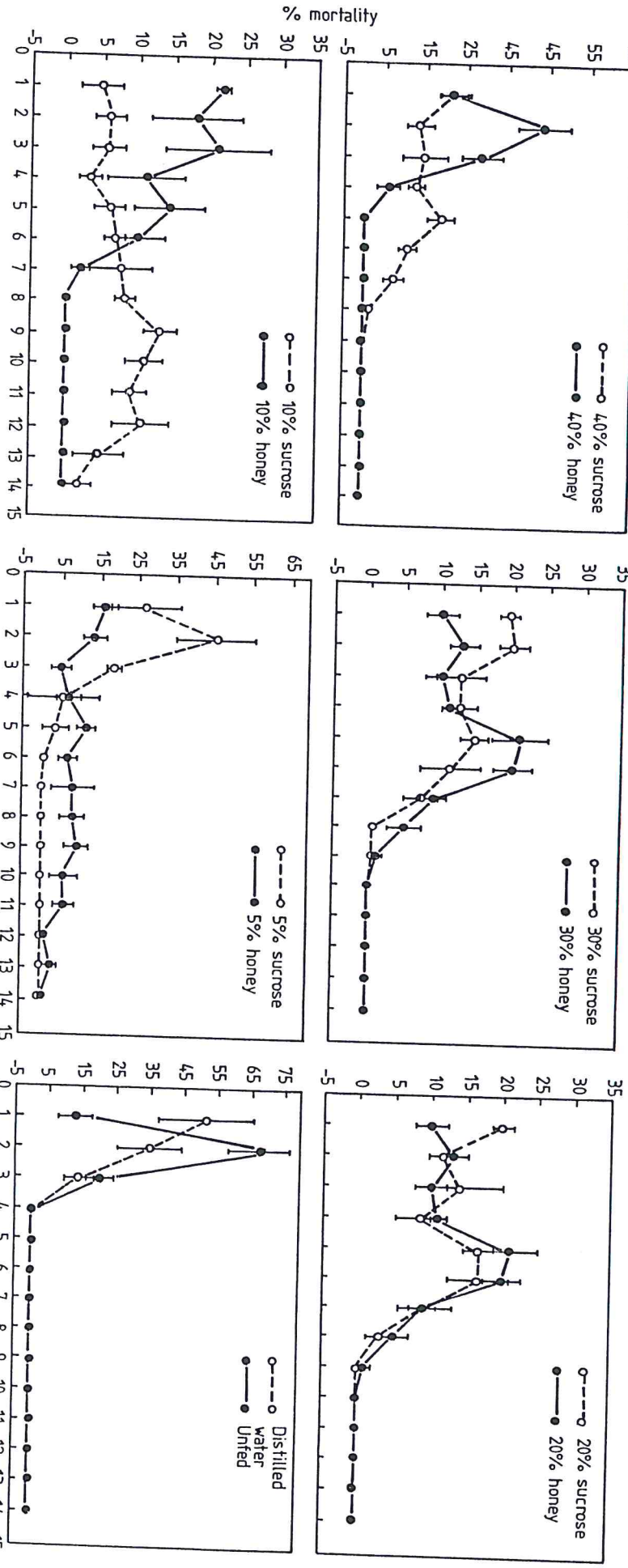

Fig. 5 Effect of diet on *P. furvus* male longivity (days S.E.% mortality)

mean value of eggs laid per host pupa was recorded when One gravid female parasitoid was exposed to two host pupa and the mean values of this parameter were : 77.25 ± 7.41 and 87.00 ± 8.04 for 12 hrs and 24 hrs. exposure times (Table 34, Fig. 6, Appendix 38).

The highest mean value of host pupae successfully parasitized (85 % and 87.50 %) was recorded at the 2:1 parasitoid-host ratio population density in hosts exposed for 12 and 24 hours (Table 35) and (Fig. 7).

Thirty five attacked hosts received an average of 250.50 eggs each (range 0-252) (Table 34), and 35 such hosts produced on the average 128 mature progeny each (range 0-148) (Table 35). At this density, there was no effect of superparasitism, small part of the host pupa usually un consumed.

Parasitoid survival and hence percentage successful parasitism was only 30 % at the higher parasitoid population densities (parasitoid-host ratio of 5:1) in hosts exposed for 12 hours; here there was an effect of superparasitism, 433 eggs on the average being laid on each *C. partellus* pupa (Table 34) and (Fig. 7), 65 mature progeny on the average being reared and the hosts usually being almost completely eaten.

TABLE 34.

Effect of Superparasitism on P. furvus oviposition at different exposure times

Parasitoid host ratio	Exposure Time: 12 hrs eggs laid/host pupa (X ± S.E.)	Exposure Time: 24hrs eggs laid/host pupa (X ± S.E.)
1:1	126.25 ±4.11 d	131.00 ±4.41 d
1:2	77.25 ±7.41 e	87.00 ±8.04 e
2:1	230.25 ±9.28 c	250.50 ±1.19 c
2:2	111.75 ±5.17 d	149.75 ±13.03 d
5:1	433.25 ±17.09 a	477.50 ±15.52 a
5:2	382.00 ±10.79 b	376.00 ±9.19 b

Means in the same column followed by different letters are significantly different at 5 % level by DMRT

TABLE 35.

Effect of parasitoid-host ratio of *P. furvus* to *C. partellus* pupae on parasitism at different exposure times

Para-host ratio	No.of host pupae exposed to parasitoids	No.host pupae parasitized/ exposure time (hours)		No. parasitoids produced/parasitized host pupae (+SE)		% host successfully parasitized (+suitability)	
		12hrs	24hrs	12hrs	24hrs	12hrs	24hrs
1:1	40	28	30	85.50+8.76b	82.67+17.12b	70	75
1:2	40	18	20	47.05+6.10c	64.10+7.85b	45	50
2:1	40	34	35	119.50+3.27a	127.50+5.24a	85	87.50
2:2	40	19	18	71.55+1.48bc	88.37+3.73b	47.50	45
5:1	40	40	40	69.60+3.54bc	65.35+5.33b	30	36
5:2	40	40	40	67.20+14.75bc	67.92+5.48b	38	39
		179	183				

Means in the same column followed by different letters are significantly different at 5 % level by DMRT.

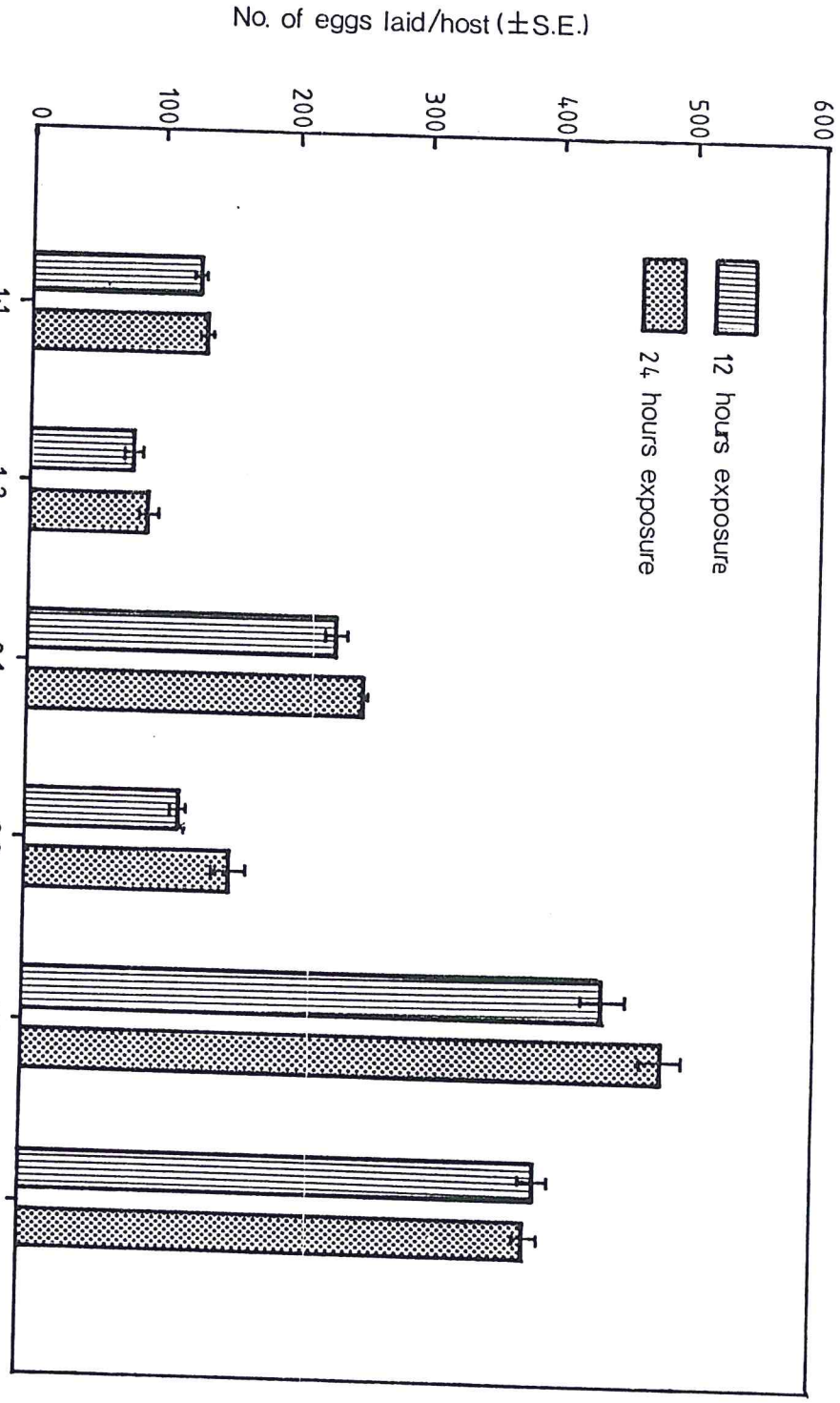

Fig. 6. influence of superparasitism on P. furvus Oviposition

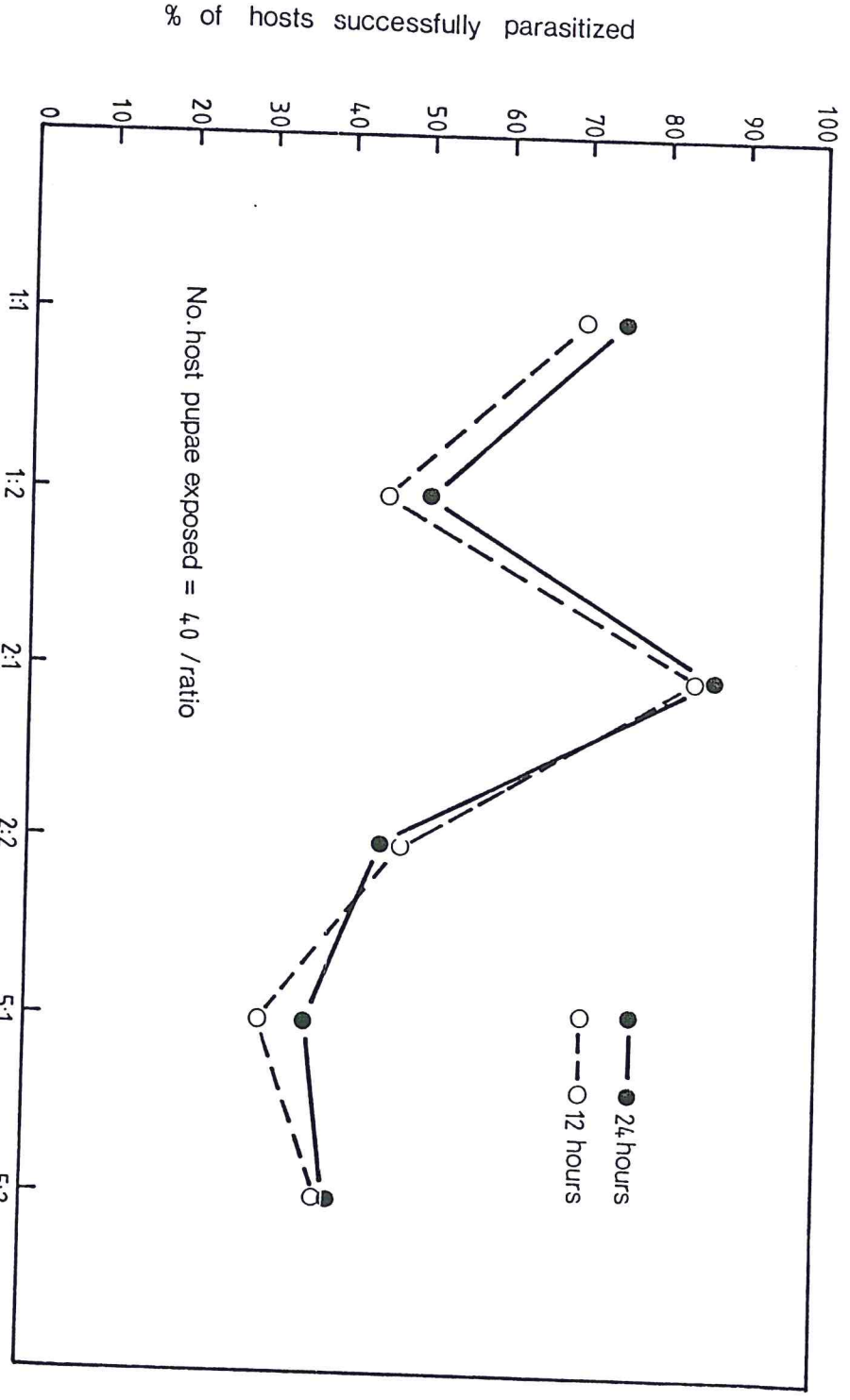

Fig.7. Influence of host - parasitoid ratio of P. furvus to C. partellus on parasitism

Superparasitism has no direct bearing on the developmental period of *P. furvus*. Rates of *P. furvus* development were similar on non-superparasitized and superparasitized hosts. Mean developmental time, from egg oviposition to adult emergence, for 179 parasitized host pupae exposed for 12 hours (Table 35); ranged from 17.60 to 19.30 days, and for 183 parasitized host pupae exposed for 24hours (Table 35); the development time ranged from a lower value of 18.81 days to a higher value of 19.77 days (Table 36). Thus, a significant retardation in the development is not noticed when exposure time remained for 12 hours (Table 36).

The results of the present studies show that superparasitism has a negative effect on the parasitoid's progeny production per host pupa. There was a significant reduction in the progeny production per host pupa as the number of parasitoid-host ratio increases. Sixty five mature progeny per host pupa were observed on 5:1 parasitoid-host ratio, while one hundred twenty eight mature progeny emerged per host pupa when the parasitoid-host ratio was 2:1 (Table 36, Appendix 36)

Superparasitism in *P. furvus* is accompanied by a preponderance of males; and as the number of parasitoids that develop on a host pupa increases, the number of males

Table 36.

Effect of Superparasitism on the parasitoid's development and progeny production at different exposure times

Parasitoid-host ratio	Exposure Time 12hrs		24hrs	
	Development (+S.E)	Progeny Production/ host pupa (+S.E.)	Development (+S.E.)	Progeny Production/ host pupa (+S.E.)
1:1	19.03 +0.23a	85.50 +8.76b	19.77 +0.23a	82.67 +17.12b
1:2	17.60 +1.20a	47.05 +6.10c	18.82 +0.21b	64.10 +7.85b
2:1	19.37 +0.07a	119.50 +3.27a	19.50 +0.00ab	127.50 +5.24a
2:2	19.30 +0.12a	71.55 +1.48bc	19.50 +0.11ab	88.37 +3.73b
5:1	18.57+ 1.19a	69.60 +3.54bc	18.97 +0.26b	65.35 +5.33b
5:2	19.27 +0.22a	67.20 +14.76bc	18.81 +0.32b	67.92 +9.13b

Means in the same column followed by different letters are significantly different at 5 % level by DMRT

produced also increases. The percentage of males in adult *P. furvus* reared on superparasitized hosts (i.e. when the parasitoid-host ratio is 5:1 or 5:2) was higher (45.80 % and 48.05 %) for 5:2 and 5:1 respectively, than that obtained from non-superparasitized hosts (Table 37).

In the present studies, the results reveal that the percentage of male per female progeny remained more or less constant in the parasitoid-host ratios of 1:1 and 2:2 for both 12 hours and 24 hours exposure times, and the mean values for this biological parameters were : 23.42 and 21.08 when exposure time was 12 hours. Similarly, percentage male per female progeny remained more or less the same at 24 hours exposure time, and the mean values for this biological parameters were : 23.68 % and 25.97 % for parasitoid-host ratios of 1:1 and 2:2, respectively (Table 37, Appendix 37).

In *P. furvus*, a detailed study of the measurements of adult parasitoids has shown that there was a significant size reduction when parasitoids were developed on superparasitized host pupae. The mean values for this biological parameter were : 1.30 mm and 1.74 mm for males and females from superparasitized host pupae. Similarly, the mean values for male and female sizes for non-superparasitized host pupae were : 1.50 mm and 2.25 mm, respectively (Table 38 Fig. 8, Appendix 39). Interestingly, the variation between male and female sizes remained un

Table-37.

Influence of superparasitism of P. furvus on Sex-ratio at different exposure times

Parasitoid host ratio	Exposure Time 12hrs % male progeny per host	24hrs % male progeny per host
1:1	23.42 ±1.15 b	23.68 ±1.36 c
1:2	14.51 ±0.84 c	18.52 ±0.42 d
2:1	46.54 ±3.41 a	49.14 ±1.38 a
2:2	21.84 ±1.27 b	25.97 ±0.69 c
5:1	48.05 ±3.64 a	42.11 ±2.33 b
5:2	45.80 ±1.22 a	42.64 ±1.06 b

* Means in the same column followed by same letters are not significantly different at 5 % level by DMRT.

Table 38

Influence of Superparasitism on P. furvus (Gah.) adult size (mm)

Treatment	Male (± S.E.)	Female
Superparasitized	1.38 ± 0.03 b	1.74 ± 0.01 a
non-superparasitized	1.50 ±0.02 b	2.25 ± 0.3 a

Means in the same row followed by different letters are significantly different at 5 % level by DMRT.

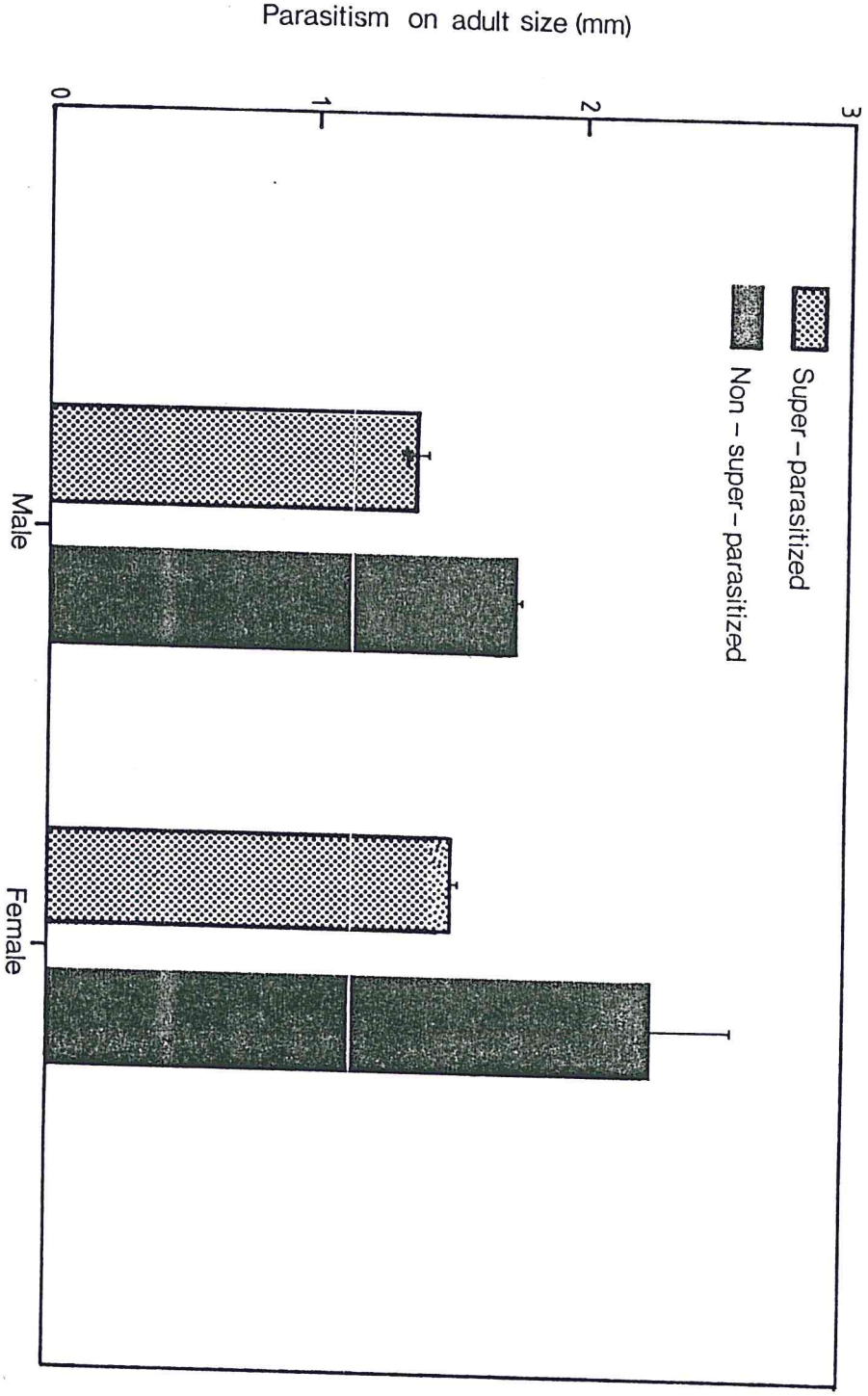

Fig. 8. Effect of Superparasitism on P. furvus adult size (mm)

affected whether hosts are superparasitized or non-superparasitized (Table 38).

4.8. Intrinsic rate of natural increase of P. furvus on C. partellus pupae

The data on the reproductive potential of *P. furvus* on *C. partellus* pupae are presented in Table 39, it is revealed that during the laboratory study, the maximum longevity of the reproducing female was 14 days, and the maximum period of reproduction was 2 days.

There was 100 % survival at the time mother *P. furvus* started ovipositing eggs but the survival rate decreased after the 2nd day of reproduction. The parasitoid started ovipositing eggs on the same day of emergence with a mean production of 80 % of its eggs.

The maximum average number of progeny was produced on the 1st day after emerging from the pupae. The mean number of females progeny produced per female over the entire reproductive period was 87. The net reproductive rate or the net replacement rate **(Ro)** was calculated to be 335.30.

The species had an approximate generation time **(Tc)** of 21.41 days, and a true generation time of 20 days. The parasitoid *P. furvus* would thus multiply 335.30 times in a single generation time occupying 20.50 days (Table 39).

Table 39.

Life table statistics of P. furvus on C. partellus pupae in the laboratory at MPFS. (26±1°C / 65±5% R.H.)

Pivotal age(days)	Proportion of femalelive at age x	No. of female progeny/female		
x	Lx	mx	Lxmx	xLxmax
0-19	1.00	immature stages		
20	1.00	95.00	95.00	1900.00
21	1.00	88.00	88.00	1848.00
22	0.95	76.00	72.20	1588.40
23	0.90	89.00	80.10	1842.30
24	0.80	00.00	0.00	0000.00
25	0.60	00.00	00.00	0000.00
26	0.50	0.00	00.00	0000.00
27	0.45	0.00	00.00	0000.00
28	0.35	0.00	00.00	0000.00
29	0.35	0.00	00.00	0000.00
30	0.20	0.00	00.00	0000.00
31	0.20	0.00	00.00	0000.00
32	0.15	0.00	00.00	0000.00
33	0.10	0.00	00.00	0000.00
34	0.00	0.00	00.00	0000.00
Total		348.00	335.30	7178.70

The cohort had the capacity for natural increase (rc) as 27 whereas, the true intrinsic rate of increase, determined was 91.06, the parasitoid had the finite rate of increase as 1.30, which means that the population would multiply 1.31 times per day at laboratory temperature fluctuating between 25 to 27 °C under relative humidity level of 65 ± 5 %.

CHAPTER FIVE

5.0. DISCUSSION

5.1. Seasonal Survey for the Incidence of P. furvus (Gah.) in maize fields in different agroecological localities in Kenya

Though *P. furvus* is known in East Africa especially in Kenya, very little information is available about its seasonal occurence and abundance relative to the host insect and other parasitoids.

An attempt study the temporal distribution pattern of the parasitoid in different agroecological localities in Kenya showed that the parasitoid was more abundant in the dry humid localities like Mombasa locality.where over 46 % parasitism on *B. fusca* pupae was recorded. Observations in different agroecological localities in Kenya during 1990 and 1991 indicated higher parasitization by *P. furvus* both in *C. partellus* and *B. fusca* pupae collections in Mombasa locality than in any other surveyed localities in Kenya.

Differences in estimates of parasitism by *P. furvus* in the different agroecological localities in Kenya can be quite marked. Overall parasitism was very low (8 %, 6 % and 3.75%, 7.9 %) for *C. partellus* and *B. fusca* in Kakamega locality followed by Kisumu locality. This apparent low

incidence of *P. furvus* parasitism in Kakamega and Kisumu localities at least partially explains that the parasitoid is either too rare or appear in the field too late to have an impact on the pest population density. Another explanation could be the relatively low densities of second generation pupae of *C. partellus* and *B. fusca* in these two localities at harvest time.

However, rates of parasitization may underestimate the total impact of *P. furvus* on populations of *C. partellus* and *B. fusca* pupae, because *P. furvus* inflicts mortality as high as 50 % by making wounds on the host pupae in an attempt to parasitize which contributes to host mortality (Pfannenstiel, 1988). Thus, in conjunction with other mortality factors in the system (e.g. other natural enemies, resistant cultivars, etc) *P. furvus* may be effective in reducing populations of cereal stem borers.

In their extensive field survey for parasitoids of graminaceous stem borers in East Africa, Mohyuddin and Greathead (1970) similarly noted *P. furvus* species to be more abundant in humid / drier areas like Mombassa. Since the per centage parasitism by *P. furvus* in general is very low in all agroecosystems surveyed, the possibility of using other mortality factors in an effective biological control programme for cereal stem borers in these agroecosystems would have to be explored in addition to manipulating the

other parasitoids that already exist, although Greathead and Waage (1983) were sceptical about dramatic success being achieved with natural enemies on annual crops.

A primary consideration for the establishment and performance of an introduced parasitoid in these localities would be its ability to adapt to long dry spells in the closed season, when host insects are either in diapause or become very scarce. Otherwise, the species would have to be amenable to mass production for inoculative or inundative releases.

5.2. P. furvus : Parasitization of C. partellus pupae and its attraction to two cultivars of maize in the field.

Parasitism of *C. partellus* pupae in the field under net caged conditions during the long rainy season of 1990 was high (96 %). However, parasitism increased to 65 % during the Short rainy season of 1990. The difference between the two seasons were partly due to the different release groups of the parasitoids. During the long rainy season of 1990 parasitoids from a field collected host pupae were used for the release while during the short rainy season of 1990 and the following long rainy season of 1991, laboratory reared host pupae on artificial diet were used for the release and so parasitism decreased from 96 % to 65 % excluding parasitism without progeny.

In addition to mortality due to parasitization, *P. furvus* was responsible for mortality of *C. partellus* pupae as high as 12 % in the field which did not result in parasite progeny. This is in parallel with work done by Pfannenstiel (1988) who reported that *P. furvus* was responsible for mortality (excluding successful parasitization) as high as 50 % among *E. loftini* under caged field, and he attributed this type of mortality to ovipositor insertion with out oviposition.

The present study indicate that *P. furvus* is capable of locating and parasitizing *C. partellus* pupae in maize stalks. However, mean percent parasitization never exceeded 96 % under netted field in any one season.

5.3. Investigation on the nature of trophic interactions between the plant, host insect and the parasitoid.

From the laboratory demonstration of host-seeking semiochemicals,(*C. partellus* and *B. fusca* larval frasses and their pupae) with the control (no stimulant), there were no significant differences (except for a combination of frass and the pupa) in the three biological parameters considered (Table 7).

Larval frass and odour from the host pupa are known to have an olfactory stimulant effect. However, the increases in biological activity reported in the present study, were not solely attributed to the presence of these olfactory stimuli in such a confined arena like the glass vial, use of the visual signals by the parasitoid to locate the host or its frass can not be ruled out.

Results from the above experiments were inconclusive, since the visual component of the host-seeking behaviour might have played a role.

The present study did not investigate the effect of olfactory cues in the field but it would concur with Lewis et *al*. (1971) observation that such host-seeking stimulants could play an important role in concentrating and holding parasitoids in a general habitat area.

The results clearly demonstrate that *P. furvus* females can use olfactory cues to locate their hosts. Female parasitoids were attracted by a combination of odors from the frass and the host itself. Such attraction should increase the parasitoids'searching efficiency in the field since females would orient towards plants or plant parts on which stem-borers are present. However, care must be exercised in extrapolating laboratory results to field conditions, as positive responses in an olfactometer do not

imply longer- range attraction (Kennedy, 1965).

Female *P. furvus* did not respond to host frass or the host pupa alone in our tests. The parasitoids did show selective responses to the different host pupae and to their larval frasses. An alternative explanation to this is that *P. furvus* females may use other than olfactory means to locate the habitat of its host pupa, such as visual cues for example. Even though this parasitoid is closely associated with *C. partellus* and *B. fusca* pupae in Kenya, its host range eleswhere in the tropical world, includes *Sesamia calamistis* (Hampson) and *Coniesta ignefusalis* (Hampson) (Mohyuddin, 1970), it also attacks *Eoreuma loftini* (dyar) (Lep: Pyralidae), and *Diatraea grandiosella* (Dyar) (Lep: Pyralidae) (Overholt and Smith, 1989).

The present study does not prove long-range attraction of *P. furvus* to hosts of *C. partellus* and *B. fusca* pupae, but it clearly shows that once in the habitat of potential hosts, the searching female has the capacity to select, via olfactory and visual cues, areas where hosts are most likely to be available, but the actual mechanisms used by this parasitoid in host habitat selection remains to be elucidated.

5.4. Effect of Temperature and Relative humidity on P. furvus parasitism

The study dealing with temperature and relative humidity levels were designed to show separately the effect of temperature on development of parasitoids and on oviposition.

Bursell (1974) has already summarized the extensive literature on the relationship between temperature and insect development. The development physiology of the local populations of *P. furvus* may be closely adapted to the peculiarities of local climates. For example, more rapid development at 25 ± 1.5°C and 30 ± 1.5°C has been observed in *P. furvus* than at 20 ± 1.5°C under same humidity levels of between 60 and 80 %. Similar observations have been reported in populations of Lepidopterous species (Danilevskii 1965), aphids (Campbell et al.,1974), mites (Beck, 1968).

In the present study, neither oviposition nor development and hence no progeny production have been recorded at the extreme low temperature of 15 ± 1.5°C and at the highest temperature of 35 ± 1.5°C at all constant relative humidity levels tested. Becouse these extreme temperatures were found to affect the oviposition behaviour of the insect parasitoid and were found to be unfavorable

for *P. furvus* development. Similar adverse relationship between temperature and developmental period have been reported by Lund (1934), Volden and Chiang (1982) and Harrison *et al.* (1985) in *Trichogramma minutum, T. ostriniae* and *T. exiguum* and *T. praetiosum,* respectively.

In the present study, exposing *C. partellus* pupae to mated female *P. furvus* adults for only 24 hours at constant temperature 20 ± 1.5°C and then transferring them to 25 ± 1.5°C had the effect of imposing growth rate and reducing the developmental period of the filial generation (Table 11).

Similarly, Starks (1945) had also advocated that rearing some species of parasitoids under fluctuating conditions would lead to the improvement in the parasitic ability of the parasitoids in mass-release programmes.

Temperature extremes, at the time of oviposition, can be a deterrent to parasitoid production possibly because the number of eggs deposited within individual pupa is reduced. Viable parasitoids did not emerge from parasitized pupae at 15 and 35 ± 1.5°C because these extreme temperatures were found to be unfavourable for *P. furvus* oviposition and / or development.

Thus, the criterion for optimum parasitoid production may not altogether be associated with unfavourable temperatures during oviposition but more importantly with temperatures at which parasitoid development takes place.

The turnover rate of the parasitoid would be greatly diminished in the field at these extreme temperatures and would thus severely affect the role of the parasitoid as a biological control agent. Thus, it is clear that survival, growth and development of *P. furvus* immatures depend apart from oviposition to a great extent on development in an appropriate environment.

From these observations it appeared that *P. furvus was rel*atively sensitive to changes in temperature but it was better adapted to a wide range of humidity. These findings would be of great value for maintaining the culture of *P. furvus* in laboratory and in accordance with the need, the emergence of the parasitoid might be delayed or stopped by regulating the rearing temperature and relative humidity. It is also important in helping workers to select optimal conditions for rearing and releasing P. furvus *for con*trol of the cereal stem-borers.

5.5. Influence of age on parasitism

The number of eggs laid per host pupa and the number of host pupae parasitized were affected by age. "Parasitism" is used in this study to describe only those host individuals from which progeny successfully emerged, while "host mortality" consists of pupal mortality not involving parasitoid emergence.

Those two parameters can be used to estimate the acceptability and suitability of the host to parasitization by *P. furvus*. Host acceptability is defined here as the ability of the parasitoid to find a potential host satisfactory to the point where oviposition is attempted (ovipositor insertion whether eggs are laid or not). In this case, the sum of percent pupal parasitism and mortality was used as a relative measure of host acceptability.

Many parasitoids cause significant host mortality by host feeding (Clausen 1940). As *P. furvus* was not observed to host feed in these experiments, parasitoid induced mortality was most likely caused by oviposition or attempted oviposition.

Gregarious pupal parasitoids have generally been observed to inflict high rates of host mortality (Lasota and Kok 1986). Host suitability can be defined as the ability of

a host, once oviposition has occurred, to support successful growth and development of the parasitoid progeny. A relative measure of host suitability is the proportion of parasitized pupae producing parasitoid progeny.

Host acceptability and suitability of both *C. partellus* and *B. fusca* exhibited variations due to host pupal age. A decrease in the number of oviposition or attempted ovipositions would be a change in host acceptability indicating that *P. furvus* is discriminating against unaccepTable host mainly after ovipositor insertion.

An increase in the ability of the host pupae to resist or defend against parasitization would indicate a change in host suitability. Specific causes for changes in host suitability were not apparent from these experiments. However,two general possibilities may be hypothesized. Fist, the female *P. furvus* may have avoided oviposition after host contact and ovipositor insertion due to some physiological conditions of the host pupae. Second, the female parasitoid may have oviposited within the host, but due to the internal physiological condition of the host, successful development of the parasitoid progeny did not follow. Numerous changes occur within the host pupae as it ages which could be responsible for this change in suitability. Possible changes in the host pupae's nutritional value, internal physical environment, or it's physiological response to

parasitization could have significant effects on the growth and survival of the parasitiod progeny. As the host pupa develops it changes both physiologically and morphologically.

As the pupa approaches the adult pharate stage it differentiates and becomes organized forming the structural and organ components that are present in the adult moth.

A decrease in the number of progeny per host pupa as the host age increases was noted in *P. furvus* which is a common occurrence among gregarious parasitoids (Clausen,1939) Purrington and Uleman 1972; Vinson and Iwantsch 1980). However, the mechanism by which this occurs is unknown. The most commonly proposed explanations are the laying of differential numbers of eggs relative to host age and the differential mortality of larvae due to competition (Vinson and Iwantsch,1980). Clausen (1940),suggested differential egg allocation for member of the genes Pleurot*ropis (=Pedio*bius) In *P. furvus* sex-ratios (proportion male) increased as host age increased. The regulation of sex ratio can be affected by many factors which were not be examined in this study.

The theory of local mate competition (Hamilton,1967) predicts that for gregarious parasitoids where sib-mating prevails the number of males per clutch will only be as many

as are needed to ensure fertilization of the female progeny (Charnov 1982, Waage 1982, Waage and Ng 1984; Waage and Lane 1984).

P. furvus prefers to oviposit in young *C. partellus* and *B. fusca* pupae and shows greatest preference for two-day-old pupae of *C. partellus* and three-day-old pupae of *B. fusca*. However, several investigators have reported host age as a factor determining the degree of parasitoid success. Differences in host hemolymph composition were suggested by Arthur et al (1969), Weseloh (1971), and Wylie (1971) to affect parasitism.

In contrast to acceptability, host suitability by P. furvus, as measured by the speed of parasitoid development, follows the reverse order of successful parasitism: Parasitoids in younger *C. partellus* pupae developed to adult more slowly than in older hosts, this is in agreement with the findings of Smilowitz and Iwansch (1973). This phenomenon is possibly caused by the increase in biomass of the host as it grows to an age capable of supporting the maximum rate of growth of the parasitoid (Salt,1941). Apparently, factors upon which acceptability is based and those on which suitability is based are quite different in developing *P. furvus* larvae.

The effect of the age of the female parasitoid on its ability to reproduce in the laboratory is clearly evident in Table 18. From the standpoint of most efficient production of parasitoids, it is obviously detrimental to hold *P. furvus* females longer than 4 days before utilizing them.

5.6. Effect of Diet on P. furvus adult longevity and fecundity

The nutritional requirements of the adult parasitoids are often associated with the type of reproductive strategy of the female (Flanders,1950). In some species of insects like the Eulophid *P. furvus* the female adult emerges with a full complement of mature eggs which are deposited during a relatively short period of time after which the female oviposits no more eggs. Such females have been termed Pro-ovigenic (Flanders,1950). *P. furvus* females generally do not require food since the development of eggs occur entirely from stored nutrients carried over from the larval stage.

Activities which are particularly well known in terms of influence of the nutritive quality of food are egg production and the development of the immature stages to adulthood. The rate of development of larval stages of *P. furvus* and their size upon emergence were found to be influenced to a considerable extent by the quality and quantity of food ingested by immature parasitoids.

In other species of insects, the larval stages may store proteins sufficient for egg production, but the adults must ingest water and carbohydrates to carry out their activities. Many mosquito spp.and other true flies fall in to this category, in which adults must usually ingest a complete diet (especially protein) in order to sustain life and produce eggs (Folsom and Wardle, 1934).

In the present study, lack of food or distilled water had shown an adverse effect on the female longevity but not on ovipositional period and fecundity of the parasitoid *P. furvus*. There was a 2.0- fold increase in longevity with 30% sucrose concentrations to a 4.6-fold increase in longevity with only 10% honey concentration. Mean female longevity (distilled water) was 2.66 days compared with 5.46 days for 30 % sucrose and 14 days with 10% honey (Table 32 and Table 33)).

Overall, 10 % honey solutions gave the highest performance for adult longevity. *P. furvus* females, had a maximum longevity of four days without nourishment. Since the ovipositional period of *P. furvus* is only four days from adult emergence, this suggests that this longevity is sufficient for the females to look for suiTable hosts in an inundative mass release programme.

As in the present laboratory study with various honey and sucrose diet concentrations, mean ovipositional period per female *P. furvus* was significantly ($P \leq 0.05$) higher during the first two days than during the rest of the female life. This was true for all the concentrations tested (Table 31). Like wise, Narayan and Moorkhejee (1956) found that 10% solutions of glucose, maltose and sucrose were not significantly different from each other, for longevity and rate of reproduction in *Trichogramma minutum*.

When the adult parasitoids were starved or given distilled water, the mortality rates were very high with parasitoids not surviving beyond the first four days (Fig. 4 and Fig. 5). Survival was much more pronounced for 10% sucrose, 10% and 20% honey diets where the parasitoids lived beyond the first two weeks of their life.

In the present laboratory study, there was no consistent relationship between diet and ovipositional period of the female parasitoid *P. furvus*. However, in some species of insect parasitoids, it evident that the location of the food sources of the adults has a strong influence on the distribution and effectiveness of these parasitoids.

If availability of host material is critical, stocks can be maintained by storing *P. furvus* adults for up to three days in the laboratory under temperature and relative

humidity of 27 ± 3°C and 65 ± 5%, but storage beyond this point results in a dramatic drop in production. We have never been able to produce an additional generation from female parasitoids held beyond four days, even though, we successfully kept parasitoids alive for as long as 18-days.

5.7. Effect of Superparasitism on the biology of the parasitoids

Dissections showed that larvae hatched from most of the eggs of *P. furvus* at all egg population densities. There was no combat among the larvae, supernumeraries being eliminated by starvation and / or suffocation. Usually, none or few of the larvae died in the first instar and most reached the third instar before they were reduced in numbers by starvation and / or suffocation. Thus, there were commonly 200 or more first instar larvae on a host pupa though not more than 133 ever matured. When 250 or more parasitoid larvae were present initially, complete consumption of the host usually caused the death of all of them, often before reaching the last instar.

High parasitoid survival on hosts with low parasitoid egg densities indicates that larvae of *P. furvus* are not harmed by a food surplus in their hosts. This contrasts with reduced survival, caused by a food surplus, of other parasitoid species (Flanders, 1935; Jackson, 1937; Salt,

1938; Taylor, 1937).

Work carried by Taylor (1937), concluded that mortality of the endoparasitic larvae of *Pediobius parvulus* Ferr.(Hymenoptera: Eulophidae) resulted from blockage of their spiracles by the unconsumed portion of their hosts.

Dead larvae of *P. furvus* species are not usually eaten by the survivors, this is also true with the findings of Salt (1961) who reported that starved gregarious species do not usually consume their survivors. However, parasitoids whose larvae are usually solitary feed on any supernumerary parasitoids they encounter; food wastage due to superparasitism is thus minimized. In *P. furvus species* the food consumed by supernumeraries is wasted and the resultant food shortage causes a size reduction in the survivors. This was shown (Table 38) by the size of the female *P. furvus* reared from a parasitoid-host ratios of 5:1 and 5:2, respectively, exposed for each time interval.

The percentage of male progeny per host pupa of *C. partellus* superparasitized was higher than that obtained from non-superparasitized host pupae.

Superparasitism is easily identified in species like *P. furvus* whose larvae are gregarious enoparasitoids and whose supernumerary larvae are eliminated by starvation or

suffocation. Here the amount of nutritive quality of the food provided by the host, as well as the number of parasitoids in the host pupa, are criteria for superparasitism. Food shortage is usually accompanied by a reduction in the number of the parasitoid progeny that mature, but if the shortage is slight, size reduction may be the only symptom of superparasitism displayed.

The results in the present study show that superparasitism can potentially modify the interaction of populations of *P. furvus* and stem borers by decreasing parasitoid survival, size and the proportion of the females in the adult progeny. Reduction in the percentage of female adults at high adult parasitoid population-densities should reduce the probability that the parasitoid will exterminate the host population and there by exterminate itself. Furthermore, the fact that the adult parasitoids are smaller at high adult parasitoid population densities probably reduces the average parasitoid fecundity, thereby temporarily reducing the total effect of the parasitoid population on that of the host and permitting continuation of the host-parasitoid interaction. Precise details of these effects of host size will, however, be apparent only after additional effects of parasitoid size on parasitism have been elucidated.

5.8. Intrinsic rate of natural increase of P. furvus on C. partellus pupae

The small variation between the mean number of progeny produced per female over its life span (87), and the net reproductive rate or the net replacement rate (Ro) which was calculated to be 83.75, could be explained on the basis of decrease in survivorship value (Lx) for the parent females most of which died earlier than the maximum life span of 18 days.

The information on demographic parameters of P. furvus obtained in the present findings is of much practical use since it relates to the speed of increase on population and not the individual factors producing it (longevity, survival and fecundity). The results would provide basis for future study of factors regulating populations in the field in which the overall mortality in the population can be determined by measuring the difference between the potential rate of increase and the observed rate of increase in the field.

SUMMARY

1. A seasonal survey for the incidence and distribution pattern of *P. furvus* in different agroecological localities in Kenya showed that the parasitoid was more abundant in the dry localities such as Mombasa where over 46% parasitism on *B. fusca* pupae was recorded.

2. However, *P. furvus* parasitism was very low (less than 8%) in Kakamega and Kisumu localities.

3. This low incidence of *P. furvus* at least partially explains the relatively low densities of *C. partellus* and *B. fusca* second generation pupae at harvest time in these localities.

4. The seasonal parasitisitization by *P. furvus* under fine mosquito net field conditions showed that more *C. partellus* pupae were recovered from INB-A in all seasons than on ICZ-2.

5. However, the parasitoid did not show any significant preference on internode levels of the maize plant for oviposition.

6. Host pupae with their larval frass played an important role as an olfactory stimulants used by the gravid female *P. furvus* which could increase the parasitoid's searching ability in the field.

7. However, results from the laboratory experiments showed that combination of frass and host pupae were the most attractive materials tested for 24hrs. old *P. furvus* female.

8. Frass alone was about half as attractive as combination of frass and host pupa.

9. However, the oriented response of the female parasitoid to test materials could have been due to olfactory stimuli, visual stimuli, or both.

10. Among a few combinations of temperature and relative humidity levels tested, the optimum temperature and relative humidity levels for the parasitoid's development, progeny production and sex ratio was found to be 25 ± 1.5 °C to 30 ± 1.5 °C under 60-70 %.

11. Low temperature resulted in longer developmental period and prepoderance of male progeny.

12. Parasitization activity increased with temperature of up to 30 ± 1.5 °C under relative humidity levels of 60-80 %.

13. Sucrose and / or honey solutions as food for the adult parasitoid increased the parasitoid's longevity but does not affect its fecundity.

14. Studies on oviposition and through dissections showed that the female parasitoid is proovigenic and oviposits only once or twice at most in her life span.

15. Age of the female parasitoid was found to affect parasitism.

16. Five-day-old or older parasitoids failed to parasitize any age of the host *C. partellus* pupae.

17. age of the host pupae as well was found to be equally important factor influencing the parasitoid's development, progeny production and sex ratio as well as the host's acceptability.

18. The optimum age for the ovipositing parasitoid and that of the host (*C. partellus*) pupae lies between 1 to 2 days , and > 5 days *C. partellus* pupae are rejected by the gravid female parasitoid.

27. The mean length of a *P. furvus* generation recorded was 21.41 days.

28. The species has a finite rate of increase as 1.31, which means the population would multiply 1.31 times per day at 25 ± 1 °C under relative humidity levels of 65 ± 5 %.

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Appendex. 1 MAIZE PRODUCTION IN THE WORLD

	AREA HARVESTED (1000 HA)				Yield (kg/ha)				PRODUCTION (1000 MT)			
Country	1979-81	1988	1989	1990	1979-81	1988	1989	1990	1979-81	1988	1989	1990
World	126346	127378	129298	129116	3353	3142	3640	3682	423724	400263	470646	475429
Africa	18219	21096	21781	20914	1567	1576	1768	1616	28553	32409	38513	337994
Algeria	2	2F	2F	1	1029	1000	1200	2400	2	2	2	2
Egypt	800	823	842	830F	3947	4965	5380	5301	3159	4088	4529	4400F
Ethiopia	7553	915	1060F	1150F	1626	1749	1781	1739	1224	1600	1888F	2000F
Kenya	1273	1451	1554	1500F	1360	1903	1882	1800	1714	2761	2925	2700
Nigeria	443	1556	1600F	1600F	1350	1337	1332	1145	599	2080	2132	1832
Somalia	151	281	265F	275F	821	1256	1129	1145	120	353	299	315F
S.Africa	4900	3657	3778	3475	2315	1983	3192	2717	13322	7253	12061	9442
Sudan	67	40	35F	50F	582	750	714	700	39	30F	25F	35F
Tanzania	1350	1850	1980	1651	1306	1264	1578	1481	1762	2339	3125	2445
Uganda	263	345	360F	380F	1363	1275	1389	1447	360	440	500F	550F
N.C.America	39400	33051	35743	37607	5392	4369	5923	6023	212384	144408	211701	226510
Mexico	6836	6506	6468	7439	1718	1629	1692	1984	11866	10600	10945	147662
USA	29661	23573	26184	27094	474	5311	7300	7437	192084	125194	191156	20150

Source: FAO 1990

Appendix: 2

Percentage parasitism of P. furvus in different agroecological locations in Kenya

Variable: Host pupae C. partellus

Source	df	SS	MS	F	P > F
Model	8	2064.39	258.04	4.35	0.0070
Error	15	890.11	59.34		
Locations	5	1827.90	365.58	6.16	0.0027
Reps	3	236.49	78.83	1.33	0.3022
C.total	23	2954.50			

R-Square	C.V.	Root MSE	Total mean
0.69	46.97	7.70	16.40

Variable: Host pupae B. fusca

Source	df	SS	MS	F	P > F
Model	8	4786.40	598.30	32.01	0.0001
Error	15	280.38	18.69		
Locations	5	4707.48	941.49	50.37	0.0001
Reps	3	78.93	26.31	1.41	0.2794
C.total	23	5066.80			

R-Square	C.V.	Root MSE	Total mean
0.94	26.83	4.32	16.11

Variable: Average number of host pupae (C. partellus) collected

Source	df	SS	MS	F	P > F
Model	8	2064.39	258.04	4.35	0.0070
Error	15	890.11	59.34		
Locations	5	1827.90	365.58	6.16	0.0027
Reps	3	236.49	78.83	1.33	0.3022
C.total	23	2954.50			

R-Square	C.V.	Root MSE	Total mean
0.69	46.97	7.70	16.40

Variable: Average number of host pupae (B. fusca) collected

Source	df	SS	MS	F	P > F
Model	8	4786.41	598.30	32.01	0.0001
Error	15	280.38	18.69		
Locations	5	4707.48	941.49	50.37	0.0001
Reps	3	78.92	26.31	1.41	0.2794
C.total	23	5066.79			

R-Square	C.V.	Root MSE	Total mean
0.94	26.83	4.32	16.11

Appendix: 3

Comparison of progeny production by locations in different agroecological locations in Kenya

Variable: Host pupae B. fusca

Source	df	SS	MS	F	P > F
Model	5	45377.71	9075.54	3.35	0.0259
Error	18	48773.25	2709.62		
Locations	5	45377.71	9075.54	3.35	0.0259
C.total	23	94150.96			

R-Square	C.V.	Root MSE	Total mean
0.48	45.15	52.05	115.29

Variable: Host pupae C. partellus

Source	df	SS	MS	F	P > F
Model	5	12262.71	2452.54	2.26	0.0923
Error	18	19526.96	1084.79		
Locations	5				
C.total	23	31788.96			

R-Square	C.V.	Root MSE	Total mean
0.38	33.71	32.93	97.71

Appendix: 4

Comparison of Sex ratio by locations in different agroecological locations in Kenya

Variable : Host pupae C. partellus

Source	df	SS	MS	F	P > F
Model	8	4.201	0.52	1.42	0.264
Error	15	5.53	0.36		
Locations	5	3.79	0.75	2.06	0.1285
Reps.	3	0.41	0.13	0.37	0.7766
C.total	23	9.74			

R-Square	C.V.	Root MSE	Total mean
0.43	16.91	6.07	35.91

Variable : Host pupae B. fusca

Source	df	SS	MS	F	P > F
Model	8	3.21	0.40	1.02	0.4596
Error	15	5.88	0.39		
Locations	5	1.81	0.36	0.92	0.4920
Reps.	3	1.40	0.46	1.19	0.3470
C.total	23	9.09			

R-Square	C.V.	Root MSE	Total mean
0.35	17.28	6.26	36.25

Appendix: 5

Seasonal collection of parasitized pupae under netted field conditions at M.P.F.S. in the Long Rainy Season of 1990

Variable: No. pupae collected

Source	df	SS	MS	F	P > F
Model	4	10120.50	2530.12	1885.19	0.0001
Error	19	25.50	1.34		
Cultivar	1	9361.50	9361.50	6975.24	0.0001
Reps	3	759.00	253.00	188.51	0.0001
C.total	23	10146.00			

R-Square	C.V.	Root MSE	Total mean
0.99	0.54	1.15	215.50

Variable: No. host pupae parasitized

Source	df	SS	MS	F	P > F
Model	4	3950.26	987.56	1003.22	0.0001
Error	19	18.70	0.98		
Cultivar	1	3862.58	3862.58	3923.79	0.0001
Reps	3	87.68	29.23	29.69	0.0001
C.total	23	3968.96			

R-Square	C.V.	Root MSE	Total mean
0.99	1.18	0.99	83.51

Appendix: 6

Seasonal collection of parasitized pupae under netted field conditions at M.P.F.S. in the Long Rainy Season of 1991

Variable: No. host pupae collected

Source	df	SS	MS	F	P > F
Model	4	27613.50	6903.37	43.75	0.0001
Error	19	2998.12	157.79		
Cultivar	1	27135.37	27135.37	171.96	0.0001
Reps	3	478.12	159.37	1.01	0.410
C.total	23	30611.62			

R-Square	C.V.	Root MSE	Total mean
0.90	7.03	12.56	178.62

Variable: No. host pupae parasitized

Source	df	SS	MS	F	P > F
Model	4	3672.35	918.08	146.66	0.0001
Error	19	118.94	6.260		
Cultivar	1	3279.74	3279.74	523.92	0.0001
Reps	3	392.60	130.86	20.91	0.0001
C.total	23	3791.29			

R-Square	C.V.	Root MSE	Total mean
0.96	3.68	2.50	67.87

Appendix: 7

Seasonal collection of parasitized pupae under netted field conditions at M.P.F.S. in the Short Rainy Season of 1991

Variable: No. host pupae collected

Source	df	SS	MS	F	P > F
Model	4	22075.50	5518.87	213.94	0.0001
Error	19	490.12	25.79		
Cultivar	1	18648.37	18648.37	722.92	0.0001
Reps	3	3427.12	1142.37	44.28	0.0001
C.total	23	22565.62			

R-Square	C.V.	Root MSE	Total mean
0.97	3.29	5.07	154.37

Variable: No. host pupae parasitized

Source	df	SS	MS	F	P > F
Model	4	2700.46	675.11	153.33	0.0001
Error	19	83.63	4.40		
Cultivar	1	2276.82	2276.82	517.12	0.0001
Reps	3	423.64	141.21	32.07	0.0001
C.total	23	2784.12			

R-Square	C.V.	Root MSE	Total mean
0.96	3.73	2.09	56.18

Appendix: 8

Seasonal parasitism of P. furvus under netted field conditions at M.P.F.S.

Variable: No. host pupae collected

Source	df	SS	MS	F	P > F
Model	8	34031.66	4253.95	28.57	0.0001
Error	15	2233.66	148.91		
Cultivar	5	33539.33	6707.86	45.05	0.0001
Reps	3	492.33	164.11	1.10	0.371
C.total	23	36265.33			

R-Square	C.V.	Root MSE	Total mean
0.94	6.67	12.20	182.83

Variable: No. host pupae collected from the upper internode

Source	df	SS	MS	F	P > F
Model	8	1796.16	224.52	24.95	0.0001
Error	15	134.97	8.99		
Cultivar	5	1754.67	350.93	39.00	0.0001
Reps	3	41.49	13.83	1.54	0.24
C.total	23	1931.13			

R-Square	C.V.	Root MSE	Total mean
0.93	14.72	2.99	20.37

Variable: No. host pupae collected from the Middle internode

Source	df	SS	MS	F	P > F
Model	8	1346.12	168.26	16.37	0.0001
Error	15	154.16	10.27		
Cultivar	5	1322.25	264.45	25.73	0.0001
Reps	3	23.86	7.95	0.77	0.52
C.total	23	1500.28			

R-Square	C.V.	Root MSE	Total mean
0.89	10.93	3.20	29.31

Variable: No. host pupae collected from the Lower internode

Source	df	SS	MS	F	P > F
Model	8	2480.83	310.10	16.91	0.0001
Error	15	275.00	18.33		
Cultivar	5	2413.14	482.63	26.33	0.0001
Reps	3	67.68	22.56	1.23	0.33
C.total	23	2755.83			

R-Square	C.V.	Root MSE	Total mean
0.90	7.63	4.28	56.12

Variable: Seasonal percentage parasitism

Source	df	SS	MS	F	P > F
Model	8	6258.17	782.27	44.69	0.0001
Error	15	262.55	17.50		
Cultivar	5	6145.65	1229.13	70.22	0.0001
Reps	3	112.52	37.50	2.14	0.130
C.total	23	6520.72			

R-Square	C.V.	Root MSE	Total mean
0.96	6.04	4.18	69.19

Appendix: 9

C. partellus parasitism and Inter-node preference under netted field conditions at M.P.F.S.

Variable: No. host pupae collected

Source	df	SS	MS	F	P > F
Model	4	25546.50	6386.62	43.31	0.0055
Error	3	442.37	147.45		
Cultivar	1	7260.12	7260.12	49.24	0.0059
Reps	3	18286.37	6095.56	41.34	0.0061
C.total	7	25988.87			

R-Square	C.V.	Root MSE	Total mean
0.98	6.04	12.14	201.12

Variable: **No. host pupae collected from the Upper inter-nodes**

Source	df	SS	MS	F	P > F
Model	4	2449.50	612.37	4.15	0.13
Error	3	442.37	147.45		
Cultivar	1	990.12	990.12	6.71	0.081
Reps	3	1459.31	486.45	3.30	0.176
C.total	7	2891.87			

R-Square	C.V.	Root MSE	Total mean
0.84	30.07	12.14	40.37

Variable: **No. host pupae collected from the Middle inter-nodes**

Source	df	SS	MS	F	P > F
Model	4	886.50	221.62	0.94	0.5400
Error	3	709.00	236.33		
Cultivar	1	50.00	50.00	0.21	0.676
Reps	3	836.50	278.83	1.18	0.447
C.total	7	1595.50			

R-Square	C.V.	Root MSE	Total mean
0.55	29.14	15.37	52.75

Variable: No. host pupae collected from the Lower inter-nodes

Source	df	SS	MS	F	P > F
Model	4	11825.50	2956.37	46.34	0.005
Error	3	191.37	63.79		
Cultivar	1	2485.12	2485.12	38.96	0.008
Reps	3	9340.37	3113.45	48.81	0.0048
C.total	7	12016.87			

R-Square	C.V.	Root MSE	Total mean
0.98	7.32	7.98	109.12

Variable: Percentage parasitism

Source	df	SS	MS	F	P > F
Model	4	3545.00	886.25	98.47	0.0016
Error	3	27.00	9.00		
Cultivar	1	800.00	800.00	88.89	0.0025
Reps	3	2745.00	915.00	101.67	0.0016
C.total	7	3572.00			

R-Square	C.V.	Root MSE	Total mean
0.99	4.00	3.00	75.00

Appendix 10

Effect of maize cultivars on the parasitoid's sex ratio and mortality without progeny

Variable: Females / host pupa

Source	df	SS	MS	F	P > F
Model	4	34.03	8.51	17.83	0.0198
Error	3	1.43	0.47		
Cultivar	1	30.69	30.69	64.31	0.0040
Reps	3	3.34	1.11	2.34	0.2521
C.total	7	35.46			

R-Square	C.V.	Root MSE	Total mean
0.96	0.98	0.69	70.14

Variable: Males / host pupa

Source	df	SS	MS	F	P > F
Model	4	0.23	0.06	0.12	0.9677
Error	3	1.51	0.50		
Cultivar	1	0.99	0.09	0.20	0.6877
Reps	3	0.13	0.04	0.09	0.9609
C.total	7	1.74			

R-Square	C.V.	Root MSE	Total mean
0.13	3.54	0.71	20.05

Variable: Mortality without progeny

Source	df	SS	MS	F	P > F
Model	4	8.58	2.14	3.09	0.1903
Error	3	2.08	0.69		
Cultivar	1	5.78	5.78		
Reps	3	2.81	0.93	1.35	0.4058
C.total	7	10.66			

R-Square	C.V.	Root MSE	Total mean
0.80	6.99	0.83	11.91

Appendix 11

Influence of Odor sources on parasitoid orientation

Source	df	SS	MS	F	P > F
Model	10	88.31	8.33	9.32	0.0001
Error	21	19.90	0.95		
Treatment	7	84.96	12.13	12.81	0.0001
Reps	3	3.34	1.11	1.18	0.3400
C.total	31	108.21			

R-Square	C.V.	Root MSE	Total mean
0.81	16.66	0.97	5.84

Appendix 12

Average number of host pupae parasitized under different temperature and relative humidity levels

Variable : Temperature regimes

Source	df	SS	MS	F	P > F
Model	10	23659.77	2365.97	100.61	0.0001
Error	21	493.82	23.51		
Tempr.	2	11195.95	5597.97	238.06	0.0001
Reps.	3	69.44	23.15	0.98	0.4200
C.Total	31	24153.59			

R-Square	C.V.	Root MSE	Total mean
0.97	10.98	4.85	44.14

Variable : Relative humidity levels

Source	df	SS	MS	F	P > F
Model	10	23659.77	2365.97	100.61	0.0001
Error	21	493.82	23.51		
R.H.	5	12394.37	2478.87	105.42	0.0001
Reps.	3	69.44	23.15	0.98	0.4200
C.Total	31	24153.59			

R-Square	C.V.	Root MSE	Total mean
0.97	10.98	4.85	44.14

Appendix 13

Influence of combined Temperature and Relative humidity on the parasitoid's biology

Variable : Developmental Period (days)

Source	df	SS	MS	F	P > F
Model	15	2705.83	180.38	56.44	0.0001
Error	36	115.06	3.19		
Tempr.X.RH	12	2698.96	224.91	70.37	0.0001
Reps.	3	6.86	2.28	0.72	0.5488
C.Total	51	2820.89			

R-Square	C.V.	Root MSE	Total mean
0.95	7.52	1.78	23.77

Variable : Progeny production

Source	df	SS	MS	F	P > F
Model	15	14420.88	961.39	9.79	0.0001
Error	36	3536.88	98.24		
Tempr.X.RH	12	14351.86	1195.98	12.17	0.0001
Reps.	3	69.02	23.00	0.23	0.8720
C.Total	51	17957.77			

R-Square	C.V.	Root MSE	Total mean
0.80	12.35	9.91	80.23

Variable : Sex Ratio

Source	df	SS	MS	F	P > F
Model	15	5880.83	392.05	20.35	0.0001
Error	36	693.53	19.26		
Tempr.X.RH	12	5832.28	486.02	25.23	0.0001
Reps.	3	48.54	16.18	0.84	0.4800
C.Total	51	6574.37			

R-Square	C.V.	Root MSE	Total mean
0.89	13.61	4.38	32.24

Appendix 14

Effect of Relative humidity levels on the parasitoid's biology

Variable : Developmental period (days)

Source	df	SS	MS	F	P > F
Model	9	2691.67	299.07	97.21	0.0001
Error	42	129.21	3.07		
RH.	4	10.65	2.66	0.87	0.4925
Reps.	3	6.86	2.28	0.74	0.5318
C.Total	51	2820.89			

R-Square	C.V.	Root MSE	Total mean
0.95	7.37	1.75	23.77

Variable : Progeny production

Source	df	SS	MS	F	P > F
Model	9	11469.74	1274.41	8.25	0.0001
Error	42	6488.02	154.47		
RH.	4	4328.30	1082.07	7.00	0.0002
Reps.	3	69.02	23.00	0.15	0.9298
C.Total	51	17957.77			

R-Square	C.V.	Root MSE	Total mean
0.64	15.49	12.43	80.23

Variable : Sex Ratio

Source	df	SS	MS	F	P > F
Model	9	5413.26	601.47	21.76	0.0001
Error	42	1161.11	27.64		
RH.	4	184.65	46.16	1.67	0.1750
Reps.	3	48.54	16.18	0.59	0.6280
C.Total	51	6574.37			

R-Square	C.V.	Root MSE	Total mean
0.82	16.31	5.25	32.24

Appendix 15

Influence of Temperature on the parasitoid's biology

Variable : Developmental period (days)

Source	df	SS	MS	F	P > F
Model	9	2691.67	299.07	97.21	0.0001
Error	42	129.21	3.07		
Tempr.	2	2674.15	1337.07	434.59	0.4925
Reps.	3	6.86	2.28	0.74	0.5318
C.Total	51	2820.89			

R-Square	C.V.	Root MSE	Total mean
0.95	7.37	1.75	23.77

Variable : Progeny production

Source	df	SS	MS	F	P > F
Model	9	11469.74	1274.41	8.25	0.0001
Error	42	6488.02	154.47		
Tempr.	2	7072.42	3536.21	22.89	0.0001
Reps.	3	69.02	23.00	0.15	0.9298
C.Total	51	17957.77			

R-Square	C.V.	Root MSE	Total mean
0.64	15.49	12.43	80.23

Variable : Sex Ratio

Source	df	SS	MS	F	P > F
Model	9	5413.26	601.47	21.76	0.0001
Error	42	1161.10	27.64		
Tempr.	2	5180.07	2590.03	93.69	0.0001
Reps.	3	48.54	16.18	0.59	0.6280
C.Total	51	6574.37			

R-Square	C.V.	Root MSE	Total mean
0.82	16.31	5.25	32.24

Appendix 16

Effect of B. fusca pupal age on the parasitoid's oviposition

Source	df	SS	MS	F	P > F
Model	11	46851.90	4259.26	12.78	0.0001
Error	168	55989.75	333.27		
Host age	8	44564.91	5570.61	16.71	0.0001
Reps.	3	2286.99	762.33	2.29	0.0800
C.Total	179	102841.66			

R-Square	C.V.	Root MSE	Total mean
0.45	16.12	16.25	113.22

Appendix. 17

Effect of C.partellus pupal age on the parasitoid's oviposition

Source	df	SS	MS	F	P > F
Model	8	19773.71	2471.71	6.03	0.0001
Error	87	35657.53	409.85		
Host age	5	18092.93	3618.58	8.83	0.0001
Reps	3	1680.78	560.26	1.37	0.25 C.total
95	55431.24				

R-Square	C.V.	Root MSE	Total mean
0.35	16.34	20.24	123.86

Appendix. 18

Effect of B.fusca pupal age on the parasitoid's biology

Variable: Developmental period (days)

Source	df	SS	MS	F	P>F
Model	15	59.59	3.97	3.65	0.0001
Error	164	178.50	1.08		
Host age	8	35.75	4.46	4.11	0.0002
Reps	3	2.13	0.71	0.65	0.5818
C.total	179	238.09			

R-Square	C.V.	Root MSE	Total mean
0.25	5.16	1.04	20.19

Variable: Progeny production

Source	df	SS	MS	F	P>F
Model	15	78039.71	5202.64	60.33	0.0001
Error	164	14141.93	86.23		
Host age	8	70831.14	8853.89	102.68	0.0001
Reps	3	305.86	101.95	1.18	0.3182
C.total	179	92181.64			

R-Square	C.V.	Root MSE	Total mean
0.85	9.02	9.28	102.95

Variable: Sex ratio

Source	df	SS	MS	F	P>F
Model	47	9110.25	193.83	29.20	0.0001
Error	132	876.18	6.64		
Host age	8	4234.64	529.33	79.74	0.0001
Reps	3	8.31	2.77	0.42	0.74
C.total	179	9986.44			

R-Square	C.V.	Root MSE	Total mean
0.91	8.46	2.57	30.44

Appendix. 19

Effect of C.partellus pupal age on the parasitoid's biology

Variable: Developmental period (days)

Source	df	SS	MS	F	P>F
Model	12	2028.12	169.01	15.71	0.0001
Error	99	1065.15	10.75		
Host age	5	1818.76	363.75	33.81	0.0001
Reps	3	1.16	0.38	0.04	0.99
C.total	111	3039.27			

R-Square	C.V.	Root MSE	Total mean
0.65	17.53	3.28	18.70

Variable: Progeny production

Source	df	SS	MS	F	P>F
Model	12	71256.02	5938.00	28.44	0.0001
Error	99	20673.40	208.82		
Host age	5	61847.66	12369.53	59.23	0.0001
Reps	3	757.07	252.35	1.21	0.31
C.total	111	91929.43			

C.V.	Root MSE	Total mean
0.77	16.34	14.45 88.43

Variable: Sex-ratio

Source	df	SS	MS	F	P>F
Model	8	24173.71	3021.71	20.73	0.0001
Error	111	16179.68	145.76		
Host age	5	24122.22	4824.44	33.10	0.0001
Reps	3	51.48	17.16	0.12	0.95
C.total	119	40353.39			

R-Square	C.V.	Root MSE	Total mean
0.59	37.05	12.07	32.58

Appendix. 20

Influence of P. furvus on its fecundity

(Host: C.partellus)

Source	df	SS	MS	F	P>F
Model	6	15322.06	2553.67	5.67	0.0001
Error	89	40109.17	450.66		
Parasitoid age	4	13641.28	4547.09	10.09	0.0001
Reps	3	1680.78	560.26	1.24	0.29
C.total	95	55431.23			

R-Square	C.V.	Root MSE	Total mean

Appendix. 21

Influence of P. furvus age on its fecundity

(Host: B.fusca)

Source	df	SS	MS	F	P>F
Model	7	21266.85	3038.12	6.41	0.0001
Error	172	81574.81	474.27		
Parasitoid age	4	18979.85	4744.96	10.00	0.0001
Reps	3	2286.99	762.33	1.61	0.189
C.total	179	102841.66			

R-Square	C.V.	Root MSE	Total mean
0.21	19.23	21.77	113.23

Appendix. 22

Effect of P.furvus age reared on B.fusca pupae on its biology

Variable: Developmental period (days)

Source	df	SS	MS	F	P>F
Model	15	59.59	3.97	3.65	0.0001
Error	164	178.50	1.08		
Parasitoid age	4	21.71	5.43	4.99	0.0002
Reps.	3	2.13	0.71	0.65	0.5818
C.total	179	238.09			

R-Square	C.V.	Root MSE	Total mean
0.25	5.16	1.04	20.19

Variable: Progeny production

Source	df	SS	MS	F	P>F
Model	15	78039.71	5202.65	60.33	0.0001
Error	164	14141.93	86.23		
Parasitoid age	4	6902.70	1725.67	20.01	0.0001
Reps.	3	305.86	101.95	1.18	0.3182
C.total	179	92181.64			

R-Square	C.V.	Root MSE	Total mean
0.84	9.02	9.28	102.95

Variable: Sex-ratio

Source	df	SS	MS	F	P>F
Model	47	9110.25	193.83	29.20	0.0001
Error	132	876.44	6 64		
Parasitoid age	4	1940.72	485.18	73.09	0.0001
Reps.	3	8.31	2.77	0.42	0.74
C.total	179	9986.44			

R-Square	C.V.	Root MSE	Total mean
0.91	8.46	2.57	30.44

Appendix. 23

Effect of P.furvus age reared on C. partellus pupae on its biology

Variable: Developmental period (days)

Source	df	SS	MS	F	P>F
Model	12	2028.12	169.01	15.71	0.0001
Error	99	1065.15	10.75		
Parasitoid age	4	208.19	52.04	4.84	0.0001
Reps.	3	1.16	0.38	0.04	0.99
C.total	111	3039.27			

R-Square	C.V.	Root MSE	Total mean
0.65	17.53	3.28	18.70

Variable: Progeny production

Source	df	SS	MS	F	P>F
Model	12	7125.02	5938.00	28.44	0.0001
Error	99	20673.40	208.82		
Parasitoid age	4	8651.29	2162.82	10.36	0.0001
Reps.	3	757.07	252.35	1.21	0.31
C.total	111	91929.42			

R-Square	C.V.	Root MSE	Total mean
0.77	16.34	14.45	88.43

Variable: Sex-ratio

Source	df	SS	MS	F	P>F
Model	7	2325.83	332.26	0.98	0.45
Error	112	38027.55	339.53		
Parasitoid age	4	2247.35	568.58	1.67	0.16
Reps.	3	51.48	17.16	0.05	0.98
C.total	119	40353.39			

R-Square	C.V.	Root MSE	Total mean
0.05	56.55	18.42	32.58

Appendix : 24

Influence of combined of host (B. fusca) and parasitoid ages on oviposition

Variable: Host age 0

Source	df	SS	MS	F	P>F
Model	7	1741.15	248.73	0.71	0.66
Error	12	4209.80	350.81		
Parasitoid age	4	1204.20	301.05	0.86	0.51
Reps	3	536.95	178.98	0.51	0.68
C.total	19	5950.95			

R-Square	C.V.	Root MSE	Total mean
0.29	15.03	18.73	124.55

Variable: Host age 1

Source	df	SS	MS	F	P>F
Model	7	4488.05	641.15	3.63	0.02
Error	12	2116.90	176.41		
Parasitoid age	4	4396.70	1099.17	6.23	0.01
Reps	3	91.35	30.45	0.17	0.91
C.total	19	6604.95			

R-Square	C.V.	Root MSE	Total mean
0.67	10.33	13.28	128.55

Variable: Host age 2

Source	df	SS	MS	F	P>F
Model	7	7462.60	1066.08	4.15	0.01
Error	12	3079.60	256.63		
Parasitoid age	4	6043.20	1510.80	5.89	0.01
Reps	3	1419.40	473.13	1.84	0.19
C.total	19	10542.20			

R-Square	C.V.	Root MSE	Total mean
0.71	12.48	16.02	128.30

Variable: Host age 3

Source	df	SS	MS	F	P>F
Model	7	5045.95	720.85	2.11	0.12
Error	12	4101.80	341.81		
Parasitoid age	4	4783.00	1195.75	3.50	0.04
Reps	3	262.95	87.65	0.26	0.85
C.total	19	9147.75			

R-Square	C.V.	Root MSE	Total mean
0.55	14.76	18.48	125.25

Variable: Host age 4

Source	df	SS	MS	F	P>F
Model	7	5513.15	787.59	4.00	0.02
Error	12	2362.60	196.88		
Parasitoid age	4	4297.00	1074.25	5.46	0.01
Reps	3	1216.15	405.38	2.06	0.16
C.total	19	7875.75			

R-Square	C.V.	Root MSE	Total mean
0.70	11.86	14.03	118.25

Variable: Host age 5

Source	df	SS	MS	F	P>F
Model	7	3195.60	456.51	1.94	0.15
Error	12	2823.20	235.26		
Parasitoid age	4	2156.80	539.20	2.29	0.12
Reps	3	1038.80	346.26	1.47	0.27
C.total	19	6018.80			

R-Square	C.V.	Root MSE	Total mean
0.53	13.62	15.34	112.60

Variable: Host age 6

Source	df	SS	MS	F	P>F
Model	7	5464.70	780.67	10.29	0.0003
Error	12	910.30	75.85		
Parasitoid age	4	4656.50	1164.12	15.35	0.0001
Reps	3	808.20	269.40	3.55	0.05
C.total	19	6375.00			

R-Square	C.V.	Root MSE	Total mean
0.86	8.03	8.71	108.50

Variable: Host age 7

Source	df	SS	MS	F	P>F
Model	7	794.95	113.56	1.32	0.32
Error	12	1035.60	86.30		
Parasitoid age	4	584.80	146.20	1.69	0.21
Reps	3	210.15	70.05	0.81	0.51
C.total	19	1830.55			

R-Square	C.V.	Root MSE	Total mean
0.43	10.36	9.28	89.65

Variable: Host age 8

Source	df	SS	MS	F	P>F
Model	7	2246.00	320.85	2.29	0.09
Error	12	1684.80	140.40		
Parasitoid age	4	756.80	189.20	1.35	0.31
Reps	3	1489.20	496.40	3.54	0.05
C.total	19	3930.80			

R-Square	C.V.	Root MSE	Total mean
0.57	14.21	11.85	83.40

Appendix 25

Effect of combined C. partellus pupal age and P. furvus age on the latter's fecundity

Variable: Host age 0

Source	df	SS	MS	F	P>F
Model	7	1647.00	235.28	0.63	0.7225
Error	12	4472.00	372.66		
Parasitoid age	4	1080.00	270.00	0.72	0.5918
Reps	3	567.00	189.00	0.51	0.6847
C.total	19	6119.00			

R-Square	C.V.	Root MSE	Total mean
0.27	14.46	19.30	133.50

Variable: Host age 1

Source	df	SS	MS	F	P>F
Model	7	2636.35	376.62	3.32	0.0331
Error	12	1362.20	113.52		
Parasitoid age	4	2267.80	566.95	4.99	0.0133
Reps	3	368.55	122.85	1.08	0.3937
C.total	19	3998.55			

R-Square	C.V.	Root MSE	Total mean
0.66	8.02	10.65	132.85

Variable: Host age 2

Source	df	SS	MS	F	P>F
Model	7	4204.20	600.60	3.90	0.0191
Error	12	1849.00	154.08		
Parasitoid age	4	3594.20	898.55	5.83	0.0076
Reps	3	610.00	203.33	1.32	0.3136
C.total	19	6053.20			

R-Square	C.V.	Root MSE	Total mean
0.69	9.05	12.41	137.20

Variable: Host age 3

Source	df	SS	MS	F	P>F
Model	7	9159.60	1308.51	4.66	0.0099
Error	12	3371.20	280.93		
Parasitoid age	4	7836.80	1959.20	6.97	0.0038
Reps	3	1322.80	440.93	1.57	0.2480
C.total	19	12530.80			

R-Square	C.V.	Root MSE	Total mean
0.73	13.26	16.76	126.40

Variable: Host age 4

Source	df	SS	MS	F	P>F
Model	7	3082.55	440.36	1.57	0.2352
Error	12	3368.00	280.66		
Parasitoid age	4	2270.80	567.70	2.02	0.1551
Reps	3	811.75	270.58	0.96	0.4913
C.total	19	6450.55			

R-Square	C.V.	Root MSE	Total mean
0.47	15.00	16.75	111.65

Variable: Host age 5

Source	df	SS	MS	F	P>F
Model	5	82.75	27.58	0.00	0.000
Error	0	0.00	0.00	0.00	0.000
Parasitoid age	0	0.00	0.00	0.00	0.000
Reps	3	82.75	27.58	0.00	0.000
C.total	3	82.75			

R-Square	C.V.	Root MSE	Total mean
1.00	0.00	0.00	86.25

Appendix: 26

Influence of B. fusca pupal age on the parasitoid's developmental period

Variable: Host age 0

Source	df	SS	MS	F	P>F
Model	7	8.56	1.22	1.63	0.22
Error	12	9.03	0.75		
Parasitoid age	4	3.48	0.87	1.16	0.3771
Reps	3	5.08	1.69	2.25	0.1348
C.total	19	17.60			

R-Square	C.V.	Root MSE	Total mean
0.48	4.33	0.86	20.02

Variable: Host age 1

Source	df	SS	MS	F	P>F
Model	7	7.81	1.11	2.16	0.1150
Error	12	6.19	0.52		
Parasitoid age	4	2.28	0.57	1.11	0.39
Reps	3	5.52	1.84	3.57	0.047
C.total	19	13.99			

R-Square	C.V.	Root MSE	Total mean
0.55	3.62	0.72	19.83

Variable: Host age 2

Source	df	SS	MS	F	P>F
Model	7	9.05	1.29	2.38	0.0895
Error	12	6.52	0.54		
Parasitoid age	4	0.82	0.20	0.38	0.820
Reps	3	8.23	2.74	5.05	0.017
C.total	19	15.57			

R-Square	C.V.	Root MSE	Total mean
0.58	3.71	0.74	19.87

Variable: Host age 3

Source	df	SS	MS	F	P>F
Model	7	4.45	0.64	2.66	0.065
Error	12	2.86	0.24		
Parasitoid age	4	2.26	0.56	2.37	0.1106
Reps	3	2.18	0.72	3.05	0.0700
C.total	19	7.31			

R-Square	C.V.	Root MSE	Total mean
0.61	2.50	0.48	19.54

Variable: Host age 4

Source	df	SS	MS	F	P>F
Model	7	6.14	0.87	2.24	0.105
Error	12	4.70	0.39		
Parasitoid age	4	3.45	0.86	2.21	0.129
Reps	3	2.68	0.89	2.28	0.131
C.total	19	10.85			

R-Square	C.V.	Root MSE	Total mean
0.56	3.11	0.63	20.14

Variable: Host age 5

Source	df	SS	MS	F	P>F
Model	7	0.85	0.12	0.34	0.918
Error	12	4.29	0.36		
Parasitoid age	4	0.53	0.13	0.37	0.824
Reps	3	0.33	0.11	0.30	0.822
C.total	19	5.14			

R-Square	C.V.	Root MSE	Total mean
0.16	2.99	0.59	20.00

Variable: Host age 6

Source	df	SS	MS	F	P>F
Model	7	4.33	0.62	1.29	0.3311
Error	12	5.73	0.47		
Parasitoid age	4	1.34	0.33	0.70	0.605
Reps	3	2.98	0.99	2.08	0.156
C.total	19	10.06			

R-Square	C.V.	Root MSE	Total mean
0.43	3.33	0.69	20.73

Variable: Host age 7

Source	df	SS	MS	F	P>F
Model	7	46.28	6.61	9.85	0.0004
Error	12	8.05	0.67		
Parasitoid age	4	38.54	9.64	14.35	0.0002
Reps	3	7.74	2.58	3.84	0.0386
C.total	19	54.33			

R-Square	C.V.	Root MSE	Total mean
0.85	3.94	0.82	20.81

Variable: Host age 8

Source	df	SS	MS	F	P>F
Model	7	60.63	8.66	15.27	0.0001
Error	12	6.81	0.56		
Parasitoid age	4	54.30	13.57	23.93	0.0001
Reps	3	6.33	2.11	3.72	0.0422
C.total	19	67.44			

R-Square	C.V.	Root MSE	Total mean
0.89	3.62	0.75	20.81

Appendix. 27

Effect of combined C.partellus and P.furvus pupal ages on the parasitoid's developmental period (days)

Variable: Host age 0

Source	df	SS	MS	F	P>F
Model	7	7.85	1.12	1.55	0.24
Error	12	8.70	0.72		
Parasitoid age	4	7.30	1.82	2.52	0.09
Reps	3	0.55	0.18	0.25	0.85
C.total	19	16.55			

R-Square	C.V.	Root MSE	Total mean
0.47	4.28	0.85	19.85

Variable: Host age 1

Source	df	SS	MS	F	P>F
Model	7	4.25	0.61	0.84	0.57
Error	12	8.70	0.72		
Parasitoid age	4	1.70	0.42	0.59	0.67
Reps	3	2.55	0.85	1.17	0.36
C.total	19	12.95			

R-Square	C.V.	Root MSE	Total mean
0.33	4.26	0.85	19.95

Variable: Host age 2

Source	df	SS	MS	F	P>F
Model	7	2.30	0.33	0.42	0.87
Error	12	9.50	0.79		
Parasitoid age	4	1.30	0.32	0.41	0.79
Reps	3	1.00	0.33	0.42	0.74
C.total	19	11.80			

R-Square	C.V.	Root MSE	Total mean
0.19	4.42	0.88	20.10

Variable: Host age 3

Source	df	SS	MS	F	P>F
Model	7	3.45	0.49	0.71	0.66
Error	12	8.30	0.69		
Parasitoid age	4	2.50	0.62	0.90	0.90
Reps	3	0.95	0.31	0.46	0.71
C.total	19	11.75			

R-Square	C.V.	Root MSE	Total mean
0.29	4.10	0.83	20.25

Variable: Host age 4

Source	df	SS	MS	F	P>F
Model	7	2.95	0.42	0.44	0.86
Error	12	11.60	0.96		
Parasitoid age	4	2.80	0.70	0.72	0.59
Reps	3	0.15	0.05	0.05	0.98
C.total	19	14.55			

R-Square	C.V.	Root MSE	Total mean
0.20	4.83	0.98	20.35

Variable: Host age 5

Source	df	SS	MS	F	P>F
Model	7	1205.08	241.01	788.78	0.0001
Error	12	1.83	0.30		
Parasitoid age	4	1204.16	602.08	1970.45	0.0001
Reps	3	0.91	0.30	1.00	0.45
C.total	19	1206.91			

R-Square	C.V.	Root MSE	Total mean
0.99	7.80	0.55	7.08

.Appendix: 28

Influence of combined host pupae (B. fusca) and parasitoid ages on the later's progeny production

Variable: Host age 0

Source	df	SS	MS	F	P>F
Model	7	556.90	79.55	0.56	0.7753
Error	12	1707.90	142.32		
Parasitoid age	4	377.30	94.32	0.66	0.6297
Reps	3	179.60	59.86	0.42	0.7416
C.total	19	2264.80			

R-Square	C.V.	Root MSE	Total mean
0.24	10.23	11.93	116.60

Variable: Host age 1

Source	df	SS	MS	F	P>F
Model	7	844.10	120.58	2.57	0.0726
Error	12	563.70	46.97		
Parasitoid age	4	730.30	182.57	3.89	0.030
Reps	3	113.80	37.93	0.81	0.513
C.total	19	1407.80			

R-Square	C.V.	Root MSE	Total mean
0.59	6.01	6.85	114.10

Variable: Host age 2

Source	df	SS	MS	F	P>F
Model	7	932.45	133.21	2.84	0.0538
Error	12	562.10	46.84		
Parasitoid age	4	408.30	102.07	2.18	0.1331
Reps	3	524.15	174.72	3.73	0.0419
C.total	19	1494.55			

R-Square	C.V.	Root MSE	Total mean
0.62	5.79	6.84	118.15

Variable: Host age 3

Source	df	SS	MS	F	P>F
Model	7	2216.80	316.68	4.60	0.0103
Error	12	826.20	68.85		
Parasitoid age	4	2071.00	517.75	7.52	0.003
Reps	3	145.80	48.60	0.71	0.566
C.total	19	3043.00			

R-Square	C.V.	Root MSE	Total mean
0.72	7.00	8.29	118.50

Variable: Host age 4

Source	df	SS	MS	F	P>F
Model	7	1561.70	223.10	2.21	0.1088
Error	12	1211.50	100.96		
Parasitoid age	4	1543.70	385.92	3.82	0.0315
Reps	3	18.00	6.00	0.06	0.9801
C.total	19	2773.20			

R-Square	C.V.	Root MSE	Total mean
0.56	8.64	10	116.20

Variable: Host age 5

Source	df	SS	MS	F	P>F
Model	7	1924.90	274.98	3.64	0.0243
Error	12	907.30	75.61		
Parasitoid age	4	1746.70	436.67	5.78	0.0079
Reps	3	178.20	59.40	0.79	0.5247
C.total	19	2832.20			

R-Square	C.V.	Root MSE	Total mean
0.67	7.74	8	112.30

Variable: Host age 6

Source	df	SS	MS	F	P>F
Model	7	1618.50	231.21	4.42	0.0120
Error	12	627.30	52.27		
Parasitoid age	4	1298.30	324.57	6.21	0.006
Reps	3	320.20	106.73	2.04	0.161
C.total	19	2245.80			

R-Square	C.V.	Root MSE	Total mean
0.72	7.76	7.23	93.10

Variable: Host age 7

Source	df	SS	MS	F	P>F
Model	7	1930.90	275.84	2.87	0.0523
Error	12	1153.30	96.11		
Parasitoid age	4	1054.70	263.67	2.74	0.0785
Reps	3	876.20	292.06	3.04	0.0706
C.total	19	3084.20			

R-Square	C.V.	Root MSE	Total mean
0.63	13.12	9.80	74.70

Variable: Host age 8

Source	df	SS	MS	F	P>F
Model	7	1201.85	171.69	2.05	0.1306
Error	12	1003.10	83.59		
Parasitoid age	4	879.70	219.92	2.63	0.087
Reps	3	322.15	107.38	1.28	0.324
C.total	19	2204.95			

R-Square	C.V.	Root MSE	Total mean
0.54	14.52	9.14	62.95

Appendix. 29

Effect of combined C.partellus and P.furvus pupal ages on progeny production

Variable: Host age 0

Source	df	SS	MS	F	P>F
Model	7	1333.50	190.50	1.95	0.14
Error	12	1170.70	97.55		
Parasitoid age	4	1097.70.	274.42	2.81	0.07
Reps	3	235.80	78.60	0.81	0.51
C.total	19	2504.20			

R-Square	C.V.	Root MSE	Total mean
0.53	9.84	9.87	100.30

Variable: Host age 1

Source	df	SS	MS	F	P>F
Model	7	2174.45	310.63	3.42	0.03
Error	12	1088.50	90.71		
Parasitoid age	4	1794.70	448.67	4.95	0.01
Reps	3	379.75	126.58	1.40	0.29
C.total	19	3262.95			

R-Square	C.V.	Root MSE	Total mean
0.66	9.25	9.52	102.95

Variable: Host age 2

Source	df	SS	MS	F	P>F
Model	7	2510.70	358.67	7.17	0.001
Error	12	600.30	50.02		
Parasitoid age	4	2388.50	597.12	11.94	0.0001
Reps	3	122.20	40.73	0.81	0.51
C.total	19	3111.00			

R-Square	C.V.	Root MSE	Total mean
0.81	6.96	7.07	101.50

Variable: Host age 3

Source	df	SS	MS	F	P>F
Model	7	2287.05	326.72	6.42	0.002
Error	12	610.70	50.89		
Parasitoid age	4	1886.50	471.62	9.27	0.0001
Reps	3	400.55	133.51	2.62	0.09
C.total	19	2897.75			

R-Square	C.V.	Root MSE	Total mean
0.78	7.26	7.13	98.25

Variable: Host age 4

Source	df	SS	MS	F	P>F
Model	7	1011.35	144.47	2.51	0.07
Error	12	691.60	57.63		
Parasitoid age	4	671.20	167.80	2.91	0.06
Reps	3	340.15	113.38	1.97	0.17
C.total	19	1702.95			

R-Square	C.V.	Root MSE	Total mean
0.59	9.91	7.59	76.55

Variable: Host age 5

Source	df	SS	MS	F	P>F
Model	7	16419.75	3283.95	107.57	0.0001
Error	12	183.16	30.52		
Parasitoid age	4	16328.16	8164.08	267.43	0.0001
Reps	3	91.58	30.53	1.00	0.45
C.total	19	16602.91			

R-Square	C.V.	Root MSE	Total mean
0.98	21.18	5.52	26.08

Appendix: 30

Influence of combined host (C. partellus) and parasitoid ages on sex ratio

Variable: Host age 0

Source	df	SS	MS	F	P>F
Model	7	128.12	18.30	3.95	0.018
Error	12	55.56	4.63		
Parasitoid age	4	89.41	22.35	4.83	0.01
Reps	3	38.72	12.91	2.79	0.08
C.total	19	183.69			

R-Square	C.V.	Root MSE	Total mean
0.69	8.01	2.15	26.85

Variable : Host age 1

Source	df	SS	MS	F	P>F
Model	7	224.89	32.12	4.64	0.01
Error	12	83.12	6.93		
Parasitoid age	4	176.73	44.18	6.38	0.005
Reps	3	48.16	16.05	2.32	0.12
C.total	19	308.01			

R-Square	C.V.	Root MSE	Total mean
0.73	9.50	2.63	27.70

Variable : Host age 2

Source	df	SS	MS	F	P>F
Model	7	159.48	22.78	0.90	0.53
Error	12	303.53	25.29		
Parasitoid age	4	157.02	39.25	1.55	0.25
Reps	3	2.45	0.82	0.03	0.99
C.total	19	463.01			

R-Square	C.V.	Root MSE	Total mean
0.34	17.81	5.03	28.23

Variable : Host age 3

Source	df	SS	MS	F	P>F
Model	7	672.93	96.13	4.36	0.01
Error	12	264.61	22.05		
Parasitoid age	4	664.20	166.05	7.53	0.002
Reps	3	8.73	2.91	0.13	0.94
C.total	19	937.55			

R-Square	C.V.	Root MSE	Total mean
0.72	11.24	4.69	41.77

Variable: Host age 4

Source	df	SS	MS	F	P>F
Model	7	558.11	79.73	1.41	0.28
Error	12	679.73	56.64		
Parasitoid age	4	319.85	79.96	1.41	0.28
Reps	3	238.25	79.41	1.40	0.29
C.total	19	1237.84			

R-Square	C.V.	Root MSE	Total mean
0.45	12.94	7.52	58.14

Variable: Host age 5

Source	df	SS	MS	F	P>F
Model	7	13058.51	1865.50	526.29	0.28
Error	12	42.53	3.54		
Parasitoid age	4	13047.87	3261.96	920.26	0.0001
Reps	3	10.63	3.54	1.00	0.42
C.total	19	13101.04			

R-Square	C.V.	Root MSE	Total mean
0.99	14.74	1.88	12.77

Appendix : 31

Influence of combined host (B. fusca) and parasitoid ages on sex ratio

Variable: Host age 0

Source	df	SS	MS	F	P>F
Model	7	181.25	25.89	10.60	0.0003
Error	12	29.30	2.44		
Parasitoid age	4	150.30	37.57	15.39	0.0001
Reps	3	30.95	10.31	4.23	0.03
C.total	19	210.55			

R-Square	C.V.	Root MSE	Total mean
0.86	6.04	1.56	25.85

Variable: Host age 1

Source	df	SS	MS	F	P>F
Model	7	206.10	29.44	10.07	0.0003
Error	12	35.10	2.92		
Parasitoid age	4	171.70	42.92	14.68	0.0001
Reps	3	34.40	11.46	3.92	0.03
C.total	19	241.20			

R-Square	C.V.	Root MSE	Total mean
0.85	6.38	1.71	26.80

Variable: Host age 2

Source	df	SS	MS	F	P>F
Model	7	206.90	29.55	10.34	0.0003
Error	12	34.30	2.85		
Parasitoid age	4	201.70	50.42	17.64	0.0001
Reps	3	5.20	1.73	0.61	0.62
C.total	19	241.20			

R-Square	C.V.	Root MSE	Total mean
0.85	6.21	1.69	27.20

Variable: Host age 3

Source	df	SS	MS	F	P>F
Model	7	199.30	28.47	2.10	0.12
Error	12	162.90	13.57		
Parasitoid age	4	188.70	47.17	3.48	0.417
Reps	3	10.60	3.53	0.26	0.8526
C.total	19	362.20			

R-Square	C.V.	Root MSE	Total mean
0.55	13.79	3.68	26.70

Variable: Host age 4

Source	df	SS	MS	F	P>F
Model	7	81.85	11.69	0.80	0.60
Error	12	174.70	14.56		
Parasitoid age	4	79.30	19.82	1.36	0.30
Reps	3	2.55	0.85	0.06	0.98
C.total	19	256.55			

R-Square	C.V.	Root MSE	Total mean
0.32	13.79	3.81	27.65

Variable: Host age 5

Source	df	SS	MS	F	P>F
Model	7	291.55	41.65	4.59	0.01
Error	12	109.00	9.08		
Parasitoid age	4	257.80	64.45	7.10	0.0036
Reps	3	33.75	11.25	1.24	0.33
C.total	19	400.55			

R-Square	C.V.	Root MSE	Total mean
0.73	10.09	3.01	29.85

Variable: Host age 6

Source	df	SS	MS	F	P>F
Model	7	852.25	121.75	24.89	0.0001
Error	12	58.70	4.89		
Parasitoid age	4	801.70	200.42	40.97	0.0001
Reps	3	50.55	16.85	3.44	0.05
C.total	19	910.95			

R-Square	C.V.	Root MSE	Total mean
0.93	6.81	2.21	32.42

Variable: Host age 7

Source	df	SS	MS	F	P>F
Model	7	702.00	100.28	17.00	0.0001
Error	12	70.80	5.90		
Parasitoid age	4	696.80	174.20	29.53	0.0001
Reps	3	5.20	1.73	0.29	0.83
C.total	19	772.80			

R-Square	C.V.	Root MSE	Total mean
0.91	6.46	2.43	37.60

Variable: Host age 8

Source	df	SS	MS	F	P>F
Model	7	2321.10	331.58	114.67	0.0001
Error	12	34.70	2.89		
Parasitoid age	4	2319.30	579.82	200.52	0.0001
Reps	3	1.80	0.60	0.21	0.88
C.total	19	2355.80			

R-Square	C.V.	Root MSE	Total mean
0.98	4.26	1.70	39.90

Appendix: 32

Influence of Diet on P.furvus fecundity

Variable: Honey concentrations

Source	df	SS	MS	F	P > F
Model	7	344.34	49.19	0.27	0.9557
Error	12	2213.95	184.49		
Parasitoid age	4	205.53	51.38	0.28	0.8863
Reps	3	138.81	46.27	0.25	0.8592
C.total	19	2558.30			

R-Square	C.V.	Root MSE	Total mean
0.13	8.88	13.58	152.79

Variable: Sucrose concentrations

Source	df	SS	MS	F	P > F
Model	7	129.75	18.53	0.13	0.9938
Error	12	1691.36	140.94		
Parasitoid age	4	67.28	16.82	0.12	0.9730
Reps.	3	62.47	20.82	0.15	0.9291
C.total	19	1821.12			

R-Square	C.V.	Root MSE	Total mean
0.07	7.82	11.87	151.80

Variable: Unfed

Source	df	SS	MS	F	P > F
Model	7	1078.74	154.10	0.50	0.8153
Error	12	3675.33	306.27		
Parasitoid age	4	1069.90	267.47	0.87	0.5079
Reps.	3	8.84	2.94	0.01	0.9986
C.total	19	4754.07			

R-Square	C.V.	Root MSE	Total mean
0.22	11.63	17.50	150.42

Appendix: 33

Influence of Diet on ovipositional period of P.furvus female

Variable: Honey concentrations

Source	df	SS	MS	F	P > F
Model	7	1.85	0.26	0.45	0.8543
Error	12	7.10	0.59		
Parasitoid age	4	1.70	0.42	0.72	0.5956
Reps.	3	0.15	0.05	0.08	0.9672
C.total	19	8.95			

R-Square	C.V.	Root MSE	Total mean
0.20	53.04	0.76	1.45

Variable: Sucrose concentrations

Source	df	SS	MS	F	P > F
Model	7	2.20	0.31	0.94	0.5100
Error	12	4.00	0.33		
Parasitoid age	4	1.20	0.30	0.90	0.4940
Reps.	3	1.00	0.33	1.00	0.4262
C.total	19	6.20			

R-Square	C.V.	Root MSE	Total mean
0.35	44.41	0.57	1.30

Appendix: 34

Influence of Sucrose Diet on P.furvus adult longevity

Variable: 5 %

Source	df	SS	MS	F	P > F
Model	5	35.98	7.19	4.51	0.0849
Error	4	6.38	1.59		
Sex	1	34.82	34.82	21.80	0.0095
Reps	3	1.16	0.29	0.18	0.9359
C.total	9	42.36			

R-Square	C.V.	Root MSE	Total mean
0.84	28.72	1.26	4.40

Variable: 10 %

Source	df	SS	MS	F	P > F
Model	5	13.92	2.78	0.65	0.6774
Error	4	17.02	4.25		
Sex	1	1.85	1.85	0.44	0.5449
Reps	3	12.06	3.01	0.71	0.6265
C.total	9	30.94			

R-Square	C.V.	Root MSE	Total mean
0.44	17.24	2.06	11.96

Variable: 20 %

Source	df	SS	MS	F	P > F
Model	5	15.07	3.01	2.55	0.1930
Error	4	4.73	1.18		
Sex	1	3.21	3.21	2.71	0.1748
Reps	3	11.86	2.96	2.50	0.1978
C.total	9	19.80			

R-Square	C.V.	Root MSE	Total mean
0.76	18.87	1.08	5.76

Variable: 30 %

Source	df	SS	MS	F	P > F
Model	5	2.60	0.52	4.08	0.0988
Error	4	0.51	0.12		
Sex	1	0.54	0.54	4.29	0.1070
Reps	3	2.05	0.51	4.03	0.1028
C.total	9	3.11			

R-Square	C.V.	Root MSE	Total mean
0.83	6.82	0.35	5.23

Variable: 40 %

Source	df	SS	MS	F	P > F
Model	5	2.10	0.42	0.51	0.76
Error	4	3.30	0.82		
Sex	1	1.60	1.60	1.95	0.2354
Reps	3	0.49	0.12	0.15	0.95
C.total	9	5.40			

R-Square	C.V.	Root MSE	Total mean
0.38	17.47	0.91	5.19

Variable: Unfed

Source	df	SS	MS	F	P > F
Model	5	2.66	0.53	18.42	0.0073
Error	4	0.11	0.02		
Sex	1	2.50	2.50	86.51	0.0007
Reps	3	0.16	0.04	1.40	0.3762
C.total	9	2.77			

R-Square	C.V.	Root MSE	Total mean
0.95	5.60	0.17	3.03

Variable: Distilled water

Source	df	SS	MS	F	P > F
Model	5	2.66	0.53	4.33	0.0902
Error	4	0.49	0.12		
Sex	1	2.18	2.18	17.71	0.0136
Reps	3	0.48	0.12	0.99	0.5041
C.total	9	3.16			

R-Square	C.V.	Root MSE	Total mean
0.84	15.94	0.35	2.20

Appendix: 35

Adult longevity of P. furvus at different Honey concentrations

Variable: 5 %

Source	df	SS	MS	F	P > F
Model	5	30.32	6.06	11.15	0.0183
Error	4	2.17	0.54		
Sex	1	28.83	28.83	53.00	0.0019
Reps	4	1.48	0.37	0.68	0.6392
C.total	9	32.49			

R-Square	C.V.	Root MSE	Total mean
0.93	7.87	0.74	9.37

Variable: 10 %

Source	df	SS	MS	F	P > F
Model	5	32.18	6.43	4.17	0.0955
Error	4	6.16	1.54		
Sex	1	27.85	27.85	18.06	0.0132
Reps	4	4.32	1.08	0.70	0.6302
C.total	9	38.34			

R-Square	C.V.	Root MSE	Total mean
0.84	9.91	1.24	12.52

Variable: 20 %

Source	df	SS	MS	F	P > F
Model	5	72.48	14 49	5.71	0.0582
Error	4	10.16	2.54		
Sex	1	65.02	65.02	25.60	0.0072
Reps	4	7.46	1.86	0.73	0.6138
C.total	9	82.64			

R-Square	C.V.	Root MSE	Total mean
0.87	22.32	1.59	7.14

Variable: 30 %

Source	df	SS	MS	F	P > F
Model	5	8.47	1.69	2.44	0.2037
Error	4	2.77	0.69		
Sex	1	7.22	7.22	10.41	0.0321
Reps	4	1.25	0.31	0.45	0.7706
C.total	9	11.24			

R-Square	C.V.	Root MSE	Total mean
0.75	12.33	0.83	6.75

Variable: 40 %

Source	df	SS	MS	F	P > F
Model	5	37.38	7.47	27.50	0.0034
Error	4	1.08	0.27		
Sex	1	34.22	32.44	125.89	0.0004
Reps	4	3.16	0.79	2.91	0.1629
C.total	9	38.46			

R-Square	C.V.	Root MSE	Total mean
0.97	13.20	0.52	3.95

Appendix: 36

Effect of Superparasitism on progeny production at different exposure times

Variable: 12hrs. exposure time

Source	df	SS	MS	F	P > F
Model	8	12582.53	1572.81	6.68	0.0008
Error	15	3529.64	235.31		
Ratio	5	11822.31	2364.46	10.05	0.0002
Reps	3	760.21	253.40	1.08	0.3887
C.total	23	16112.17			

R-Square	C.V.	Root MSE	Total mean
0.78	19.99	15.34	76.74

Variable: 24hrs. exposure time

Source	df	SS	MS	F	P > F
Model	8	11772.38	1471.54	3.71	0.0138
Error	15	5943.33	396.22		
Ratio	5	11618.06	2323.61	5.86	0.0138
Reps	3	154.31	51.44	0.13	0.9400
C.total	23	71715.71			

R-Square	C.V.	Root MSE	Total mean
0.66	24.08	19.90	82.65

Appendix: 37

Effect of Superparasitism on P. furvus development at different exposure times

Variable: 12hrs. exposure time

Source	df	SS	MS	F	P > F
Model	8	13.31	1.66	0.78	0.6300
Error	15	32.04	2.13		
Ratio	5	9.31	1.86	0.87	0.5200
Reps	3	4.00	1.33	0.62	0.6100
C.total	23	45.35			

R-Square	C.V.	Root MSE	Total mean
0.29	7.75	1.46	18.85

Variable: 24hrs. exposure time

Source	df	SS	MS	F	P > F
Model	8	3.87	0.48	2.45	0.060
Error	15	2.96	0.19		
Ratio	5	3.37	0.67	3.42	0.030
Reps	3	0.49	0.16	0.84	0.490
C.total	23	6.83			

R-Square	C.V.	Root MSE	Total mean
0.56	2.31	0.44	19.23

Appendix: 38

Effect of Superparasitism on egg production at different exposure times

Variable: 12hrs. exposure time

Source	df	SS	MS	F	P > F
Model	8	449619.33	56202.41	127.28	0.0001
Error	15	6623.29	441.55		
Ratio	5	449132.87	89826.57	203.43	0.0001
Reps	3	486.45	162.15	0.37	0.777
C.total	23	456242.62			

R-Square	C.V.	Root MSE	Total mean
0.98	9.26	21.01	226.87

Variable: 24hrs. exposure time

Source	df	SS	MS	F	P > F
Model	8	473343.66	59167.95	131.58	0.0001
Error	15	6745.29	449.68		
Ratio	5	473118.64	94623.64	210.42	0.0001
Reps	3	225.45	75.15	0.17	0.9100
C.total	23	480088.95			

R-Square	C.V.	Root MSE	Total mean
0.98	8.64	21.20	245.29

Appendix: 39

Effect of Superparasitism on size of adult P. furvus

Variable: Non-superparasitized

Source	df	SS	MS	F	P > F
Model	4	1.166	0.291	99.00	0.0016
Error	3	0.0088	0.0029		
Size	1	1.163	1.163	394.73	0.0003
Reps	3	0.0037	0.0012	0.42	0.751
C.total	7	1.1754			

R-Square	C.V.	Root MSE	Total mean
0.99	2.89	0.05	1.87

Variable: Superparasitized (dwarfs)

Source	df	SS	MS	F	P > F
Model	4	0.26	0.06	31.84	0.0086
Error	3	0.0062	0.0021		
Size	1	0.25	0.25	120.98	0.0016
Reps	3	0.013	0.004	2.13	0.275
C.total	7	0.2716			

R-Square	C.V.	Root MSE	Total mean
0.97	2.92	0.04	1.56

Appendix 40

Influence of Superparasitism on the parasitoid sex ratio at different exposure times.

Variable: 12 hours.

Source	df	SS	MS	F	P > F
Model	8	4676.44	584.55	31.21	0.0001
Error	15	280.91	18.73		
Ratio	5	4596.28	919.25	49.09	0.0001
Reps.	3	80.16	26.72	1.43	0.200
C.total	23	4957.35			

R-Square	C.V.	Root MSE	Total mean
0.94	13.02	4.33	33.24

Variable: 24.hours.

Source	df	SS	MS	F	P > F
Model	8	3149.32	393.66	58.31	0.0001
Error	15	101.27	6.75		
Ratio	5	3118.37	623.67	92.38	0.0001
Reps.	3	30.94	10.31	1.53	0.2481
C.total	23	5250.59			

R-Square	C.V.	Root MSE	Total mean
0.96	7.71	2.59	33.67