THE BIOLOGY OF *CERANISUS MENES* (WALKER) (HYM., EULOPHIDAE), A PARASITOID OF THE BEAN FLOWER THRIPS *MEGALUROTHRIPS SJOSTEDTI* (TRYBOM) (THYS., THRIPIDAE):A COMPARISON BETWEEN AFRICAN AND ASIAN POPULATIONS

BY

KHADY DIOP

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A thesis

submitted to the Department of Crop Science of the Faculty of Agriculture, University of Ghana, Legon in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Crop Science (Entomology)

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Declaration

I hereby declare that the work contained in this thesis for the Doctor of Philosophy degree in Crop Science (Entomology) is the result of my own investigations and has not been submitted for a similar degree in any other University.

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Professor J. N. Ayertey
University Supervisor

Dr. M. Tamò
IITA supervisor

Dedication

To my mother Nafy Gueye.

To my two adoptive mothers,

Khady Diagne and Awa Gueye, peace on them

Abstract

Cowpea is an important food crop in Africa, but suffers from a variety of insect pests. Among those is *Megalurothrips sjostedti* (Trybom), a major pest which is not successfully controlled by its local natural enemies. One of them, *Ceranisus menes* (Walker), a cosmopolitan endoparasitoid of thrips larvae, provides an efficient control of thrips populations in Southeast Asia. This has necessitated a study of this insect which involves a comparison of the biology of the African and Asian populations of *C. menes*.

To achieve this, three (3) objectives were set: 1) to identify potential candidate for the adoption of the Novel Association Approach of biological control against *M. sjostedti*, using the Southeast Asian populations of this parasitoid; 2) to diagnose the problem of the local population in failing to provide good control of *M. sjostedti*, 3) and to obtain more information on the biological diversity of the different geographical strains of *C. menes*.

Three (3) strains selected from Southeast Asia, i.e. one from Malaysia and two from India, and the local strain from Benin were studied. Quantitative evaluation of their biological characteristics, when *M. sjostedti* was offered as host, were obtained and compared. Based on these data, the compatibility of the different strains of *C. menes* with *M. sjostedti* for successful parasitism were assessed. On the question of the problem of the local strain, this study used as control the most compatible host-parasitoid pairings: *M. usitatus*-Malaysian, or *Frankliniella schultzei*-Indian strains, to evaluate the compatibility of the pairing *M. sjostedti*-local strain.

A series of 3 laboratory experiments simulating the natural chronological sequence of events during the parasitization process were conducted. The first experiment studied the behaviour of host thrips larvae and *C. menes* parasitoid at the host selection phase. For this, a model of their behaviour was developed. Parameters were defined, and determined for host resistance, host acceptance, and host handling time, from the various reactions of the host larva, and the wasp. Host resistance refered to the defensive behaviour of the thrips, and host acceptance, to that of the parasitoid

accepting the thrips larva for oviposition. Each of five (5) female wasps of the Malaysian strain, and ten (10) females of the other strains of the parasitoid, was observed, interacting with the thrips larvae during a total period of 300 minutes per strain. For each species of thrips, three different age-groups of larvae, 0-24 hours, 24-48 hours, and 48-72 hours, were used as host, in order to determine any effect of host age on the behaviour of the parasitoid. Each female parasitoid was offered a unique category of host at a time. In the second experiment, host suitability for the local and the two Indian strains was studied. It was evaluated from the immature survival rate of the parasitoid on the host. In the last experiment, the developmental time and the demographic parameters of the parasitoid were studied, to compare the potential of each strain to maintain and build up its population on the host. All data were analyzed at the 5% level of significance. Host handling times were compared between treatments using Kruskal-Wallis test. Host resistance, and acceptance parameters, the immature survival rate, and the population sex ratio were compared using the logit loglinear model analysis. The jacknife method was used to analyze and compare the intrinsic rate of natural increase (r_m) of the different populations of *C. menes*.

During the first series of tests, it was found that the one and two days old larvae were slightly faster to handle, and also significantly less resistant, and more likely to be accepted by all strains of *C. menes*. Thus larvae from these two age groups were used to maximize parasitization success in the subsequent second and third tests.

The results of this investigation indicated that there were in fact biological differences between the four strains of *C. menes*, on *M. sjostedti* host. There were significant differences between strains in the sub-components of the host handling time, but no difference in the overall host handling time. The average host handling time for the Malaysian, the two Indian strains, and the local strains were respectively 27.4, 29.0, 25.8, and 31.6 seconds.

It was also found that the four strains of *C. menes* were slightly different in their ability to overcome the resistance of *M. sjostedti* larvae. The results showed that 40.6 and 46.4 percent of larvae encountered by the Malaysian and local strains respectively, were resistant to the parasitoid. With the two Indian strains they were 53.2, and 53.5

percent. The analysis indicated no difference between the Malaysian and local strains; or between the two Indian strains. The first two strains were however slightly better to overcome *M. sjostedti* host resistance, than the two Indian strains.

The acceptance of *M. sjostedti* was definitely more successful with the local than with the exotic strains. More than twenty five percent (25.5%) of the non resistant larvae were accepted by the local strains for oviposition. Acceptance of this thrips species decreased significantly in the order: the two Indian strains (4.7 and 3.3 percent), Malaysian strain (0.4 %).

Thus, at the host selection phase of the parasitization process, the behaviour of the local strain was found to be the most compatible for a successful parasitization of *M. sjostedti*. However, in the physiological test, the suitability of *M. sjostedti* was found to be very poor for the local strain, as well as for the second Indian strain (**Indian2**). Their survival rates (proportion of eggs that survive up to adult stage) in this species of thrips was estimated at 0.06 for both strains. Unexpectedly, it was significantly higher (0.36) for the first Indian strain (**Indian1**).The possibility that *M .sjostedti* could have co-evolved with the Asian population of *C. menes* in the past was discussed.

The results of the life history notes in the last test confirmed those of the first and second tests. The Indian2 strain was not able to reproduce in *M. sjostedti*, in contrast to the local and Indian1 strain. The sex ratio of the offspring population was 0 for the local, as compared to 0.67 for the Indian1 strain. On the other hand, the total fecundity of the Indian1 strain was very low, as compared to that of the local strains: Ten (10) female wasps of Indian1 strain produced an average of two (2) offspring, whereas the same number of females of the local strain produced an average of up to 867 offspring. As a consequence, the population growth parameters R_0 and r_m were null for all the 3 strains of *C. menes*. The mean developmental time of the Indian1 and local strains were respectively 23.0 and 21.0 days for males.

In fact, each of the 4 populations of *C. menes* was unique in the biological features it exhibited when *M. sjostedti* was offered as host. This can be seen as the onset of biotypes differentiation among the 4 populations of this species of parasitoid. The difference on the two Indian strains, both originating from the same geographical area are discussed.

When comparing the local strain on *M. sjostedti* against the Asian strains on their respective check hosts *F. schultzei* and *M. usitatus*, the results of the first test showed that the host handling time by the local strain (31.6 seconds) was not significantly different from those of the two Indian strains (24.1, and 30.0 seconds). Host resistance against the local strain (40.6%) was also not significantly different from that against the Malaysian (47.2%). Host acceptance by the local strain (25.5%) was also not significantly different from that of the Malaysian strain (27.9%). However there were significant differences in the suitability of their respective check hosts, suggesting that physiological incompatibility must have been the only reason why the local strain could not perform as well on *M. sjostedti* as the Asian strains were doing on their check hosts. The survival rate of the local strain (0.06) was significantly lower than that of the first and second Indian strains, which were 0.20 and 0.46 respectively. The mean developmental time for males of the local strain (21.0 days) was higher than that of the Indian2 strain (18.7 days), but it was lower than that of the Indian1 strain (22.5 days). The possible explanations for the lack of suitability of *M. sjostedti* to the local strain of *C. menes* are also discussed.

In conclusion, this study has brought some insight into the biological diversity among the different geographical populations of *C. menes*. It has demonstrated that none of the 4 selected strains of *C. menes* from Southeast Asia and Africa would be able to parasitize successfully *M. sjostedti*. Each of them was hampered by behavioural and/or physiological incompatibility with this thrips species. The possibility of manipulating the Asian population to obtain better success with *M. sjostedti* is discussed

The validity of the model and the critiques of the methodology used for the behaviour study are also discussed.

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AWLAE	"African Women Leaders in Agriculture and Environment". This is the IITA-Winrock Collaborative Programme for Agricultural and Leadership Fellowships for West African Women Agricultural Professionals
IITA	"International Institute for Tropical Agriculture"
ISRA	"Institut Senegalais de Recherches Agronomiques"
NAA	"New Association Approach" of biological control
WAU	"Wageningen Agricultural University"

Chapter 1
GENERAL INTRODUCTION

Cowpea, *Vigna unguiculata* (L.) (Walker), an indigenous plant of Africa, is a valuable leguminous crop grown in tropical, sub-tropical zones of Africa, Asia, and America. The value of this crop, especially in the sub-sahelian region of Africa, resides first in its high level of tolerance to heat, drought, and soil mineral deficiencies (Hall *et al.*, 1979), which enables it to grow in the Semi-Arid zone, where low rainfall, and poor soil fertility are the most important limiting factors for many agricultural crops. Secondly, cowpea grains, as well as both its pods and leaves which are consumed as vegetable, represent an important source of cheap protein for millions of Africans living in this area.

Several constraints have kept farmers' yields constantly low at levels between 350 and 700 kg/ha, although yields of 2500 kg/ha are achievable. Despite the efforts made at IITA to improve cowpea production by developing high yielding, and disease-resistant cultivars, insect pests still remain a major constraint to production. Traditional plant breeding to introduce insect resistance has yielded limited success. Thus, average yields cannot be contemplated unless cowpea cultivation is accompanied by heavy doses of insecticides. One most important pest that requires regular insecticide spraying for the farmer to achieve a good yield is *Megalurothrips sjostedti* (Trybom) (Thysanoptera: Thripidae), commonly referred to as the "bean flower thrips" or "cowpea thrips". However, beside its undesirable ecological and health consequences, insecticide dependence is also not an economical solution in Africa, since cowpea is cultivated mostly by resource poor farmers in small holdings. A more sustainable and environmentally friendly method of controlling the cowpea thrips had to be found.

The first attempt to study systematically the factors that make this insect a key pest on cowpea was done by Tamò and co-workers (1993). They found that three factors were mainly responsible for the pest status of this insect in West Africa : (1) the existence of a wide range of alternative host plants in the zone, (2) the low damage

threshold of the thrips on cowpea, and (3) the low performance of the local natural enemies in controlling the pest.

A search for natural enemies of *M. sjostedti*, through sampling from the exotic plant *Tephrosia candida* (Fabaceae), an alternative host for *M. sjostedti*, revealed for the first time in Africa, and in this species of thrips, the presence of *Ceranisus menes* (Walker) (Hymenoptera: Eulophidae), a larval endoparasitoid of many other thrips species.

C. menes is a cosmopolitan species with great variations among as well as within geographical strains of this insect, and with an unclear taxonomy. The tropical area of the East Asiatic region is ecologically similar to the West African zone. In addition, it has the largest diversity in species of this parasitoid, that keeps under control the populations of thrips species like *M. usitatus* and *M. typicus*, which are phylogenetically close to *M. sjostedti.*

It has been proved in many cases that natural enemies controlling the close relatives of a pest can be very successful against the pest (Dodd, 1940; Pimentel, 1963). Therefore, the populations of *C. menes* from this region could be considered as a potential biological control candidate against the cowpea thrips in the West African region.

It is well known that taxonomy is very important in biological control. Therefore, the accurate identification especially at the subspecies level, can be very crucial for the success of a biological control programme (Gonzales *et al.* 1979). As stated above, *C. menes* presents lots of variations at this sub-species level, so it is important to be aware of the existence of any biotypes among this insect, before time and effort are wasted in trying to work with a wrong biological control agent.

In this type of biological control, known as "New Association Approach" (NAA) (Hokkanen, and Pimentel, 1984; 1989) the knowledge of the behavioural and physiological compatibility of the natural enemy with the target host, as well as its biological attributes contributes to understanding or helping to predict the performance of the natural enemy (Hokkanen, and Pimentel, 1984; 1989; van Lenteren, 1988;

Wiedenmann and Smith, 1997). These parameters can also be used to compare populations of different species, or of a species occurring at different locations (van Lenteren, 1988).

Another important reason to investigate the diversity of this parasitoid, is to have a sound understanding of what is being done, as recommended by Sabrowsky (1955): this particular biocontrol programme would seek to introduce *C. menes* in West Africa where it already exists. Thus, before the natural situation is confused by mixing all the *C. menes* populations, now is the best chance to get fundamental information, and establish the relation and status of the Asian and African forms of this parasitoid. This can be a significant exercise for both biological control and taxonomic researches.

The objective of this work was therefore, to estimate and compare the biological characteristics of different populations of *C. menes* from tropical Asia and West Africa. This knowledge was expected to help first explain the low performance of the local population of *C. menes* to control the cowpea thrips in West Africa. Secondly, it was also expected to help identify the potential effectiveness of the East Asian populations, for future use in a NAA of biological programme against the cowpea thrips, and hopefully, to provide information for the review of the taxonomy of *C. menes*.

Chapter 2
LITERATURE REVIEW

2.1. The insect pest: *M. sjostedti*

2.1.1. Reproduction and damage

Although males have been observed, the reproduction of *M. sjostedti* is mostly parthenogenetic. The adult female inserts its eggs in the plant tissue of the buds, pods, or stem of the host plant. After hatching, the young larvae come out of the plant tissue, and the feeding activity of both the immature and adult thrips on the reproductive structures causes an excessive shedding of the flowers and buds, resulting in an important loss of yield (Singh and Taylor, 1978).

It is only in the last 30 years that *M. sjostedti* was recognized as a pest on cowpea in West Africa (Singh and Taylor, 1978) where the importance of the crop has consequently justified many studies in the 1970s to develop resistant varieties, and programmes to optimize the use of insecticides against this pest.

This species is again the only one in the genus to have reached pest status on an agricultural crop (Palmer, 1987). In East Asia, its closely related species are not serious pests, as their populations are kept under control by the activity of natural enemies (Tamò *et al*, 1997). This is one of the supporting arguments for the hypothesis of the foreign origin of *M. sjostedti* suggested by this author.

2.1.2. Origin, distribution, and history

M. sjostedti was recorded for the first time on the African continent at the beginning of this century (Trybom, 1908). Not only is its distribution range restricted to the African continent, it is also the unique species in the genus found in Africa (Palmer, 1987; 1989). Its closely related species, *M. typicus* (Bagnall), and *M. usitatus* (Bagnall), and

M. distalis are found in East Asia (Palmer, 1987). For many years, *M. sjostedti* was considered as *Taeniothrips sp.*

2.1.3. Taxonomy

The cowpea thrips, *M. sjostedti*, belongs to the large family of Thripidae, a sub-division of the suborder Terebrantia., characterized by a conical last abdominal segment in the male, and a small external saw-like ovipositor in the female (Palmer, 1990). Species in the genus Megalurothrips can easily be identified in the field by their large size. Adults are black and the immature stages are reddish (Plate 2.1 "a" and "b"). From the taxonomical point of view, they are also characterized by the presence on the abdominal tergite VIII, of a comb of microtrichia grouped laterally to the spiracle (Palmer, 1990). Within the genus, the asymmetrical positioning of the median posteromarginal setae on the sternite VII of the female individual allows one to distinguish *M. sjostedti* from its South-East Asian sister species, *M. usitatus*. This seta is located at the posterior margin in the former, and at the anterior margin in the latter.

Plate 2.1: Larva (a) and female adult (b) of *Megalurothrips sjostedti*

a) b)

(x 300)

2.2. The parasitoid: *C. menes*

2.2.1. Origin and Distribution

C. menes is a solitary, koinobiont, endoparasitoid of the larval stages of the thrips. It is found in a variety of habitats, host plants, host thrips species. This lack of ecological specificity must probably be related to the high diversity in biological attributes found among the geographical strains of this parasitoid.

The distribution of *C. menes* is almost worldwide (Fig.2.1). Despite the fact that early records originated from Europe (Vuillet, 1914; Buhl, 1937), most materials described recently were collected from East Asia (Japan, Korea, Taiwan, Indonesia etc..) which is thought to be the area of origin of this species (Loomans, 1991). It is also found in America (DeSantis, 1961), has been introduced in Hawai (Sakimura, 1937b), and reported also in West Africa (Tamò *et al.*, 1993).

2.2.2. Synonyms

Several synonyms have preceded "*C. menes* ", since the first holotype was described by Walker in 1839. They are listed chronologically (Loomans and van Lenteren, 1995).

Pteroptrix menes Walker 1839,
Diglyphus aculeo Walker 1848,
Asecodes aculeo (Walker) Dalla Torre 1898
Thripoctenus brui Vuillet 1914,
Epomphate auriventris Girault 1915,
Epomphate rubensteina Girault 1934,
Ceranisus menes (Walker) Graham 1959,
Ceranisus rosilloi De Santis 1961.

Figure 2.1: World distribution of *Ceranisus menes* (Walker) (from Loomans and van Lenteren, 1995)

Circles are the origins of the populations studied in this paper

2.2.3. Taxonomy

2.2.3.1. Taxonomic characters for the identification of *C. menes*

The taxonomy of *C. menes* is still obscure (Loomans *et al.*, 1994, Loomans and van Lenteren, 1995). This family of parasitoids, the Eulophidae, has been studied to some extent in certain regions of the world, like the Palearctic (Peck *et al.*, 1964; Graham, 1963), the Holarctic (Schauff, 1991), the Oriental region (Hayat, 1985), and the Australian/Asian region (Boucek, 1976, 1988). For the specimens collected in these areas, generic keys for their identification are available.

A taxonomic key to the species level, provided by Graham (1963) and Erdös (1971) exists only for the European species. The characters used in this key to separate *C. menes* from the other species of Ceranisus, and classify it under this taxon are mostly structural external characters, and are summarized by these two authors as follows:

> "Females are 0.66 mm (DeSantis, 1961) till 1.06 mm (Buhl, 1937) in size, the males somewhat smaller (Ishii, 1933). *C. menes* is characterized by head and thorax black and all legs yellow; the hyaline wings can be distinguished from other Ceranisus species by the characteristic bare space below the subcubital vein strongly sinuately curved upward....The male differs from the female in its antennae and its truncate brownish abdomen, pale towards the base (Ishii, 1933; Tachikawa, 1986)."

So, based on this key and on reference catalogues, it was possible to distinguish from among materials collected worldwide, 14 well described species within the genus Ceranisus, which are reviewed by Loomans and van Lenteren, (1995).

2.2.3.2. Taxonomic problems

2.2.3.2.1. Variations in external and biological characters

Subsequent to this, several other variations have been identified within the species. First, a polymorphism in the colour of the abdomen has been found as another structural variation within *C. menes*. The abdomen of the females in specimens collected in different parts of the world varies from yellow to black, passing through four to five intermediate colours (Loomans, 1991; Loomans and van Lenteren, 1995). Some of them are uniformly coloured, and others present one or several narrow dark stripes across the abdominal tergites. The first material described by Walker (1839), as well as the original holotype (Vuillet, 1914), are of the uniform yellow type. The African specimen is of the three-striped brown type, and the materials that were collected in the South-East Asian region present all the different variants (Tamò, pers. coll.)

Secondly, biological variations within *C. menes* have been reported in early studies (Sakimura, 1937; Hirose, 1989; Daniel, 1986; Murai, 1990), and lately, some differences in biological parameters have again been detected within the European populations of *C. menes*, depending on their colour types or geographical origins (Loomans, 1993; 1994).

2.2.3.2.2. Variations in efficiency

There is a significant variation among the different populations in their ability to control efficiently their associated thrips hosts. The African population of *C. menes* is inefficient in controlling the cowpea thrips, *M. sjostedti*. In this area, parasitism was not found in all the host plants of *M. sjostedti*. Thrips larvae collected from the cowpea flowers for example, were not found parasitized when this parasitoid was first discovered in Benin (Tamò *et al.*, 1993). The parasitism of *M. sjostedti* from cowpea plant started later on (Tamò, *et al.*, 1997). Nevertheless, the percent parasitism observed on larvae from any host plant was still low, probably due to a high larval mortality of the parasitoid (Tamò *et al.*, 1993). In East Asia, different species of

Ceranisus, among which *C. femoratus* (Gahan), *C. vinctus* (Gahan), and *C. menes* (Walker) found parasitizing *Megalurothrips* spp, are thought to keep them below the pest status level (Tamò *et al.*, 1997).

2.2.3.2.3. Lack of taxonomic keys

The lack of taxonomic keys for most localities of this parasitoid range is another problem for the accurate identification of this insect. Apart from Europe, investigations on the taxonomy of Ceranisus have so far been limited. For the specimens of Ceranisus collected from any other part of the world including the South East Asiatic region and the African continent, identification is done just by reference to catalogues (Loomans and van Lenteren, 1995).

All these problems have cast doubt on the present taxonomic status of this species, and on the reliability of identification of the materials collected throughout the world (Tamò *et al.*, 1993; Loomans and Murai, 1994; Loomans and van Lenteren, 1995).

2.2.4. Ecology of *C. menes*

The ecology of this insect is reviewed by Loomans and van Lenteren, (1995).

2.2.4.1. Habitat and host plant range

C. menes is found in various biotopes. It has been collected alongside roads, in natural as well as agricultural ecosystems (Buhl, 1937; Hirose, 1989; Loomans, 1991; Hirose *et al.*, 1992, Tamò *et al.*, 1993). This parasitoid has also been collected from more than 20 different families of host plants, mostly the Leguminosae, but comprising also some Compositae, Cruciferae, Solanaceae, Euphorbiaceae, Liliaceae etc... In Benin, *C. menes* seems to prefer the exotic host plant *Tephrosia candida* to the indigenous cultivated crop cowpea. But later on, it has been sampled from cowpea (Tamò *et al.*, 1997). This differential parasitism on host plants could be explained by a lack of recognition of the cowpea crop as habitat for its hosts. On the plant, *C. menes* is found

in the organs or parts of the plant infested by the host: leaves of onion, potato, eggplant, or flowers of citrus, legumes etc... The wasp can sneak into very narrow spaces such as in between the petals of cowpea flowers, or leaves of onions to search for hosts.

2.2.4.2. Host range on thrips

C. menes is reported in the literature to attack a wide range of thrips hosts comprising at least 18 species of thrips, most of them of the genera Thrips, Frankliniella, Megalurothrips found in the African, Asian and European regions, including the species of Megalurothrips: *M. typicus*, *M. usitatus* (Chang, 1990), and *M. sjostedti* (Tamò *et al.*, 1993), all belonging to the same sub-family of Thripinae (Loomans *et al.*, 1992; Loomans *et al.*,, 1994). As pointed out by these authors, this host range could be overestimated: some of these thrips species are considered hosts only because they are found as adults in association with the female parasitoid searching for hosts in the flowers of the plants. There is no evidence that these thrips species collected in these plants flowers are actually established and feed on the plants, nor is there any evidence that the parasitoid can develop in all of them after attacking those larvae. It could be that thrips and/or parasitoids were just visiting the plant at the time of sampling.

On the other hand, the physiological range of *C. menes* could be wider than its ecological range. Several thrips species that have never been found associated with this parasitoid in the field, are found to be parasitized in the laboratory. The actual thrips host preference of *C. menes* is yet to be established.

2.2.4.3. Sex ratio and mode of reproduction of *C. menes*

In some regions, such as Europe and Africa, only females are found when sampling the host plant flowers in the field. In Europe, the female individuals collected reproduce parthenogenetically by theletoky (i.e. they asexually produce only female offspring). In Benin (West Africa) however, males exist too, although they are practically absent from the field samples collected (Tamò, 1993). They are usually obtained from field-parasitized larvae, collected and reared in the laboratory, and which give emergence to both males and females. The sex ratio in the samples is yet to be determined. The

question about where males and females of this parasitoid meet in the natural environment for copulation remains a dilemma.

In Asia, both males and females are collected in the field from the host plant flowers. In some areas, the sex ratio is around 1:1 (Hirose, 1989), but in most, the females predominate (van Heurn, 1923; Sakimura, 1937a; Daniel, 1986; Murai, 1988). So the strains of *C. menes* from Asia and Benin in Africa, have a bisexual type of reproduction. It has been reported however, that this parasitoid in Japan, has switched from a bisexual form of reproduction in the field, to an asexual form producing only females, after 5 generations of laboratory culture on *Frankliniella intonsa* (Murai, 1988). Again during laboratory culture, a switch from a 1:1 sex ratio in the first generation, to a progressively males predominating sex ratios through the following generations on *Thrips tabaci* has been reported (Carl, 1971).

2.2.5. Field parasitism

High field parasitism is reported only in Asia. In this region, the incidence of the parasitoid can vary from one area to the other, but generally, the climatic conditions, and pesticide application in agricultural crops are the main factors affecting field parasitism by *C. menes*. At the peak of the host *T. tabaci*, population in onion crops (mid-February, March and April), up to 100% parasitism was recorded in Japan (Sakimura, 1937b), 12-18% parasitism in India (Saxena, 1971), and 48% parasitism of *Z. ricini* on ricin plant (*Ricinus communis*) in Madras, India (Anathakrishnan, 1984). There is no parasitism when temperature falls below 20°C during dry season, or rises above the 30°C during the wet season (Sakimura, 1937b; Saxena, 1971). In Thailand, pesticide application in egg-plant gardens caused a significant decrease in the level of parasitism of *Thrips palmi* by *C. menes* (Hirose, 1989; 1990; Hirose *et al.*, 1993).

There are few reports on field parasitism in Europe. The only records are the 35.1% parasitism on the univoltine host species *Kakothrips pisivorus* in Germany (Buhl, 1937), which is relatively high compared to recent records of 8-25% parasitism found on Thripine hosts in several countries in Europe. In Benin (Africa), Tamò and co-workers (1997) reported a very low level of parasitism of *M. sjostedti* on cowpea plant

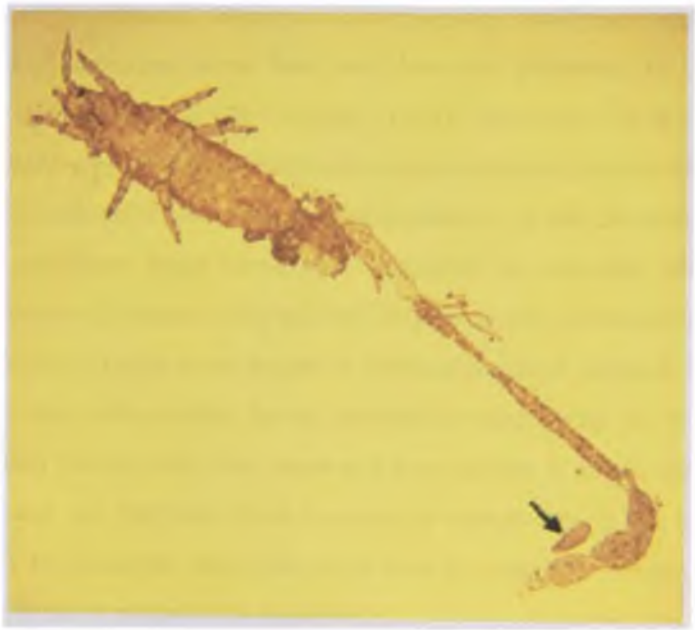
(< 1%), not much higher than on other naturally-occurring host plants. The parasitism in the other local thrips species in the environment has yet to be checked in Benin.

2.2.6. Life history of *C. menes*

The egg

C. menes lays its egg in the abdomen (Saxena, 1971) but preferentially in the thorax (Loomans, 1991), of the thrips larva. The egg of *C. menes* has a bean-like shape, more filiform in one of its sides than in the other (Plate 2.2). Its dimensions vary between 3 x 8 microns and 7 x 17 microns. This variation in size of the egg is probably due to a difference in their sexes. There is no record of encapsulation and melanization of the egg of *C. menes* as a defense reaction of the thrips larvae. Such mechanisms of resistance are however common in many endoparasitoid-host relationships, and could be a cause of failure of parasitization by *C. menes*. The incubation time of this parasitoid egg is unknown.

Plate 2.2: Egg of *Ceranisus menes* (indicated by the arrow) pulled out from the body of the host



(x 500)

The larva

After hatching, the larva of this endoparasitoid starts feeding and developing inside the host which is killed only just before pupation. The total duration of the egg and larval development of *C. menes* reported in the literature varies between 5.8 days and 22.8 days, depending on the temperature, the geographical origin of the parasitoid, and the species of thrips host (reviewed by Loomans and van Lenteren, 1995). It is well known that the host quality, as affected by the host species, affects the survival of the parasitoid larva feeding on it (Salt, 1940; Corrigan and Lashomb, 1990). Thus, a female *C. menes* accepting hosts that are not suitable as food jeopardizes the life of her offspring. This is another way by which the process of parasitization could be interrupted. Some species of thrips have been observed attacked by *C. menes,* without subsequent development of parasitism in the host larvae (Murai, 1988; 1990), and nothing is known whether or not this failure of the parasitization results from the death of the parasitoid larva within the host larva due the poor food quality.

The symptoms of parasitization on the thrips larva

The larva of the parasitoid develops in the apparently healthy growing thrips larva. The symptoms of parasitized larvae have been described extensively by many authors and reviewed by Loomans and van Lenteren, (1995): The symptoms of parasitism become apparent only at pre-pupation which occurs approximatively on the 6th to 7th day after oviposition under laboratory temperature conditions. At that moment, both parasitized and non parasitized thrips larvae hide themselves in concealed areas to pupate. In nature, this usually occurs in the soil for Thripine species, in between dried vegetation. In the laboratory thrips larvae pupate in between sheets of paper, at the bottom of the container. But unlike healthy larvae, parasitized thrips larvae do not develop wings; instead, they become with time, more and more tubular in shape, and creamy white in colour. Later on, the thrips larva presents an orange spot in the center of its body (Fig.2.2)). In fact at this stage, the thrips larva is completely consumed internally, and occupied by the prepupa of the parasitoid.

Figure 2.2: Prepupa of *Ceranisus menes* within the remains of the host larva (from Loomans and van Lenteren, 1995)

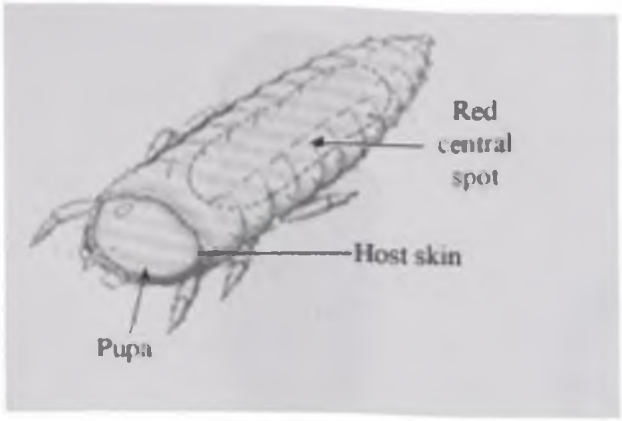
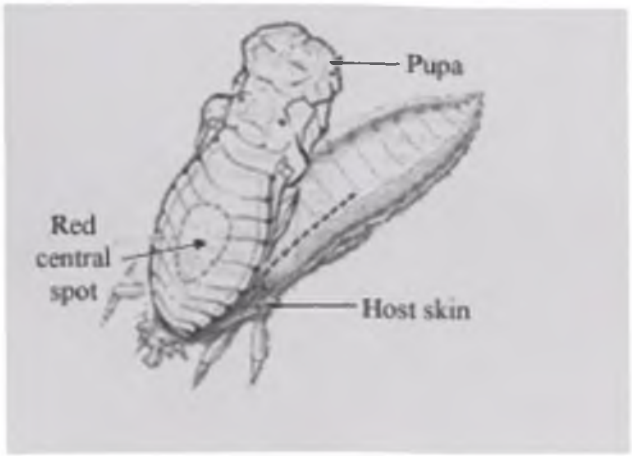


Figure 2.3: Posture of the pupa of *Ceranisus menes* after emergence (from Loomans and van Lenteren, 1995)



The pupa

The next day, the pupa of the parasitoid splits the dorsal tegument of its host, then, still stuck to the substrate with the tip of its abdomen, it raises its anterior part out, leaving behind it the host skin and its own moulting exuvia and remains tilted in a characteristic way (Fig. 2.3). Melanization and sclerotization process of the newly formed pupa is completed within a few hours, and the pupa turns dark brown with the red spot still visible in the thorax, or abdomen (Plate 2.3) of the pupa. Thus pupation occurs in the 7th to 8th day after oviposition.

Plate 2.3: Pupa of *Ceranisus menes*

The adults

A couple of weeks later, the head capsule of the pupa splits, and the adult parasitoid emerges, through the hole, head first. The males are smaller, have a black abdomen, and usually emerge one or two days earlier than the females. The females are easily recognized by their large size, and their coloured and swollen abdomens (Plate 2.4). Sometimes, the adult emerges keeping the orange spot in the abdomen (pers. observation). This way, it can be mistakenly sexed as female, specially when dealing with large size individuals. The aspect of the antennae is a more reliable character than the colour of the abdomen to sex *C. menes*. The eggs are mature soon after emergence of the adult (Sakimura, 1937a), and the parasitoid observes a pre-oviposition period of 1-2 days (Sakimura, 1937a) or 2-3 days (Daniel, 1986), but some authors have reported no gaps between the time of the wasp emergence and the beginning of oviposition (Murai, 1988; Loomans, 1991).

The total developmental time from egg to adult reported in the literature, and reviewed by Loomans and van Lenteren, (1995), is highly variable, depending obviously on the ambient temperature, but also on the thrips host species, and on the strain of *C. menes*

(see references on table 5.4). This parasitoid develops in a short time like 10.8 days at 28° C, in *Zaniothrips vicini* host, a species of the Panchaetothripinae sub-family (Daniel, 1986). At the other extreme, its developmental time can take up to one year, following the physiological growth of its univoltine host, *Kakothrips pisivorus* in Germany (Buhl, 1937). This parasitoid also overwinters along with the host *T. tabaci* in Japan, to produce only four generations per year (Sakimura, 1937b). Within the Thripinae, which constitute the majority of hosts tested in Europe, its developmental time takes intermediate values with large variations between them. It is found to be longer (more than 30 days on the average), and more variable for the yellow abdomen type than for the brown abdomen type of *C. menes* (Loomans, and Murai, 1994). There is no report on the developmental time of the parasitoid for the African strain of *C. menes*.

As with many parasitoids (Charnov, 1979; Charnov *et al.*, 1981; Waage and Godfray, 1985; Waage, 1982), the quality of the food obtained from the host could also affect some biological features of *C. menes*, such as the developmental time, the viability and fitness of the adults offspring. For *C. menes* nothing is known yet about the effect of the thrips species, among the wide range of thrips species considered as host for *C. menes*, on the biology of this parasitoid.

2.2.7. The behaviour of *C. menes*

C. menes attacks preferentially second instar larvae (Saxena, 1971), in which it may deposit its egg. During the host-parasitoid interaction, the behaviour of the female *C. menes* and that of the host thrips larva have been widely described by many authors, and reviewed by Loomans and van Lenteren (1995). The different events occurring during this interaction can be classified in two categories: those which favor the parasitization process, the acceptance behaviour of the wasp, and those that interrupt the parasitization process which can be either the reactions of the thrips larvae resisting against it, or the reaction of the wasp itself rejecting the host

Plate 2.4: Female adult of *Ceranisus menes*.

(x 2000)

The arrow indicates the sinuated margin of the bared area at the base of the forewing, characteristic of the species

2.2.7.1. Host acceptance behaviour of *C. menes*

The antenning

Once a parasitoid after searching for sometime encounters a larva, an interaction between the two organisms begins. Loomans and co-workers (1992) have subdivided this interaction into different steps. The wasp first starts with the "antenning" phase (Plate 2.5a), by feeling the body of the larva with her antennae. The antennae of many parasitoids are usually provided with sensory receptors which allow them to "read" size, shape, texture (Salt, 1935, 1958; Arthur, 1981; Vinson, 1985) or chemicals (Strand and Vinson, 1982; 1983a; 1983b) present on the surface of the hosts body. These bits of information are then used by the parasitoid as cues to "feel" the suitability of the host as an oviposition site. It is at this antenning phase that *C. menes* tests externally the suitability of the thrips larva as host for oviposition.

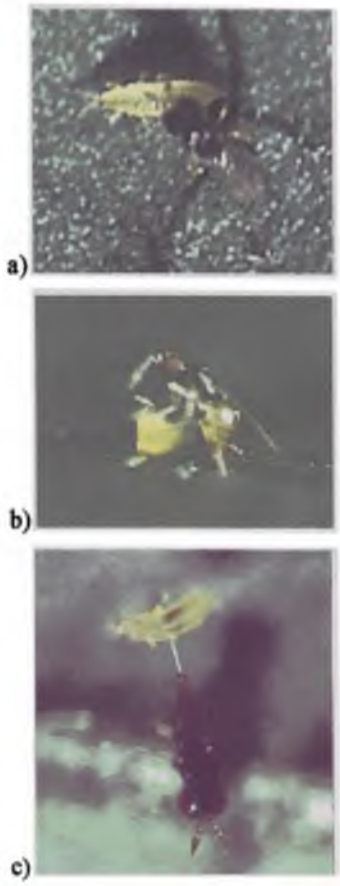
The attack

The wasp proceeds then to the "attack" phase (Plate 2.5b): with her abdomen bent onward in between her legs, in a position ready to sting, she goes into a short struggle with the thrips larva to subdue it (Loomans, 1991). Therefore, like in any physical competition, the outcome of this struggle, i.e. its success or failure, and its duration, may depend on the relative physical strengths of the two antagonists. This attack phase is found to last longer with the older larvae which are physically stronger than the younger ones (Loomans *et al.*, 1992). It is also mentioned that the most vulnerable hosts for attack by this parasitoid, are the weak young larvae (Fullaway, 1934; Loomans *et al.* 1992), or the motionless newly moulted ones (Loomans and van Lenteren, 1995). Nevertheless, the relative motivation of the parasitoid to parasitize the host may also have a significant role in the success of the attack.

The insertion

Next, the insertion phase (Plate 2.5c) starts when she finally manages to sting the larva. This species of Ceranisus has a particular way of handling the host larva

Plate 2.5: The host acceptance behaviour of *C. menes*: the antenning (a), the attack (b), and the insertion (c) phases of the interaction with a host larva



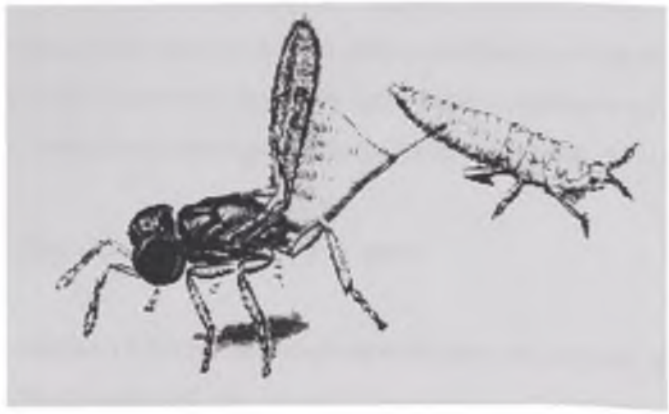
during the insertion of the ovipositor for egg deposition, which is typical among parasitoids, and has been described by many authors (Carl, 1971; Murai, 1988; Loomans, 1991; Galazzi and Bazzocchi, 1993): She afterwards, turns very quickly her ovipositor back, either lifting the larva up in the air (the "lifting" position) (Fig. 2.4a) or leaving it on the floor (the "tail-to-tail" position) (Fig. 2.4b) when she is unable to handle the weight of a larva (Loomans *et al.*, 1992). In this later position, some larvae, attempting to walk free from the wasp, end up dragging the parasitoid behind them for some distance before they separate from each other. Studies reviewed by Godfray

(1994) have revealed that some parasitoids, such as the Ichneumonid wasp *Itoplectis conquisitor* and some species of Trichogramma inspect the quality of their host using chemical cues detected by means of sensillae located at the tip of their ovipositor, after probing their host. With *C. menes*, it is probable that internal examinations take place during this last phase of the interaction with the host larvae.

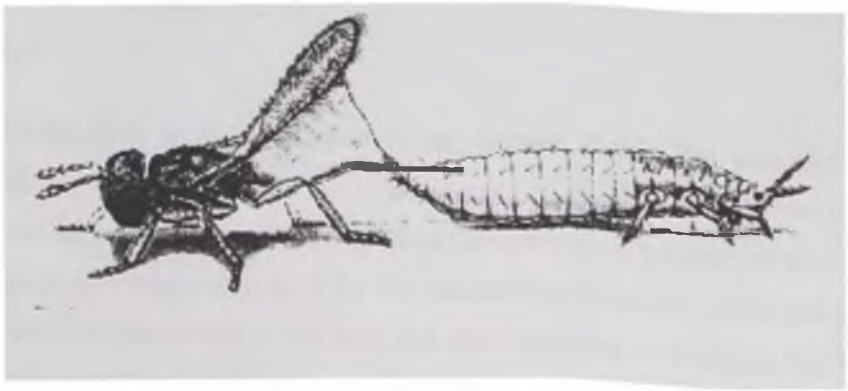
Oviposition

After internal examination of the host, the female of *C. menes* reacts by ovipositing into the larva, when this latter is found acceptable.

Figure 2.4: *Ceranisus menes* oviposition postures: (a) lifting, (b) tail-to-tail (from Loomans and van Lenteren, 1995)



(a)



(b)

2.2.7.2. The host resistance reactions

The interaction between thrips larvae and *C. menes* can be interrupted at any moment by successful defense reactions of the host larvae, trying to escape from paratisization (Loomans *et al.*, 1992).

Running away. One of these reactions is to run away at the first contact with the parasitoid, i.e. the antenning phase.

Wriggling and fluid excretion. Another reaction, mostly used by old larvae, is to wriggle, i.e. project violently their abdomen, as they often do against other thrips larvae when in conflict, to dissuade the wasp from getting close or to get free from her ovipositor (Saxena, 1971; CAB, 1971; Loomans *et al.*, 1992). The excretion of a liquid from the anus, may go along with the wagging tails of the thrips. This strategy is also used by many other insect hosts as a defense mechanism, in an attempt to drown or to discomfort their aggressor, so that the latter would spend most of her time cleaning out the mess, rather than pursuing the attack (Hays, and Vinson, 1971; Van Alphen, 1980).

2.2.7.3. Host rejection behaviour of *C. menes*

The interruption of the parasitization process may also depend on the decision of the wasp following external and internal examinations of the host at the antenning or insertion phases.

The retreat

Unacceptable hosts could be rejected at any moment during this interaction, as described by Loomans *et al.*, (1992). In the absence of any defensive reaction of the host larvae, this rejection can be distinguished through various reactions of the female *C. menes*. One of these reactions is for the parasitoid to retreat i.e., either she walks away, instead of proceeding to the next step after antenning or attacking the thrips larva, or she restrains herself from ovipositing after probing the larva.

Host feeding

After inserting a larva, *C. menes* sometimes "host feeds" upon it. Loomans (1991) describes the host feeding behaviour of *C. menes*: The wasp feeds on the juice coming out from one or several punctures she makes with her ovipositor in the body of the larva. Host feeding is considered as another reaction response of the parasitoid rejecting a host which is not found fit for the development of the parasitoid. In this case, instead of retreating and releasing such larva, the parasitoid might find it more useful as food for herself.

So, host resistance and host acceptance are factors that have opposite effects in the parasitization by *C. menes*. Host resistance is an attribute of the thrips larva that affects negatively the parasitization, by interrupting the host-parasitoid interaction. On the other hand, host acceptance is an attribute of the parasitoid, encouraging the parasitization process. In some way, these two factors may be related. Many authors (Fullaway, 1934; Sakimura, 1937; Saxena, 1971) have reported the non preference of old hosts by this parasitoid presumably due to their resistance. Others (Loomans *et al.*., 1993) mentioned the negative correlation existing between host age (which is a correlate of the host resistance), and host acceptance by *C. menes*. The cause-and-effect relationship between the behaviour of the two antagonists, host resistance and host acceptance by *C. menes*, is not clear; yet, by studying the relative importance of each of these two factors, in the interaction between *C. menes* and the thrips larva, one should be able to know whether or not there is any compatibility in their behaviour for a successful parasitization of the host.

Chapter 3
GENERAL MATERIALS AND METHODS

All exotic insects materials came through established import procedures with permits obtained from the Dutch and Benin Plant Protection Services. The studies on the behaviour of the different strains of *C. menes* were carried out in the insectaries of Wageningen Agricultural University (WAU) in The Netherlands and the Biological Control Center of IITA (International Institute of Tropical Agriculture) in Benin. Therefore, the materials and the methods used to conduct some of the experiments in the two stations are slightly different

3.1. Strains of *C. menes*

Four different populations of *C. menes*, from three geographical areas, were used in this work; Information about these populations is summarized in Table 3.1.

Malaysian strain

This strain is originated from Malaysia. It was collected as adults and in parasitized larvae from *Pueraria phaseoloides* plant around Keluang (Johor province) in South Malaysia. At the time of collection, the plants were hosting two species of Megalurothrips, *M. usitatus*, and *M. distalis*. The Malaysian strain has a brown abdomen with two or three stripes on the dorsum. The studies on the behaviour of this strain were done in November-December 1995 in the insectary of WAU, while the insect was under quarantine. The colony of the parasitoid shipped to Benin in November 1995 could not be sustained on *M. sjostedti*. So the colony was lost before any further experiments could be conducted on it.

Table 3.1: Information on the different strains of *C. menes*

***C. menes* Strain**	**Abdomen colour**	Original			**Size of the founderess population**
		Locality (year)	**Host plant**	**Host thrips**	
Malaysian	Brown	Malaysia (1995)	*Pueraria phaseoloides*	*M. usitatus* *M. distalis*	
Indian1	Brown	India (1996)	*Pongamia glabia*	*M. usitatus* *M. typicus*	1 female
Indian2	Yellow & Brown	India (1997)	*Pongamia glabia*	*M. usitatus* *M. typicus*	98 females
Local	Brown	Benin	*T. candida* & others	*M. sjostedti*	

First Indian strain

This is the first strain of *C. menes* that was collected around Hyderabad (Andhra Pradesh) in December 1995, and shipped to the insectary of IITA in January 1996. In this paper, it will be referred to as "**Indian1**" It was collected from the *Pongamia glabia* plant hosting two species of Megalurothrips, *M. usitatus*, and *M. typicus*. It was also a brown abdomen type. The first attempt to rear this strain on *M. sjostedti* failed again, and the unique female recovered from the first generation was found to be successfully reared on *Frankliniella shultzei*. It produced the actual population on which these experiments were conducted. In consequence, there is a high risk of genetic bottle-neck effect, due to the reduced size of the founder population. As a result, the population studied is far from being representative of the wild population in India, upon which these studies want to draw inferences.

The second Indian strain

A second shipment from India, that will be referred to as "**Indian2**", was also collected around Hyderabad in April 1997 from *Pongamia glabia* hosting *M. usitatus*, and *M. typicus*. It was received from quarantine in May 1997, as mixture of yellow and brown abdomen types. At the first generation it was noticed that this trait was not really fixed. Individuals with a yellow abdomen (identified from the WAU quarantine) have produced in the successive generation, offspring for which the yellow colour of the female abdomen, was more or less pronounced from one individual to the other. So all specimens were bulked into one single population considered as brown abdomen type. It started from a total of 98 females which were reared very successfully on *F. schultzei*. Experiments on this strain began on the third generation. Consequently, the population studied is relatively more representative of the natural population of this strain in India, compared to the laboratory population of the first shipment.

The local strain

As "local", it is referred to the local population of *C. menes* in Benin. This strain was collected from a variety of local plants hosting *M. sjostedti* : *Tephrosia* spp, Canavalia etc... mostly from the exotic *T. candida* growing in the IITA station. Because of the difficulty of maintaining a mass rearing of this strain on *M. sjostedti* or on *F. schultzei*, the first generation of adults emerging from on-field parasitized, or in-laboratory parasitized larvae were mostly used for our experiments. Therefore, the population studied would represent fairly well the natural population of *C. menes* in Benin.

3.2. Thrips hosts

For the stock parasitoid rearing

The native host *M. usitatus* was used to maintain the rearing of Malaysian strain in the insectaries of WAU. In Africa, the native hosts of the Asian strains are not available. For lack of it, *F. schultzei*, a thysanopteran with no pest status in Benin, and which has been very successful for the rearing of the two Indian strains, was used as host for their stock rearing in the insectaries of IITA. Some of the adults of the local strain used in

this experiment were reared on *M. sjostedti* larvae. However, most of them were obtained directly from parasitized larvae collected from the field.

For the experimental parasitoid rearing

In addition to *M. sjostedti*, the host of interest, a second species of thrips on which each strain is known to develop best, was tested as host check to have a reference upon which the potential of the strain could be evaluated. *M. usitatus*, the native host of Asian strains, was used as check in WAU for the Malaysian strain. *F. schultzei* was used as check host for these two strains in Benin. *M. sjostedti*, the known native host of *C. menes* in Benin, was thus both check and test host for the local strain in this study.

3.3. Plant hosts

The thrips were reared on field or green house grown cowpea organs (peduncles and pods), except for the experiment concerning the Malaysian in which the thrips hosts, *M. usitatus* and *M. sjostedti* were reared on bean pods (*Phaseolus vulgaris*). It was assumed then, that the nature of the food for the thrips host would not affect parasitoid behaviour or its biology.

3.4. The insect rearing techniques

The materials and methods of rearing of the insects are summarized in Table 3.2. This was done in a controlled environment chamber at WAU (25°-30°C, 75% RH, and 16 hours of photoperiod), and in laboratory conditions at IITA station (Annual mean: 27°C, 75% RH, and 16 hours of photoperiod).

For the experiment conducted at WAU with the Malaysian strain of *C. menes*, the bean pods methods of rearing, as described by Loomans (1991), and Loomans and Murai (1994), was used respectively, for the rearing of the parasitoid, and of the thrips.

Table 3.2: Summary of stock and experimental rearing methods of the insects materials

Strain of *C. menes*	Malaysian	Indian1	Indian2	Local
Stock rearing host thrips	*M. usitatus*	*F. schultzei*	*F. schultzei*	*M. sjostedti (?)*
Experimental rearing host thrips: test:	*M. sjostedti*	*M. sjostedti*	*M. sjostedti*	*M. sjostedti*
check:	*M. usitatus*	*F. schultzei*	*F. schultzei*	*M. sjostedti*
Rearing host plant	Bean	Cowpea	Cowpea	Cowpea
plant organ:	pods	peduncles and pods	peduncles and pods	peduncles and pods

3.4.1. Thrips rearing

For the rearing of the thrips, this method consisted of three units.

Oviposition unit

Adult female thrips were introduced into a one-liter candy glass jar, covered with a fine mesh, onto freshly cut bean pods (*Phaseolus vulgaris*) as feeding and oviposition substrate, plus bee pollen as additional food.

Feeding unit

Three to four days later, i.e. before the hatching of the thrips eggs, the adults thrips and bee pollen were removed from the oviposition jar, and fresh pods added into the jar every other day for one week, to feed the larvae emerging from the oviposition pods. Also, a bunch of 10-15 layers of coarse paper (4-5 cm) was placed on the bottom of the jar as a pupation site.

Pupation unit

After 10-11 days, i.e. around the pre-pupation period, the pods were removed to prevent them from rotting in the feeding jar. Then the pupation papers, with prepupa and pupa of the thrips in between the sheets of paper were left inside. The adults that emerged later were collected to start a new culture.

3.4. 2. Parasitoid rearing

The parasitoid rearing technique was composed of two units.

Oviposition/feeding unit

In one of the thrips feeding jars, containing the growing 1 to 2-days-old thrips larvae on pods, adults of the parasitoid that have been together for 24 hours to assure mating

of the females, were introduced to oviposit on the larvae. Droplets of honey were placed on top of the mesh covering the jar for the adult parasitoids to feed on.

Pupation unit

After about two weeks, the pupation papers with the parasitoid pupae stuck on them were carefully removed and placed in a smaller vial containing agar, to maintain the humidity. This unit was checked regularly. The emerged adult thrips were collected and used for thrips rearing. The emerged adult parasitoids were collected into a small glass vial with a streak of honey on the wall, and kept at 15°C until ready for use.

For the experiments conducted at IITA with the other strains of *C. menes*, the one-liter candy glass jar of the oviposition and feeding units was replaced with a Plexiglas tube of 4.0 cm in diameter and 11.0 cm in height. The pupation unit was a petri dish containing a humidified piece of filter paper, on which the parasitoid pupae collected from the oviposition unit were transferred. The petri dish was then tightly closed with a parafilm to prevent desiccation. The modified pods method for rearing the thrips, was re-modified, by replacing the bean pods with cowpea peduncles, i.e the stalks bearing the flower bud, as oviposition substrate for the adult thrips, and with cowpea pods as feeding substrate for both larvae and adults.

3.5. Biological characteristics studied

3.5.1. Behaviour compatibility of *C. menes* with the host

The biological characteristics of interest in this work are first, the behavioural characteristics of *C. menes* at the individual level. Moreover, this first study serves as a preliminary work for the next one (below), in the determination of the oviposition rate of the parasitoid. It is also a way of screening the different populations of *C. menes* on different host species, and host age, in order to select the host categories that are accepted by a strain of *C. menes*, and which will later be used as support for the life-table study of the parasitoid.

3.5.2. Physiological compatibility of *C. menes* with the host

Next, the ability of the different strains of *C. menes* to overcome the physiological resistance of the host, i.e. the host suitability will be studied. This will determine the immature survival of the parasitoid, which is also required to set up the life-and-fertility tables of the parasitoid for the next study

3.5.3. Mean developmental time, and demographic parameters of *C. menes*

Finally, the last observations will be on the mean developmental time and the population characteristics of *C. menes*. For this, the life-history notes of each strain of *C. menes* on any host which allows a complete development of the parasitoid will be studied.

These three (3) studies were carried out to determine and compare the above biological parameters of the different strains for biotypes differentiation, and for selecting the one that showed the highest compatibility with *M. sjostedti* to recommend for the biological control of this pest.

Chapter 4

A COMPARISON OF THE BEHAVIOUR OF AFRICAN AND ASIAN POPULATIONS OF *CERANISUS MENES* WALKER (HYMENOPTERA: EULOPHIDAE) DURING HOST SELECTION IN PARASITIZATION

4.1. Introduction

Vinson (1976) has described in a chronological way the different phases involved in the parasitization process by an insect parasitoid. These involve: a) the habitat finding, b) the host plant finding, c) the host finding, all of which Salt (1935) termed the "ecological selection", and finally d) the host selection phase, which refers to host acceptance, and eventually host suitability.

It is obvious that the behaviour of the parasitoid during each of these steps will have a significant effect on parasitism. At the host selection phase, i.e. during the interaction between the wasp and its host, the outcome of the parasitization is determined a) through the behaviour of the wasp rejecting or accepting the host, or b) through the defensive reactions of the host, resisting parasitism.

As already stated (Chapter 2), the behaviour of both *C. menes* and of the thrips larvae can affect the outcome of parasitism. There are already large variations in the structure, biology and in the level of field parasitism among the different populations of this species of Ceranisus. It is possible also that variations in their behaviour exist among them. Three strains of *C. menes* from Southeast Asia were identified for testing their potentials as candidates for biological control of the cowpea thrips, *M. sjostedti*. Because of the absence of a coevolutionary history between this thrips species and the populations of *C. menes* from Asia, it was considered important to investigate behavioural variations among the different geographical strains of this parasitoid, and determine how this can affect their efficiencies as biological control agents.

As reported by Loomans *et al.*, (1992) most of the early reports on the behaviour of *Ceranisus spp* are limited to the descriptive level and, therefore, can not be used as

reference to compare objectively different populations of this insect. In a series of experiments, this author and his co-workers (1992; 1993) for the first time attempted to quantify some of the behavioural characteristics of *C. menes*. The objective of this first part of the current work was therefore, to estimate and compare at the host selection level of the parasitization process, the behaviour of different populations of *C. menes* when exposed to the different species and ages of host larvae. It was expected that this would make it possible to separate the different populations of *C. menes* based on their behaviour, to see how these characteristics could affect the parasitism of the different thrips species, particularly *M. sjostedti*, and finally to select the strains of *C. menes* whose characteristics would be most adapted for a successful parasitism of *M. sjostedti*, and on which biological studies would particularly be emphasized in the second part of this work.

For this, the parameters considered important to study were:

a) The host handling time (HHT) of the parasitoid. A short handling time of the host is a favorable characteristic for a parasitoid. In theory, it should allow the wasp more time for host searching, thus increase her chance to encounter more of them. However, its absolute value by itself, is meaningless; when compared to the time that is allocated to the parasitoid for searching and parasiting its hosts, it helps provide an insight of the parasitoid efficiency (Hassell, 1978).

b) The host physical resistance to parasitization. This is the same parameter as the ability of the wasp to overcome the host resistance. It measures the relative aggressiveness of the two antagonists. Host resistance is another factor that can hamper the process of parasitization. When it does not prevent the parasitization to take place, a resistant host can at least increase the host handling time of the parasitoid, and thereby affect indirectly the resulting parasitism. For *C. menes*, the attack sub-component of the host handling time is affected by host resistance (Loomans *et al.*, 1992). The power of the wasp to overcome the host resistance is also a good characteristic for a successful parasitism. For example host size or host age, as mentioned in Chapter 2, would not be a limiting factor for such parasitoid to accept a

host. This would make available to the wasp, more categories of larvae in her choice for acceptance.

c) The host acceptance. This is the last prerequisite factor in host selection for a successful parasitization, although it does not guarantee it. It is defined as the attribute of the wasp accepting a host as an oviposition site (Vinson, 1976), as evidenced by her depositing an egg into that host.

4.2. Materials and methods

The insects, materials and their stock rearing techniques are as described in Chapter 3.

4.2.1. Experimental rearing technique

To obtain the synchronized ages of the thrips larvae necessary for the experiment, the same technique as in the stock rearing was used. As soon as they emerged from the pods used for oviposition in the feeding unit, the first instar larvae tend to move on to the fresh pods provided for feeding. So the feeding pods with newly emerged larvae, aged 0-24 hours (one day-old larvae), were removed and isolated in a new feeding unit. These provided the two-days-old larvae the next day, the three-days-old ones the following day, and so on..., so that any desired age groups of larvae could be obtained on schedule, to run this experiment.

4.2.2. Experimental set-up and observations

The experiment on the Malaysian strain was conducted under the laboratory conditions at WAU (25°C). The experimental set-up was based on the method used by Loomans and co-workers (1993):

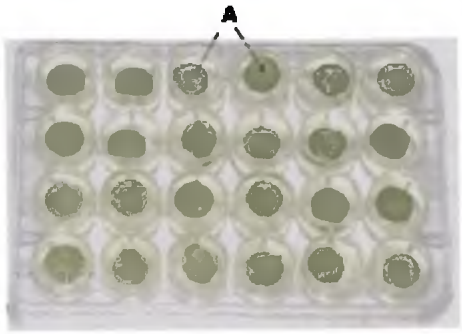
The larvae were divided into three (3) age groups, namely 0-1,1-2, 2-3 days old larvae. Thirty to forty individuals of each age group of thrips larvae were placed in a modified Munger cell (Plate 4.1). A single 1-2 days-old female was introduced in the cell, and observed under a binocular continuously for one hour. Five individual females were observed with each age group of larvae for each species of thrips.

For the other strains of *C. menes* which were studied in the insectary of the Biological Control Center of IITA in Cotonou, the time of observations was limited to 30 minutes for each wasp. In the previous experiment with the Malaysian strain, it was noticed that after 30 to 40 minutes of intense activity, the wasp stopped searching, and remained inactive for the remaining time out of the preset 60 minutes of observation, probably due to fatigue or to egg depletion of the female parasitoid. Therefore, the number of female wasp replicates was doubled to 10 females, so that the total duration of observation of a strain of *C. menes* is kept constant at 300 seconds per host category (Appendix 4.1).

Using the "Observer" Computer Programme (Noldus Information Technology, Wageningen) (Appendix 4.2), the different events referring to wasp and larvae behaviour described earlier (i.e. the "antenning", "attack", "insertion", and "host feeding" phases), and their sequences were recorded, and timed for each female parasitoid. In addition, events which interrupt the parasitization process such as the rejection of the host by the wasp (i.e. "retreat"), or the resistance of the larva (i.e. "escape"), and the occurrence of oviposition in inserted larvae, were also recorded using the "Observer". The inserted larvae were first, isolated on leaf discs in small tubes (Plate 4.2). Then at the end of the observation period, they were dissected to check for the presence of the parasitoid egg, and the result added to the data already recorded in the "Observer" programme.

Plate 4.1: The Munger cell

Plate 4.2: Tubes containing leaf discs (A) floating in water, used for the isolation of inserted larvae before their dissection.



4.2.3. Data collection

4.2.3.1. The acceptance and resistance parameters

Host resistance was assessed by the thrips behaviour, by contrast to host acceptance which was measured by the wasp behaviour. For each female parasitoid, on each age-group of host larva, and each species of thrips, the total number of each event were obtained from the "Observer" Report files, and the combinations of events from the Sequence files. They were used to calculate the acceptance and resistance parameters.

When a host larva is encountered by a female*C. menes*, three possible outcomes, as represented in Fig. 4 1, can result:

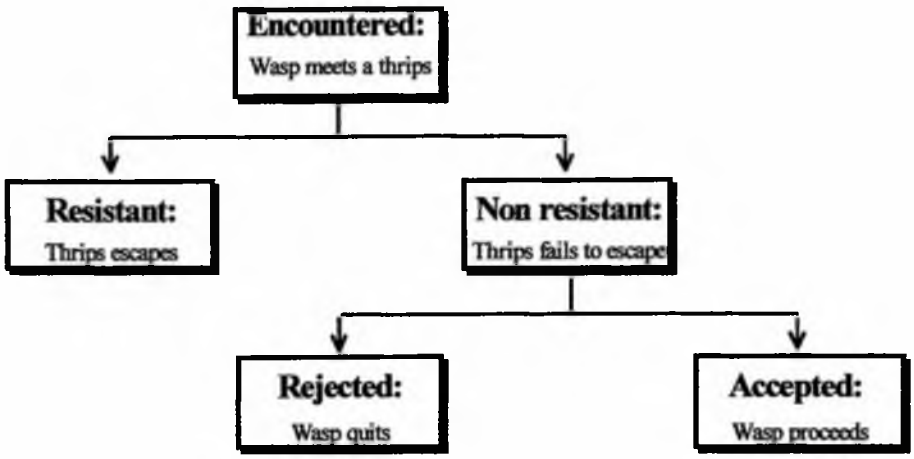


Figure 4.1: Diagram representing the possible outcomes of encountered larvae during the interaction with *C. menes*

1) The host larva can escape with a probability equal to the total number of hosts that escape (es), over the total number of hosts encountered (en) during the interaction. So the overall resistance (S) of the host is measured by the proportion:

$$S = es/en$$

This total resistance is further broken down into its different components at the different stages of the interaction namely:

11) The resistance at the encounter phase (S_{en}):

$$S_{en} = es_{en}/en$$

12) The resistance at the attack phase (S_{at}):

$$S_{at} = es_{at}/en$$

13) The resistance at the insertion phase (S_{in}):

$$S_{in} = es_{in}/en$$

where es_{en} , es_{at} , and es_{in} are the frequencies of escapes at the encounter, attack, and insertion phases respectively.

Among the remaining that could not escape, i.e. the total number of encountered (en) minus the total number of escaped (es) larvae, the host larva is either rejected, or accepted by the wasp.

2) The host is rejected, with a probability equal to the total number of "retreats" (re) and "host feeding" (hf) (which represent the total rejection by the parasitoid), over the total number of hosts encountered without resistance (i.e. "en" minus "es"). So the overall rejection (R) by the wasp is measured by:

$$R = (re + hf)/(en - es)$$

Again, this total rejection is broken down into its different components:

21) The rejection after the encounter phase (R_{en}):

$$R_{en} = re_{en}/(en - es)$$

22) The rejection after the attack phase (R_{at}):

$$R_{at} = re_{at}/(en - es)$$

23) The rejection after the insertion phase by retreating (i.e. no ovipositing (R_{in}) :

$$R_{in} = re_{in}/(en - es)$$

24) The rejection after the insertion phase by host feeding (R_{hf}):

$$R_{hf} = hf_{in}/(en - es)$$

where re_{en} , re_{at} , and re_{in} are the frequency of retreats after encounter,, after attack, and after insertion respectively, and hf_{in} is the frequency of host feeding after an insertion.

3) The final possibility is that the host is accepted with a probability equal to the total number of oviposition responses from the wasp (ov), over the total number of larvae encountered without resistance (i.e "en" minus "es"). So the acceptance (A) of the host is:

$$A = ov/(en - es)$$

4.2.3.2. The Host Handling Time (HHT) parameter

For every female wasp tested, the data file was used to select all the antenning, attack, insertion, and host feeding events. Their individual durations were calculated also. Then the sequence file was used to single out combinations of events, such as all the insertion events preceding an oviposition event, those preceding a retreat event, and those preceding a host feeding event. Similarly, their individual durations were calculated. This work was done for all the (5 or 10) replicate wasps of each strain of the parasitoid, with every age group, and species of the host larvae; It was made easy by using a computer macro programme developed in Lotus 123 version 5 software.

The HHT is calculated as the time interval between the first antennal contact (i.e. beginning of the antenning phase) with a host and the release of this same host (end of the insertion or of the host feeding phases). Thus it is the sum of the duration of the antenning, the attack, and the insertion followed by an oviposition or a retreat event when the host was not fed upon. And when the host was used by the parasitoid for feeding it becomes the sum of the duration of the antenning, the attack, the insertion preceding a host feeding event, plus the host feeding duration. The average duration of

these sub-components of HHT were used to estimate the overall HHT of the parasitoid.

4.3. Statistical analysis

4.3.1. The terms of comparisons

Considering the three main objectives of this work stated already in introduction, it is necessary to compare first, the behaviour of the local strain on *M. sjostedti* host versus that of the Asian strains on their check host species. This comparison would enable to determine whether there is any problem of behavioural compatibility between the local and *M. sjostedti*, which would make the local strain less efficient on *M. sjostedti* than the Asian strains are on their native hosts, in other words, to answer the first objective.

Next, a comparison of the behaviour among all the four strains of *C. menes* when *M. sjostedti* is offered as a host, would enable to answer objectives 2 and 3, concerning respectively, the identification of the best biological control agent against *M. sjostedti*, and the question about the existence of different biotypes among the four strains of *C. menes* studied.

4.3.2. The hypothesis

Thus, two hypotheses are tested to investigate for these objectives. The first one tests the null hypothesis ($H_0$1) that there is no difference in the behavioural parameters between the local and the Asian strains of *C. menes*, when their respective check hosts are offered, against the alternative (H_a1) that they are different (i.e. the local-*M. sjostedti* behaviour patterns are less compatible for successful parasitization than the Asian strains-checks behaviour). The second hypothesis tests "$H_0$2" that these behaviour are the same for all the four different populations of *C. menes* when *M. sjostedti* (i.e. a same host) is offered as host, against the alternative (H_a2) that they are different on this host.

4.3.3. The nature of the variables

In this study, the data to be analyzed are the 3 types of behavioural parameters, the host acceptance, host resistance, and the HHT. As computed above, the acceptance and resistance parameters consist of categorical derived variables expressed in proportion (p/(p+q)), i.e. the ratio of two measured variables. For the acceptance parameter, the measured variables are the frequency of accepted (p) and of non resistant larvae (p+q, where q = frequency of rejected larvae). For the resistance parameter, they are the frequency of resistant (p) and of encountered larvae (p+q, where q = number of non resistant larvae). The host handling time is a continuous variable, measured in unit of time (seconds).

4.3.4. Analysis of acceptance and resistance parameters

Certain characteristics of categorical data in proportion (p/(p+q)), for instance their lack of accuracy, continuity, unknown distribution etc.., as explained by Sokal (1995), and the non linear property of the logistic equation:

$$p = e^{a+bx}/1+e^{a+bx}$$

cause problems for the statistical analysis of such data to test differences between the two proportions. It is suggested that the odd expression form of the proportion (p/q) is most appropriate for their statistical analysis. It can be log transformed into logit, which is approximately normally distributed, and also make the logistic function linear:

$$\ln(p/q) = a+bx$$

In this form, the difference of two logits, in other words, the natural logarithm of the ratio of two odds or "ln odd ratio" can be computed to compare data expressed in proportion, such as, in this case, the host acceptance or resistance parameters between any two strains of *C. menes*.

For this reason, these two behavioural parameters will be compared using their odd instead of their proportion expressions.

4.3.4.1. The statistical technique

The logit log linear model analysis computes estimates of the logarithm of the odds (ln odd), and odd ratios (ln odd ratio). Then it tests (H_0) that they equal "0" (i.e. odd = 1), and provides their asymptotic standard error and 95% Confidence Interval. The analysis was carried out on SPSS 7.5 for Windows.

4.3.4.2. The data

A thrips larva that was encountered by a female wasp is classified according to four factors: A, the strain of the wasp, B, the species of the larva, C, the age of the larva, and D, the response of the wasp or the host after the interaction. According to the behavioural parameter under study, the response is whether the larva is accepted or rejected by the wasp, or whether the larva succeeds to resist or not to the parasitoid attack.

For the logit loglinear model analysis, the variable "strain of *C. menes"* (A) is an independent class variable, with 4 levels: (i) = {Malaysian, Indian1, Indian2, local}. The variable "host species" (B) is another independent class variable with 3 levels (j) = {*M. sjostedti*, *M. usitatus*, *F. schultzei*}. And "age of the host larva" (C) is the third independent class variable with 3 levels (k) = {1, 2, 3} day(s) old}. The dependent class variable is the response (D) about the behavioural parameter under study. It is a dichotomous variable, for which the 2 levels (l) are {yes or no}. When the response "D" refers to the resistance of host to the parasitoid, (l) = {resisted, not resisted}, and when "D" refers to the acceptance of host by the parasitoid, (l) = {accepted, rejected}. The data consist of the frequencies (f_{ijkl}) of larvae in samples of each combination of the above variables.

4.3.4.3. The model

The model equation. This technique models the log of the odd. For this study, in which the response of the parasitoid is tested over the range of an independent variable, e.g.

the strain of *C. menes*, a 2x4 table of contingency is constructed with the variables "response" (D), and the independent variable in the model. It is known from previous studies (Loomans *et al.*, 1993; Sakimura, 1937b) that the age of the host larva might play a role in the outcome of the response. Thus when testing the effect of *C. menes* strain or that of the host species on the response of the wasp, the variable "age" must be controlled. This is achieved by having all ages of larvae represented in the samples to be analyzed. The model equations for testing the effect of the strain of *C. menes*, the species of host, or the interaction effect of strain and host species on the response of the parasitoid are shown in Appendix 4.3.

In all tests, the response "no" is selected as reference response. For the test of the effect of a single variable, "strain" (A) for instance, one of the strain "x" is selected as reference strain, upon which the others strains are compared, with respect to their odds of responding "yes". Afterward, the other strains are selected in turn, to obtain all paired comparisons between the strains.

The model parameters. The parameter ($\lambda^{D}_{(i)}$) for the response factor represents the natural logarithm (Ln) of the odd for the reference strain(x) responding "yes", while the parameter ($\lambda^{AxD}_{(il)}$) for the interaction term is the log of the ratio between two odds: the odd for strain(i) responding "yes" in numerator, and the odd for the reference strain (x) responding "yes" in the denominator (Appendix 4.3).

The loglinear technique provides estimates of these lambda parameters "$\lambda^{D}_{(i)}$" and "$\lambda^{AxD}_{(il)}$, ", their standard errors , and 95% Confidence Interval (CI), then tests the null hypothesis (H_0): that they are 0 (i.e. their odd equals "1", or the two terms of the ratio are the same). In other words, it tests the odd response (yes/no) against the odd of 1:1 under the null hypothesis, and the odd ratio (the ratio between the odd response of strain (i) over odd response of strain (x)), against the ratio of "1" under the null hypothesis, i.e. similarity in response between strain(i) and strain (x).

4.3.4.4. Interpretation of the analysis

The analysis of the response parameters "$\lambda^{D}_{(l)}$" measures the magnitude of the behavioural response within the reference strain(x). For the acceptance response of the parasitoid, the failure to reject the null hypothesis

$$H_0: \lambda^{D}_{(l)} = 0$$

implies that the parasitoid (i.e. the reference strain (x)) was equally likely to accept, as to reject the larva. This is rated in this study, as a "medium" acceptance level. Otherwise, if H_0 is rejected, the parasitoid was more likely to accept than to reject the host larva when the estimate "$\lambda^{D}_{(l)}$ "has a positive sign, and less likely to accept than to reject it when the estimate has a negative sign. Then the acceptance level is rated as "high" and "weak" respectively. Similarly, the analysis of the resistance response of the larva is interpreted the same ways, and rated as "medium", "strong", and "weak" resistance level.

The analysis of the interaction term parameters ($\lambda^{AxD}_{(il)}$) compares the responses between strains. Again for the acceptance behaviour, the failure to reject the null hypothesis

$$H_0: \lambda^{AxD}_{(il)} = 0$$

means that the odd for strain (*i*) accepting the host larva rather than rejecting it, is equal to the same odd for strain (x). In others words, their host acceptance are equivalent. Otherwise if H_0 is rejected, the acceptance of strain (*i*) is higher, or lower than the acceptance of strain(x), depending on the sign of the value $\lambda^{AxD}_{(il)}$. Likewise, the host resistance against strain(*i*) is equivalent, stronger, or weaker than resistance against strain(x) depending on the acceptance or rejection of the null hypothesis (H_0) about the interaction term, and on the sign of its estimate.

4.3.5. Analysis of the components of the host handling time parameter

The data are the duration of each of the different actions of the parasitoid, i.e. the antenning, attack, insertion, and host-feeding on the host larvae. The nonparametric

statistics procedure was chosen in this study to analyze the duration of the different actions of the parasitoid, because of the unknown distribution of these data. First, the samples were separated on the basis of the 3 ages of host larvae, the 3 species of host larvae, or the 4 strains of *C. menes*. Next, each set of data was tested for equality of their median duration. Kruskal-Wallis (Stell and Torrie, 1980) were used to test the hypothesis (H_0) that the four (4) samples of data come from identical populations with the same median, against the alternative that their medians are different. After eventual rejection of H_0, the groups in the samples were separated using Siegel and Castellan. (1988) method.

The level of significance of 0.05 was chosen for all analysis.

4.4. Results and discussions

Examples of the 3 types of outcome files obtained from the "Observer", i.e. data, sequence, and report files, are shown in Appendix 4.4, 4.5 and 4.6 respectively. The results of the experiments are summarized in Tables, and Figures "4".

4.4.1. The Host Handling Time (HHT)

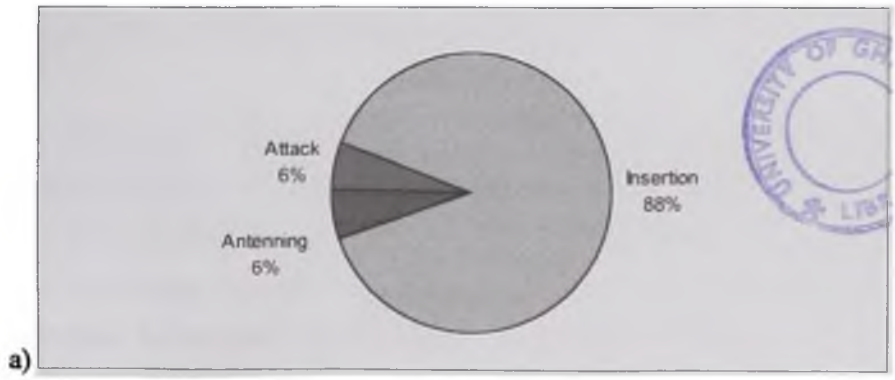
4.4.1.1. The different components of the parasitoid host handling time

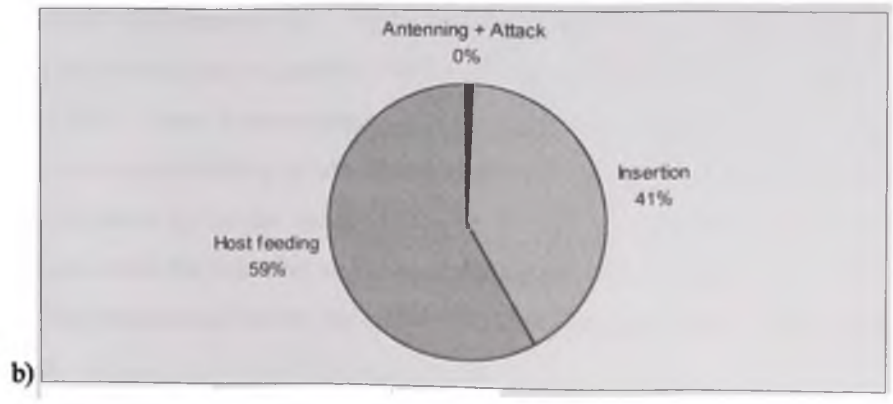
The frequency distribution graphs and the descriptive statistics of the different components of the HHT (Appendix 4.7 and 4.8) show that these data are strongly skewed to the right, with their means much larger than their medians. The test of normality performed on these data rejects the null hypothesis ($p < .001$), even after transformation of the data (by the inverse transformation). All these justify the choice of the non parametric statistic to test the results of this experiment. The large variations found in these results in the components of the HHT of *C. menes*, were also observed in other studies (Loomans *et al.*, 1992; Loomans *et al.*, 1993).

4.4.1.1.1. Antenning and attack duration

As shown in the pie representation graphs (Fig. 4.2a and 4.2b) the antenning and attack phases of the parasitoid-host larva interaction were relatively very brief compared to the insertion and the host feeding phases. Most of the time, they lasted less than one second. The antenning, which is the external examination of the larva by the wasp took on average 1.8 second. In few cases, it has been recorded to be as low as zero second, i.e. below the tenth of a second, that cannot be detected by the "Observer" programme. On the other extreme, it has lasted up to 58 seconds (Appendix 4.8). The attack, or the struggle between host larva and the female wasp, took about

Figure 4.2: Relative importance of the different components of the host handling time on host used for parasitization (a), and host used for feeding (b) by *C. menes*





the same amount of time as the examination (1.7 second), but also varied greatly, between 0 and 157 seconds (Appendix 4.8). In this experiment, the attack phase was found to last longer with recalcitrant hosts, which most often escaped the parasitoid.This long attack time of resistant larvae has been also reported in other studies (Loomans *et al.*, 1991; Loomans *et al.*, 1993).

4.4.1.1.2. Insertion and host feeding duration

The insertion and host feeding were by far the longest events in this parasitoid-host interaction (Fig. 4.2a, and 4.2b).

Insertion

Like most koinobiont parasitoids, *C. menes* produces large yolky egg type (unpublished data) that may take time and effort to be pumped out. This must explain the long oviposition time observed with this parasitoid.

As it was also mentioned by several authors, the duration of the insertion varied greatly depending on whether or not, the host would subsequently be used by the wasp for feeding or for oviposition. Insertion preceding a host feeding took much longer time (Fig. 4.3). The average duration of this insertion was found to be 196.6 seconds, but varied between 5.2 seconds and 24 minutes (Appendix 4.8). These results are comparable with the 251.7 seconds found for the European brown abdomen type of this parasitoid (Loomans *et al.*, 1993). The relatively long duration of insertion preceding the feeding may be justified by the process of tube building as explained by Godfray (1994). Some hymenopteran parasitoid including Eulophidae, have to go through a process of building a tube in the body of the host, through which the host fluid will be taken up by the wasp. And since it takes much longer time than the insertion preceding the rejection and release of the larva, it can allow to predict the host feeding phenomenon before the end of the interaction between *C. menes* and the host larva.

4.4.1.2. The relative importance of the sub-components in the parasitoid HHT

Figs. 4.1 "a" and "b" indicates that the insertion and host feeding duration were the most determinant components of the HHT of this parasitoid. Thus, HHT varied considerably depending on whether or not the host was fed upon. In the absence of host feeding, the duration of antenning and attack represented just 12 % of the total HHT, and all the remaining time was covered by the insertion period (Fig. 4.2a). When the parasitoid host fed, however, almost 59% of the HHT was covered by the feeding activity duration, and 41% by the insertion time (Fig. 4.2b). Therefore, any factor that affects the insertion component, or the feeding behaviour of the parasitoid, should be expected to have a significant impact on the overall HHT.

4.4.1.3. The parasitoid HHT

The HHT of this parasitoid varied from 3 to 19 minutes, with an average of 8 minutes when host is used for feeding (Fig. 4.4a), and from 0.3 and 1 minute, with an average of 0.5 minute, when the larva was used only for parasitization (Fig. 4.4b). Results of studies obtained with Asian *C. menes* on various species of thrips (Sakimura, 1937b; Carl, 1971; Daniel, 1986; Hirose, 1989; Loomans, 1991; Loomans *et al.*, 1992; Loomans *et al.*, 1993) and reviewed by Loomans and van Lenteren (1995) showed different ranges of values for *C. menes* HHT, which include the results found in this experiment.

The absolute value of the HHT of a parasitoid by itself, is meaningless. But when compared to the time that is allocated to the parasitoid for searching and parasiting its hosts, it helps provide an insight of the parasitoid efficiency (Hassell, 1978). In the natural situation, this time allocation would be the entire lifespan of the female wasp, but in the context of this laboratory experiment, it was limited to the 30 minutes of observation during which the female wasp was allowed to interact with the host larvae. The 495 seconds for handling host used for feeding represent 27% of the whole time allocated to *C. menes* for searching a host in this experiment. In other words, the wasp

would not be able to encounter more than 4 larvae during this period, provided that all of them were used for feeding. Under the situation when the wasp does not feed upon the host larvae, HHT takes just 2% of this time, which would allow the parasitoid to encounter up to 50 larvae during the 30 minutes period of observation.

Thus, host feeding activity of *C. menes* is by about 10 fold, as more time consuming activity for the wasp as the normal host-parasitoid interaction for parasitization. Furthermore, if host feeding is considered as a form of rejection of the host, it becomes then, a waste of time for the process of parasitization, and results in reducing considerably the time available for searching hosts. The efficiency of *C. menes* can be in this case, affected negatively by the host feeding activity of the parasitoid.

After reviewing cases of a number of parasitoids, Hassell (1978) estimated that values which are far below "1" for the ratio HHT over the wasp longevity could be considered acceptable for an efficient parasitoid. For *C. menes*, this ratio which was 0.02 and 0.27 for host parasitization and host feeding respectively, is already low on the basis of the 30 mn time allocation in this experiment. It would be probably much lower than these values, would the whole longevity of a female *C. menes* taken into consideration.

4.4.1.4. Effect of host age on the components of HHT

The results shown in Table.4.1 indicates that handling time of larva of different ages by *C. menes* differs at the antenning and at the attack stages. They were longer on older larvae. The longer time to antenning the 3 days-old larvae suggests that the wasp must have been hesitating to attack them, probably by fear of their violent defense reactions. The increase of the attack duration with age of the host larvae, was also reported (Loomans, 1991; Loomans *et al.*, 1993), as the consequence of the difference in resistance between young and old hosts. At the attack, the parasitoid needed also a longer time to overcome the resistance of stronger older larvae. Nevertheless, due to

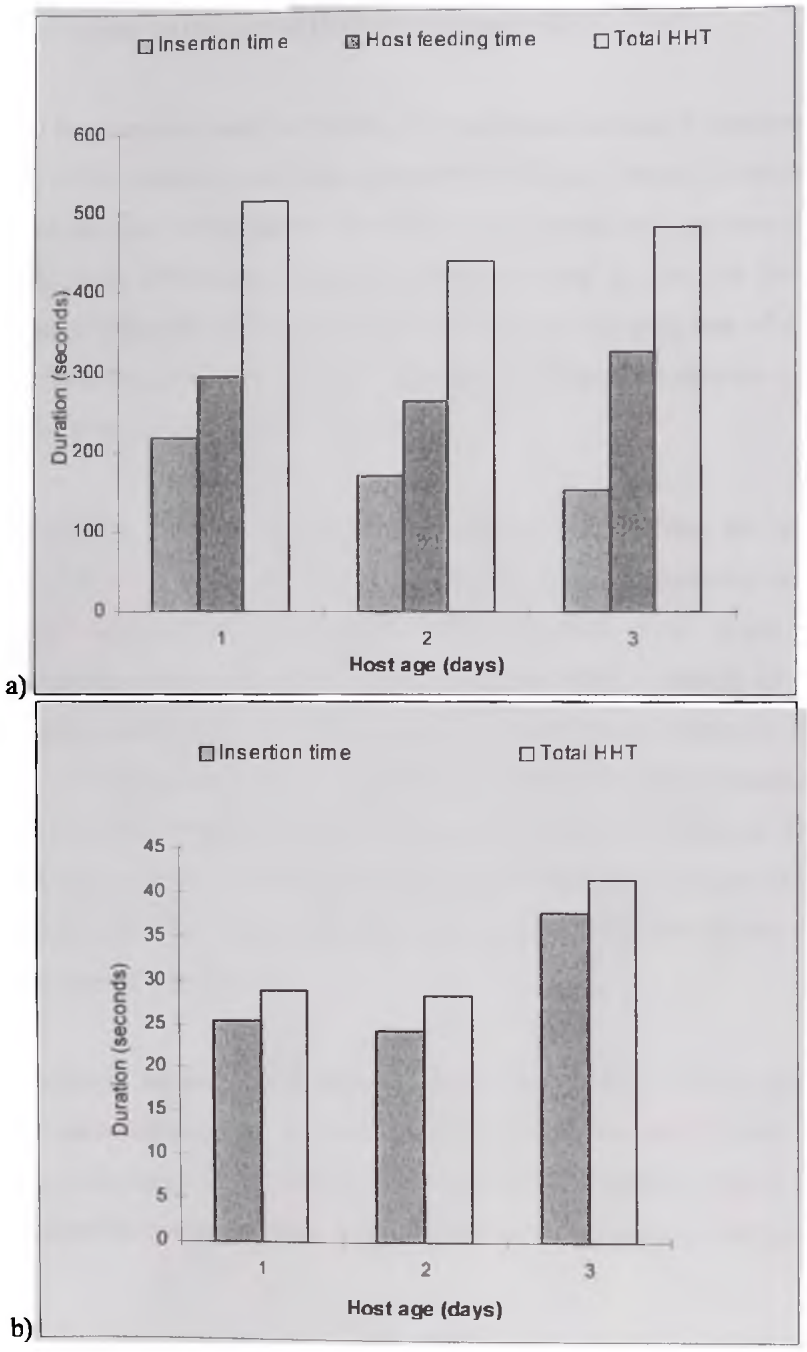


Figure 4.4: The handling time of larvae from the different age groups by *C. menes*, in host feeding (a), and without host feeding (b) situations

the relative short duration of the interaction at these steps, the differences should not have much impact on the overall HHT of this parasitoid.

When the host was not used for feeding, the results also indicate a significant increase with age, of the insertion time. This induced the HHT of *C. menes* to increase slightly as well, on the older thrips larvae. Nevertheless considering the total time allocated to the wasp, these differences between handling a young and an old larva are not substantial. Irrespective of the age of the host larva, the handling time of a larva used as oviposition site, remained around 2% of the 30 minutes allocated to the wasp for searching a host in this experiment.

In situation when *C. menes* was feeding on the host after insertion, the reverse trend was observed: HHT decreased with age of the larva, following again the same trend as the corresponding long insertion, and host feeding duration. In fact, it was particularly with the one day-old larvae that the parasitoid was observed wandering for a long time with the larva suspended on her ovipositor before she begun feeding on it. Meanwhile, she might go walking around for some distance, sometimes even attempting to attack other larvae while having its ovipositor still occupied with the probed one. The analysis did not, however, detect any difference between the different age groups of the host, in the duration of insertion and host feeding (Table 4.1). This is probably due to the large variations observed on the data.

In conclusion, *C. menes* handles faster the younger larvae of 1 or 2 days, than the older ones for parasitization, but without improving much its rate of host encounter. Therefore as far as *C. menes* HHT is concerned, larvae from any of the 3 age-groups can be chosen for rearing purpose, without affecting the efficiency of this parasitoid.

Table 4.1: Average duration (in seconds) of the different components of the host handling time (HHT) by *C. menes*, on the different age groups of host larvae

	Host age (days)	Antenning	Attack	Insertion	Host feeding	Total HHT
Without host feeding:	1	1.8 a	1.5 a	25.4 a	-	28.7
	2	1.8 ab	2.1 b	24.2 a	-	28.1
	3	1.9 b	1.8 b	37.6 b	-	41.4
With host feeding:	1	1.8 a	1.5 a	216.9	293.7	514.0
	2	1.8 ab	2.1 b	170.4	263.0	437.3
	3	1.9 b	1.8 b	152.6	324.6	480.9

Numbers within a column followed by the same letters are not significantly different (after Kruskal-wallis test at $\alpha = 0.05$)

4.4.1.5. Comparison of components of the HHT between strains

4.4.1.5.1. *M. sjostedti* host handling time

When *M. sjostedti* larvae were offered to the different strains, the female wasp of the Malaysian strain took a longer time to examine and attack these larvae, than do the other strains (Table 4.2) The remaining 3 strains showed the same speed to handle *M. sjostedti* larvae during antenning and attack phases. On the last steps of the interaction, there was no difference in the insertion time between strains of *C. menes*, when the host was not used for feeding. Otherwise the Malaysian spent less time in the insertion before feeding, and more time in feeding than the other strains. On the other hand, the local strain took a longer insertion time before host feeding, but adversely, a short host feeding period. The end result was that HHT turned out to be somewhat equal for all the 4 strains of *C. menes* (Table 4.2).

It is assumed that for many parasitoids, the HHT is constant within the same species, although variations of its sub-components may exist among different populations of the species (Hassell, 1978); This is again demonstrated in this study with *C. menes*. As presumed by this author, differences in some of these sub-components like the insertion and host feeding duration, tend to cancel each other out, while others, like the antenning and attack duration of this parasitoid, have relatively little effect on the overall HHT.

In conclusion there is no difference in the HHT of *M. sjostedti* between the 4 strains of *C. menes* studied in this experiment, but just a slight variation on the behaviour patterns they exhibit in handling this species of thrips. In this regard, the local and the two Indian strains show behaviour patterns more similar to each other than to the Malaysian strain.

Table 4.2: Average duration (in seconds) of the different components of *M. sjostedti* host handling time (HHT) by the different strains of *C. menes*

	Strain of *C. menes*	Antenning	Attack	Insertion	Host feeding	Total HHT
Without host feeding:						
	Malaysian	2.6 b	3.2 b	21.6	-	27.4
	Indian1	1.4 a	2.6 a	25.0	-	29.0
	Indian2	1.6 a	3.7 a	20.5	-	25.8
	Local	1.7 a	1.3 a	28.6	-	31.6
With host feeding:						
	Malaysian	2.6 b	3.2 b	152.8 a	390.8	549.4
	Indian1	1.4 a	2.6 a	174.3 ab	194.0	372.3
	Indian2	1.6 a	3.7 a	202.4 a	166.9	374.5
	Local	1.7 a	1.3 a	253.9 b	116.4	373.3

Numbers within a column followed by the same letters are not significantly different (after Kruskal-wallis test at $\alpha = 0.05$)

4.4.1.5.2. The check hosts handling time

When the check host was offered to each of the four strains of *C. menes*, the results of the component of the HHT of the parasitoid were more diverse than was observed when the same host species, *M. sjostedti*, was presented to all 4 strains of the parasitoid (Tables 4.2. and 4.3). This obviously reflects the difference in thrips species used as check hosts.

The results (Table 4.3) indicate that for parasitization purposes (i.e. when the parasitoid is not host feeding), the local showed a shorter insertion time, thus a shorter handling time, than the Malaysian strain on their respective check hosts. But the local was not significantly different from the two Indian strains, as far as the handling time of their respective check hosts was concerned. When they were feeding on their respective check hosts, the local spent more time for the insertion, but less time for feeding than do any of the Asian strains (Table 4.3). As a result, the total HHT of the local got closer to those of the Asian strains. In term of the HHT, these two results suggest that the behaviour of the local with *M. sjostedti* as host, was not different from that of the Asian strains on their check hosts.

4.4.2. Host resistance

The tables of analysis are presented in tables "a" and "b" in Appendix 4.9-4.13. Tables "a" are results on the magnitude the resistance of a larva, expressed in the odd term, and tables "b" are results of their comparison between age groups of the larvae, species of host thrips, or strain of *C. menes*. The data and results of the analysis are summarized in the graphs where host resistance is expressed in percent.

A total of 3395 individuals thrips larvae encountered by the parasitoid. All thrips species, larval age, and parasitoid strain confounded, have been analyzed for their resistance against the parasitoid. Almost half of these larvae (44%) exhibited some

Table 4.3: Average duration (in seconds) of the different components of the host check handling time (HHT) by the different strains of *C. menes*

	Strain of *C. menes*	Host species	Antenning	Attack	Insertion	Host feeding	Total HHT
Without host feeding:	Malaysian	*M. usitatus*	2.7 d	1.8 c	45.8 c	-	50.4
	Indian1	*F. schultzei*	1.5 b	0.9 a	21.7 a	-	24.1
	Indian2	*F. schultzei*	0.8 a	1.1 a	28.1 b	-	30.0
	Local	*M. sjostedti*	1.7 c	1.3 b	28.6 ab	-	31.6
With host feeding:	Malaysian	*M. usitatus*	2.7 d	1.8 c	220.4 bc	276.8 ab	501.8
	Indian1	*F. schultzei*	1.5 b	0.9 a	141.3 a	255.9 ab	399.6
	Indian2	*F. schultzei*	0.8 a	1.1 a	157.0 ab	348.4 b	507.3
	Local	*M. sjostedti*	1.7 c	1.3 b	253.9 c	116.4 a	373.3

Numbers within a column followed by the same letters are not significantly different (after Kruskal-wallis test at $\alpha = 0.05$)

kind of physical resistance to avoid parasitization. The host resistance measured on these larvae was found highly associated to the age, species of the thrips larvae offered to the wasp, as well as to the strain of *C. menes* involved. Depending on these same variables, it was also found to manifest at certain specific stages of the interaction between the host and the parasitoid.

4.4.2.1. Host resistance at the different steps of the host-parasitoid interaction

A total of 1478 individuals larvae out of the 3395 contacted, were resistant to the attack of the parasitoid. The majority of this sample of thrips larvae (more than 70%) resisted at the first contact with the parasitoid, i.e. at the antenning phase of their interaction. This was observed at all age groups of larvae (Fig. 4.5) and with most of the parasitoid-host combinations (Fig. 4.6). The proportion of larvae that resisted at the attack was about 3 times less, and was negligible at the insertion phase.

In fact, a resistant larva had a greater chance to escape at the moment of antenning when the parasitoid just touched its body for examination. Most of these larvae quickly run away, or projected violently their abdomen against the wasp to defend themselves. But once the larva failed to escape at this stage, the struggle the wasp underwent afterward, at the attack phase, reduced considerably the chance of the larva to escape. Very few larvae were found to escape from the ovipositor of *C. menes* after being probed and lifted up, despite the long duration of this insertion phase, and the vehement wagging tail of the thrips larvae to free themselves. Host lifting behaviour must be an adaptive strategy for this parasitoid to overcome physical resistance of the host during the long time necessary for the process of oviposition.

However, two exceptions were found with the Indian2 on *F. schultzei* host and with the Malaysian on *M. usitatus* host larvae. On these two host-parasitoid pairings, the proportion of larvae that resisted at antenning, attack and insertion phases were approximately equal. In other words, rejection at antenning was relatively low compared to the other host-parasitoid pairings.

4.4.2.2. Effect of the host species on resistance

This study showed that the host resistance was also strongly influenced by the species of thrips. The tables "a" and "b" of analysis (Appendix 4.9) indicate that the resistance of *M. sjostedti* and that of *M. usitatus*, rated "medium", were stronger than the resistance of *F. schultzei* species which was rated "weak".

Sakimura (1937b), Loomans and co-workers (1993), by comparing host resistance between young and old thrips larvae, considered the physical strength of the host larva as the major mechanism of its resistance. The stronger resistance of *Megalurothrips* spp compared to *F. schultzei* could also be explained by the difference in strength between the two species of thrips. The genus Megalurothrips is a big size, thus strong type of thrips larvae. *M. sjostedti* larvae in particular, were observed to be more violent in their defensive reactions, and to move faster than larvae of any of the other thrips species, including *M. usitatus*. This specific characteristics of Megalurothrips larvae must explain why they were able to resist better than *F. schultzei* larvae.

However the table "b" of analysis (Appendix 4.10) indicate that there was a significant effect of the strain of *C. menes* to which these species of host were faced. The resistance of *M. sjostedti* was by far stronger than the resistance of *F. schultzei* host species when offered to the two Indian strains; but with the local and Malaysian strains, there was no difference in resistance between *M. sjostedti*, *M. usitatus* and *F. schultzei* species.

Thus, the physical strength of the host larva cannot account for the success of the *F. schultzei* resistance against the local strain. This species of thrips, unlike *M. sjostedti*, is characterized by its smaller size, its slow reactions. Despite this, *F. schultzei* resistance was as successful as *M. sjostedti* resistance against the local strain. Host kairomones are known to have a major importance in parasitoid behavioural response (Beck, 1965). For instance, the persistance of a searching wasp to locate the host (Srivastava and Singh, 1988), and her determination to overcome the host resistance, are governed by the strength of the stimuli they received

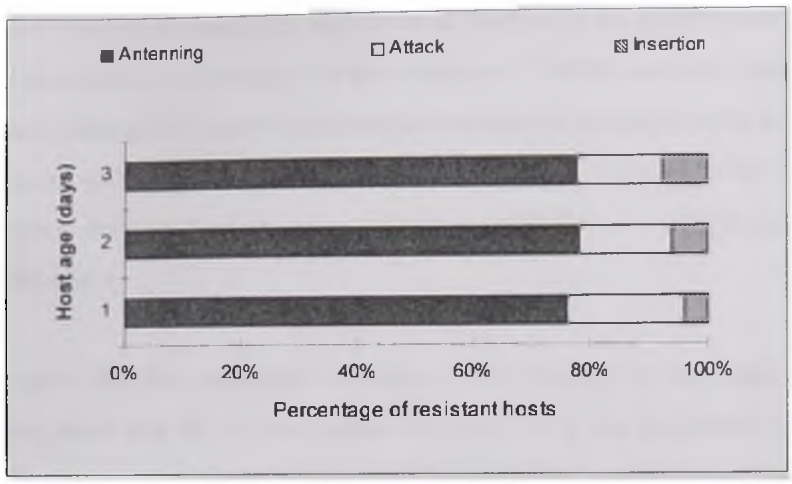


Figure 4.5: Resistance of larvae of the three different age groups, at the different stages of the host-parasitoid interaction

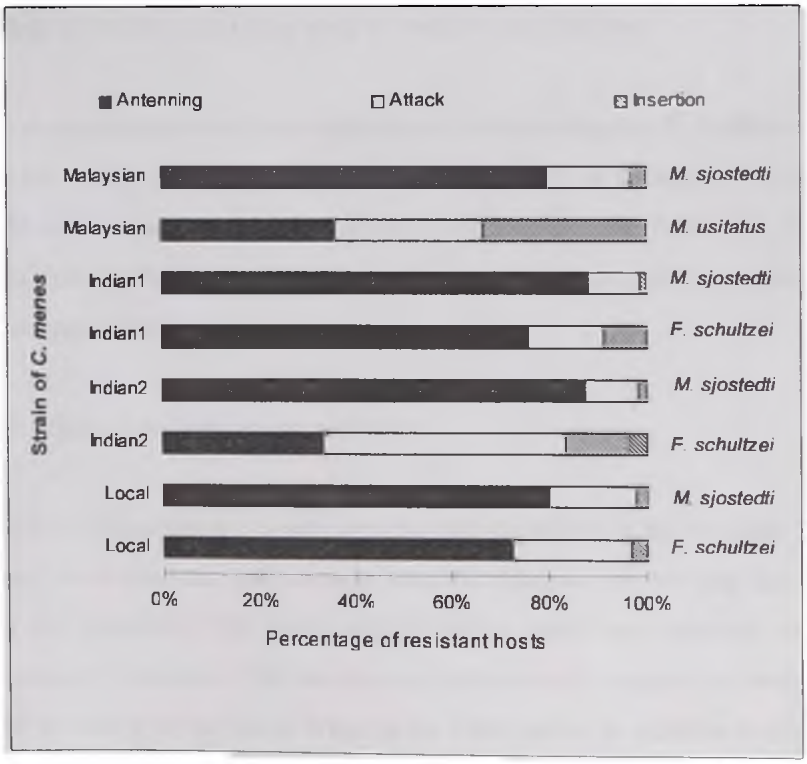


Figure 4.6: Resistance of the different species of host against the different strains of *C. menes*, at different stages of the host parasitoid interaction

from the host kairomones. Negative stimuli as defined by Beck (1965), induce behaviour that are incompatible with the host acceptance for parasitization, such as a lack of motivation to overcome the host resistance. On the contrary, positive stimuli from host kairomones induce behaviour that encourage acceptance for parasitization. The success of *F. schultzei* resistance against the local strain probably resulted to a large extent, from the lack of interest of this strain of *C. menes* to win the struggle at the attack phase.

This implies that the successful resistance of *M. sjostedti* to the Indian strains of *C. menes* could also be to some extent, the result of a low acceptance of this host, which made the *M. sjostedti* larva succeed more easily its resistance than if it were accepted by the parasitoid. By the same token, positive stimuli, probably received by local and Malaysian strains from *M. sjostedti*, must have induced in these two strains a strong motivation, and thus trigger their aggressiveness to overcome the resistance of *M. sjostedti* larva. So it seems that the full expression of a host resistance is mostly dependent on the decision of the wasp to reject or not, the host.

This study has demonstrated that with respect to host resistance, *F. schultzei* was more compatible with the two Indian strains than *M. sjostedti* for a successful parasitization, while *M. usitatus* and *M. sjostedti* were equivalent vis-à-vis the Malaysian strain. Thus, the host species chosen as check for each of the exotic strains, were effectively the most adequate hosts in this regard.

4.4.2.3. Effect of the host age on resistance

The analysis (Appendix 4.11) indicated that the resistance of the two and three days-old ones, were medium, and stronger than the resistance of the one day-old larvae against the parasitoid. The young and old larvae have been observed with various mechanisms of resistance. The one day-old larvae usually escaped by running away at the first contact with the wasp. Whereas the older larvae, in addition to this means of escape, used the method of wagging their abdomen against the wasp. With the help of

their strength, they got more successful results than the young larvae did, to discourage the wasp from attacking.

The graphical representation (Fig. 4.7) shows a general trend of stronger resistance on older hosts, which confirms results obtained in previous studies on this parasitoid (Loomans *et al.*, 1993). However, the analysis did not indicate any difference in resistance between the 2 and 3 days old larvae. This significant effect of host age on resistance to *C. menes* justify the decision to control the age effect in all analysis in this behaviour study. Being less resistant, the one day old larvae should by consequence, be more easily available to *C. menes* for parasitization. Thus there could be an advantage in offering young larvae to *C. menes*, for the success of the parasitization.

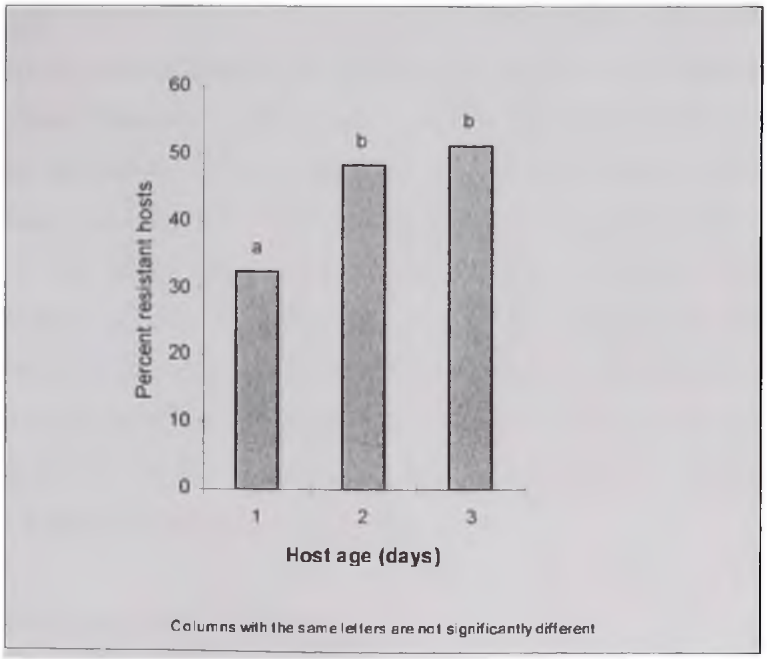


Figure 4.7: Resistance of hosts of the three age groups of larvae against *C. menes*

4.4.2.4. Comparison of host resistance between strains of *C. menes*

4.4.2.4.1. *M. sjostedti* host resistance

The results of the analysis (Appendix 4.12) show that the resistance of *M. sjostedti* was weak against the local strain, but medium against the exotic strains, i.e. Malaysian, and the two Indian strains. However, there was no significant difference in its resistance between the Malaysian and the local strains on one hand, and between the two Indian strains on the other (Fig. 4.8). It implies that the local and Malaysian strains had better ability to overcome the resistance of *M. sjostedti* host than did the two Indian strains. Although, these differences were not so important. *M. sjostedti* resistance to the Malaysian and local strains, were respectively 1.3, and 1.6 times stronger than the resistance to any of the Indian strains (Appendix 4.12). These differences could be explained by the different conditions under which these parasitoids have been maintained in the laboratory. In fact, Malaysian and local were reared for several generations on *Megalurothrips* spp, which are bigger, stronger and more resistant species than *F. schultzei* on which the two Indian strains were reared. In other words, the ability of Malaysian and local strains to handle *M. sjostedti* more successfully than do the Indian strains could be explained by their having more experience on the stronger resistance of *Megalurothrips* spp than do the Indian strains. It would be interesting to find out how the Indian strains would handle *M. sjostedti* larvae, if they were also reared on one of their native Megalurothrips host species such as *M. typicus*, *M. usitatus* or *M. distalis*.

4.4.2.4.2. Check host resistance

The tables of analysis (Appendix 4.13) indicates that the resistance of the host checks against the parasitoid, was in fact weak for all strains, except the Malaysian one for which it was medium. It also indicates that resistance against the local strain was stronger than against the Indian1 by 1.7 fold, and stronger than against the Indian2 by 4.07 fold. However, there was no difference in the resistance the Malaysian and the

local strains have to face from their check hosts, *M. usitatus* and *M. sjostedti* respectively (Fig. 4.8). These results imply that there is at least one Asian strain, in occurrence the Malaysian one, which is equivalent to the local strain in terms of their ability to overcome resistance of their associated hosts.

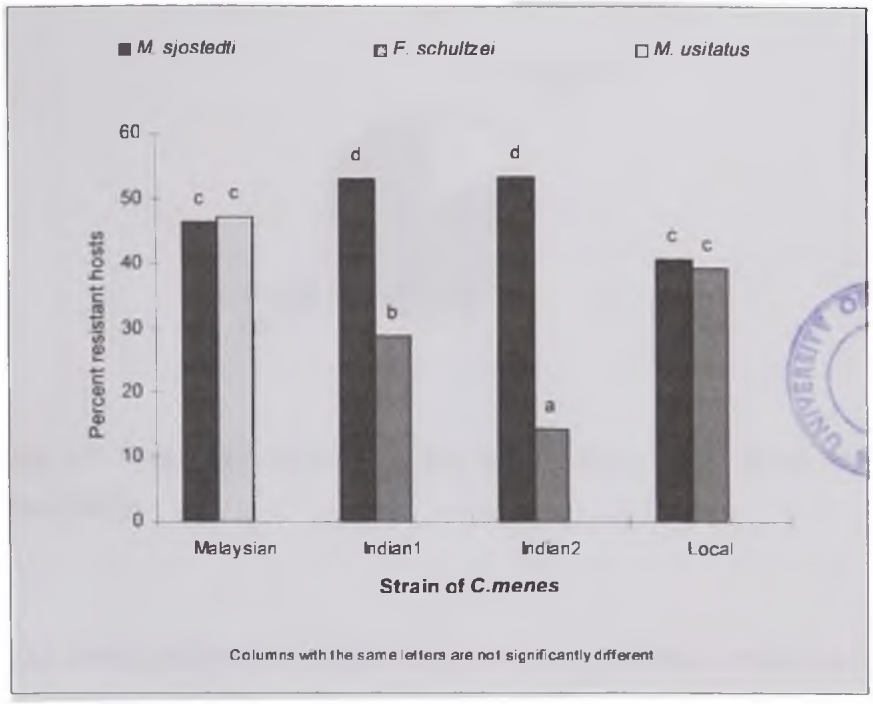


Figure 4.8: Resistance of the different species of host against the different strains of *C. menes*

4.4.3. Host acceptance

Just like in the previous section on host resistance, the tables labeled "a" of the analysis (in the appendices) are results on the magnitude of the host acceptance, expressed in the odd term, and the tables "b" are the results of their comparison between host age groups, host species, or strains of the parasitoid. Again, data and results of the analysis are summarized in graphs where, host acceptance are expressed in percent.

The remaining thrips larvae that did not succeed to resist the wasp represented a total of 1917 larvae, which were available for the parasitoid to accept or reject. Fig. 4.9

shows that a large proportion of them (about 75%), ended up being rejected at some stage of their interaction. The acceptance of the thrips larvae by the parasitoid was weak, regardless of the category of host larvae (Appendices 4.14a, 4.15a and 4.16a).

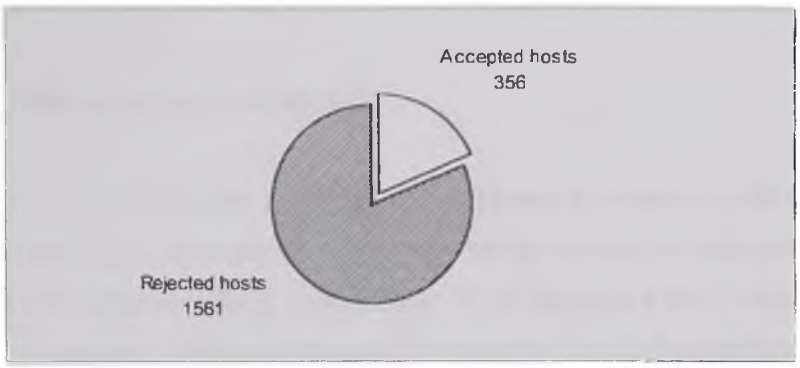


Figure 4.9: Sample size of accepted and rejected hosts by *C. menes* among non resistant larvae

4.4.3.1. Host rejection at the different steps of the host-parasitoid interaction

The results of the study show that *C. menes* rejected host larvae at any stage of their interaction. The large majority (about 74%) of the larvae that were under the control of the female wasp *C. menes*, were rejected by this parasitoid very soon, after external examination of the host at the antenning phase (Fig. 4.10). The remaining few ones that were accepted up to this stage, were rejected later on, almost all (24%) after the insertion. This proves that acceptance recorded just at the attack phase of the host-parasitoid interaction, would overestimate the actual acceptance rate of this parasitoid.

The results also indicate that there were some effects of the host age, host species, and also effect of the strain of *C. menes* on the stages of the interaction at which the rejection occurs. For instance, at the antenning phase, rejection was more frequent on the one and two days-old larvae than it was on the three days-old ones (Fig. 4.10). At this step of the interaction, the rejection by the Asian strains of the check hosts

M. usitatus, and *F. schultzei*, was also minimal (Fig. 4.11). This same trend (i.e. minimal resistance) was observed in the previous section, about the host resistance at antenning on the same combination of host-parasitoid. This suggests the possible existence of a correlation between the host acceptance and host resistance. Thereby, it confirms the conclusion of analysis discussed in the previous section, that the host resistance may depend to a large extent, on its acceptance by the parasitoid.

4.4.3.2. Effect of host age on acceptance

The results in Fig. 4.12, show a general trend of decreasing acceptance with the age of the host larva, but no difference was found between the one and two days old larvae in terms of their acceptance by *C. menes* (Table "b" in Appendix 4.14). However, the 3 days old larvae were significantly less accepted than the 2 and 1 days-old larvae. Their acceptance rates were respectively 21.8, 19.3, and 12.4 percent. Loomans, and co-workers (1992) found acceptance rates of 59.9%, 62.8%, and 33% respectively for the 1, 2, and 3 days-old larvae of *F. occidentalis*, using the brown abdomen type of a European strain. However, acceptance in that study, was defined as the ratio of the number of attack over the number of encountered larvae. In this one, it is the number of oviposition over the number of non resistant larvae. Therefore values obtained from these two studies might not be comparable, but they both indicate that younger larvae are more readily accepted by this parasitoid than the older ones. Like the HHT and host resistance, the results of the analysis on the host acceptance of this parasitoid again suggest that younger larvae must be more appropriate for rearing *C. menes*.

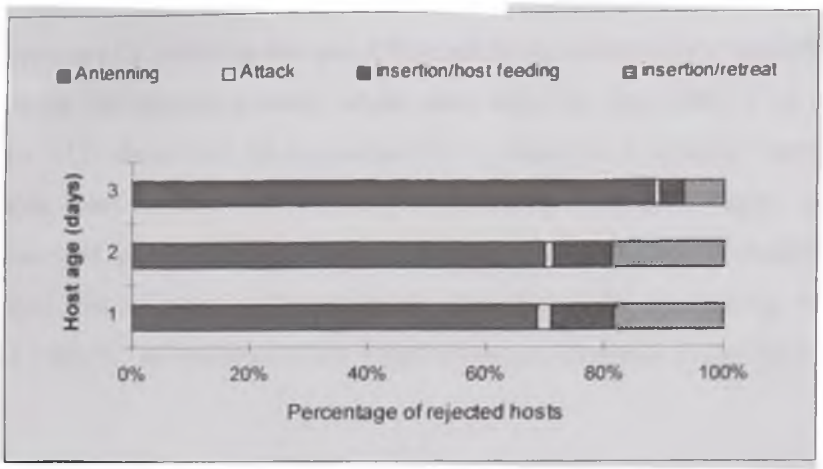


Figure 4.10: Rejection by *C. menes*, of hosts of the different age groups of larvae, at the different stages of the host-parasitoid interaction

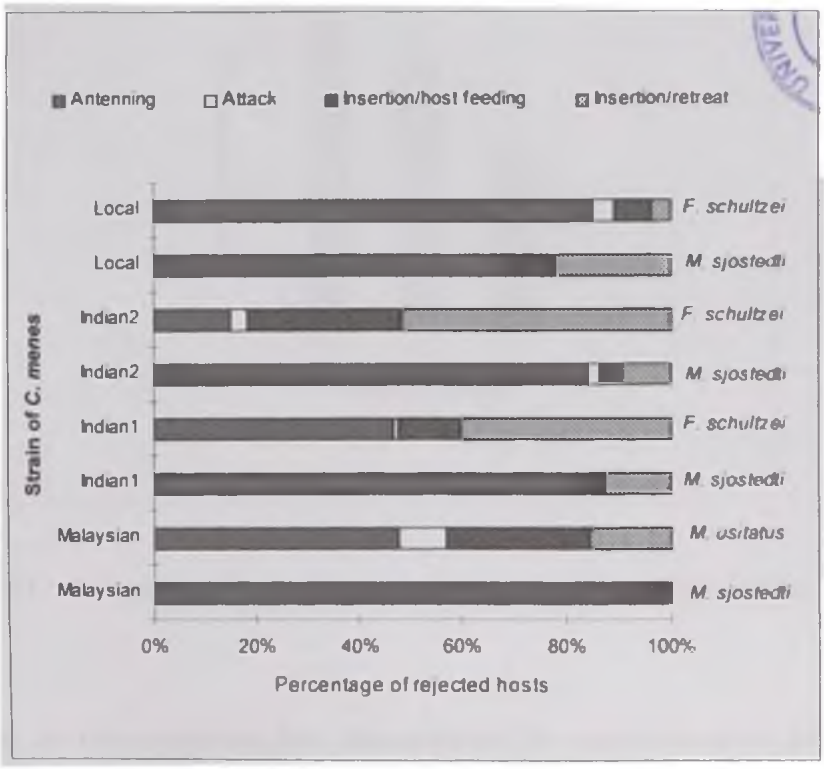


Figure 4.11: Rejection by *C. menes*, of hosts of the different thrips species, at the different stages of the host-parasitoid interaction

4.4.3.3. Effect of host species on acceptance

The acceptance of a host larva was also influenced by the species of the host offered to the parasitoid, but depending mostly on the strain involved. The Table "b" of analysis (Appendix 4.15) shows that the acceptance of *M. usitatus* or *F. schultzei* host, which were check hosts for the Asian strains, was several times much higher than the acceptance of *M. sjostedti* host by the same Asian strains. Contrarily, the acceptance of *F. schultzei* host was almost 3 times lower than that of *M. sjostedti* by the local *C. menes* (table "c" of Appendix 4.15). These results are illustrated in Fig. 4.13. Thus,

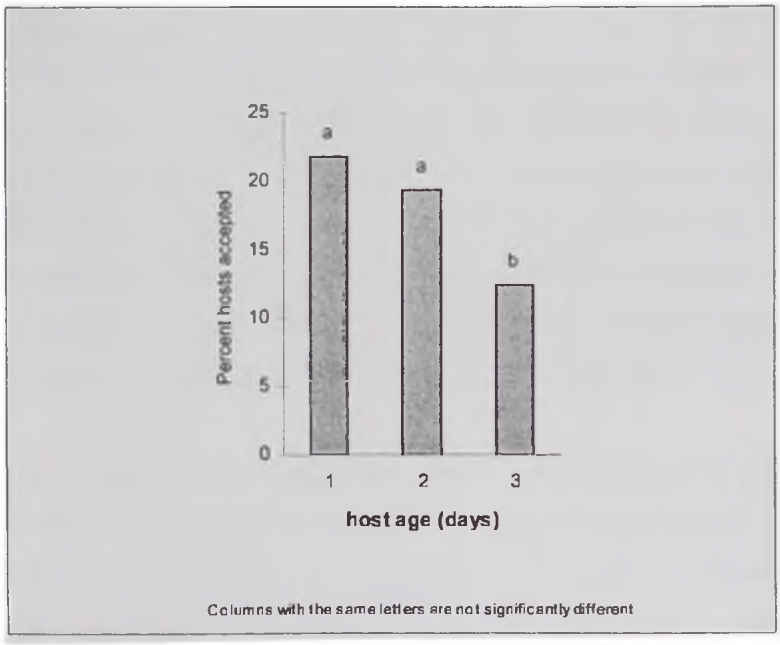


Figure 4.12: Acceptance of hosts of the three age groups of larvae by *C. menes*

between the two species that have been presented to each strain of the parasitoid, *M. sjostedti* was by far less accepted by all the three Asian strains. Adversely, it was preferred over *F. schultzei* by the local one. With respect to the host acceptance, the

species of host chosen as check for each of the exotic strains had once again proven to be the best hosts for them.

4.4.3.4. Comparison of host acceptance between strains of *C. menes*

The host acceptance rates of thrips larvae by the different strains of the parasitoid were low for all strains, except that of *F. schultzei* by the Indian2 strain, for which it is medium (Tables "a" of Appendices 4.16 and 4.17). A larva of this species of thrips had the highest chance of 50:50 to be accepted by the Indian2 strain.

4.4.3.4.1. Acceptance of *M. sjostedti* host

The analysis (Appendix 4.16) indicates that *M. sjostedti* was significantly more accepted by the local strain than by any of the Asian strains. Actually, this species of thrips was totally rejected by the Malaysian strain (Fig. 4.13). Twenty five percent (25%) of the non resistant larvae encountered by the local strain of *C. menes* received the parasitoid egg, compared to just 4%, and 0% for the Indian strains and Malaysian strain respectively. Thus, among the Asian populations, the Malaysian strain was less likely to accept *M sjostedti* than the two Indian strains, and there was no difference between these two strains in their acceptance of *M. sjostedti* larvae.

Thus, the analysis indicates that the 4 strains of *C. menes* can be classified into 3 groups which are in order of increasing acceptance of *M. sjostedti*, the Malaysian strain, followed by the two Indian strains, then the local strain. This is another proof of the better adaptation of the local than the Asian strains for the parasitization of *M. sjostedti*.

4.4.3.4.2. Acceptance of check hosts

The analysis (Table "b" of Appendix 4.17) indicates that the acceptance of *F. schultzei* by any of the two Indian strains was higher than that of *M. sjostedti* by local strain, and also higher that of *M. usitatus* by the Malaysian strain. However, no significant

differences were found between the acceptance of *M. usitatus* by Malaysian, and that of *M. sjostedti* by the local strain. On *F. schultzei* host, there was a difference between the two Indians strains: the Indian2 strain showed a higher acceptance of *F. schultzei* than the Indian1 strain. The analysis (Appendix 4.18) shows that both Indian strains had a higher acceptance rate of *F. schultzei* than the local strain (Fig. 4.13).

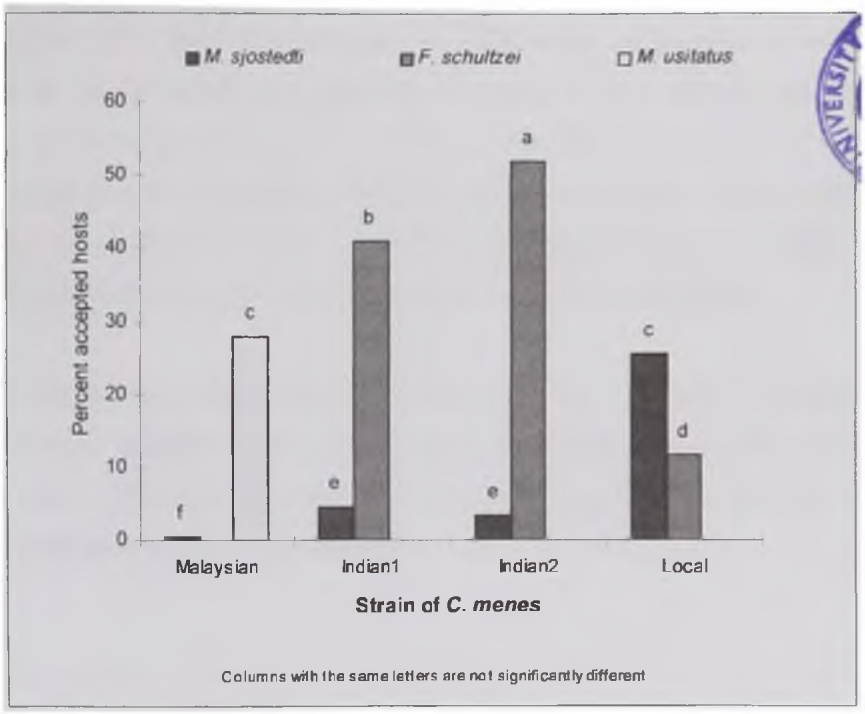


Figure 4.13: Acceptance of the different host species by the different strains of *C. menes*

Thus, the analysis has demonstrated that the local strain showed equivalent acceptance as the Malaysian vis-à-vis their respective check hosts, which were, however, relatively low compared to the acceptance of *F. schultzei* by the two Indian strains. Thus, it should be expected that the local strain would perform as well on *M. sjostedti* host, as the Malaysian strain is on *M. usitatus*, which is in contradiction to observations in the

laboratory rearing (Loomans, pers. com.) as well as in the field parasitism (Tamò *et al.*, 1993).

4.5. Conclusion

In this experiment, the number of hosts encountered by actively searching parasitoid during the 30 minutes period of interaction varied considerably from one individual wasp to the other, even within the same population of *C. menes*. This is illustrated in the example (Appendix 4.19), showing the encounter rate of host larvae by a female parasitoid. After the host resistance, just 25% of the encountered larvae were left available for the parasitoid to parasitize. Only 26% of these non resistant hosts were accepted for oviposition, i.e. just 6.5% of the total larvae encountered by this parasitoid. Considering this low proportion of encountered larvae that are likely to be accepted, it is important that this parasitoid has a good ability to overcome the host physiological resistance, in order to maximize the rate of parasitization.

This first experiment has demonstrated that there were variations in the behaviour of the different geographical strains of *C. menes*. Nevertheless, none of the exotic strains had shown behaviour patterns more compatible than those of the local strain for successful parasitization of *M. sjostedti*.

Chapter 5

ASSESSMENT OF THE SUITABILITY OF TWO HOST SPECIES OF THRIPS TO AFRICAN AND ASIAN POPULATIONS OF *CERANISUS MENES* WALKER (HYMENOPTERA: EULOPHIDAE)

5.1. Introduction

At the host selection phase of the parasitization process, it was found in the previous experiment, that the behaviour of *C. menes* to accept *M. sjostedti* for oviposition varies among the different strains of the parasitoid. The local strain had proven to be more able to fight off the physical resistance of this thrips species, and more likely to oviposit into the host larvae. However, even after the egg of the parasitoid has been deposited into the body of the host, the success of parasitization cannot always be guaranteed. Some insect hosts can continue to resist against parasitization, using physiological means. The most common defense mechanisms used against endoparasitoids of larval hosts are the encapsulation or melanization of the parasitoid egg, through the reaction of the host immune system. Other insect hosts, simply by their poor nutritional value as food for the feeding stage of the parasitoid, are naturally unfit to allow the growth and development of the parasitoid. The difference in relative amount of various nutrients among host species or host age, is believed to affect the growth of the parasitoid (Sandlan, 1982). With these types of insect hosts, characterized as unsuitable, or physiologically incompatible with the parasitoid, the immature stages of the parasitoid may be killed inside the host body. At the best, it may try to regulate the host physiology, thereby, take a longer time to complete its development in the host. Otherwise the parasitoid may end up producing abnormal adult progenies that are unable to grow its own population on the host. After the host acceptance, the host suitability is therefore crucial for the success of parasitization.

Among this category of unsuitable hosts, are natural hosts of the parasitoid that, in the course of evolution, have developed resistance against the parasitoid. Factitious hosts may also fall into this category. In this work, which is about associating Asian populations of *C. menes* with a novel host, the African species of Megalurothrips,

M. sjostedti, the physiological compatibility between the host and the parasitoid is a particularly important factor to be considered, while selecting parasitoids for the biological control of this insect pest. As host suitability should primarily depend upon its ability to support the parasitoid growth, the immature survival is the first indication of host suitability.

The objective of this study was therefore to assess the survival of the immature parasitoid, as a complement of the biological characteristics studied in Chapter 4. It is used first, to compare the physiological compatibility of the different strains of *C. menes* with the different species of thrips. Secondly, this information will be used for the construction of a life table of the parasitoid in the final part of this work.

5.2. Materials and Methods.

This experiment was carried out with 3 strains of *C. menes*: the Indian1, Indian2, and the local strains, and with two species of thrips, *M. sjostedti*, the host species to be tested, and *F. schultzei* which were used as check for the most adequate host for the two Indian strains. The materials and the methods of rearing both thrips and parasitoid insects are the same as in Chapter 3.

The survival of an immature insect is measured by the ratio between the number of eggs laid and the number of adults emerging from these eggs. Since *C. menes* does not necessarily oviposit in every larva she has probed (as found in Chapter 4), it becomes necessary to be able to ascertain the existance of the egg inside the host. The method used in the previous experiment (Chapter 4), is obviously not appropriate for this study, as it kills the parasitoid egg along with the thrips larva. So, the initial number of eggs of the parasitoid had to be estimated from the oviposition rate in inserted larvae. In a cohort of inserted larvae, the number of eggs deposited by the parasitoid was evaluated from the oviposition rate, then followed until emergence of the adult parasitoids.

5.2.1. Determination of the oviposition rate

Data of the previous experiment were used to obtain the oviposition rate of each strain on the different species of thrips. All larvae that were inserted (n_i), and checked for presence of the parasitoid eggs, were sub-divided into two groups of larvae with (ovi+) and without (ovi-) egg of the parasitoid. The oviposition rate (p) which corresponds to the acceptance after insertion in Chapter 4, was calculated by the ratio (ovi+)/n_i, It was obtained for each strain of *C. menes* on each species of thrips.

5.2.2. Determination of the survival of the immature parasitoid.

The survival rate of the immature stages of the parasitoid is the proportion of adults emerging from an initial number of eggs. Two days old larvae were selected for this experiment to study the survival rate of immature *C. menes*., because they had the highest acceptance rate, and were least preferred for host feeding (Chapter 4).

First, about 15 to 20 larvae of the desired thrips species were introduced into the Munger cell. Females of the parasitoid to be tested (0 to 2 days old) were also introduced one at a time into the cell, and their interaction with the thrips larvae followed until a total of about 100 larvae were stung by the parasitoid.

The actual number of inserted larvae (N_i) which had not been used for feeding by the wasp, was then recorded. In these inserted larvae, the frequency of larvae carrying egg of the parasitoid (N_e), was estimated by multiplying N_i with the oviposition rate value (p) measured previously for each host species-strain of *C. menes* pairing. These larvae were then transferred into a parasitoid rearing jar, and checked until the emergence of the adult parasitoids. The total number of emerged adult offspring (N_a) was afterward recorded.

The number of larvae carrying an egg of the parasitoid (N_e) is the same as the number of eggs present in the cohort of inserted larvae. Finally, after the adults emergence, all the (N_e) eggs of the parasitoid were subdivided into two groups, the observed

survivors (N_a) and the dead immature parasitoids. The immature survival (π_o) of each strain of the parasitoid on each host species was obtained with the ratio N_a/N_e:

$$\pi_o = N_a / N_e.$$

This ratio measures also the host suitability, which was defined in this experiment, as the ability of the parasitoid to complete development in the host (regardless of the quality of the adult progenies emerging from the host).

5.2.3. Statistics

Like the acceptance and resistance parameters studied in the Chapter 4, the host suitability parameter is also a categorical derived variable, expressed in the ratio of two measured variables: the number of emerged adult parasitoids, and the initial number of eggs. The oviposition rate is also a categorical variable, as it is expressed in the ratio of the number of egg deposited by the wasp, over the number of inserted larvae.

Unlike with the host resistance and acceptance parameters studied in the previous section, the interest is on the exact magnitude of these two proportions. This is because the value of the oviposition rate is needed for the estimation of the initial eggs number in the cohort, which is required next for the estimation of the pre-imaginal survival. Similarly, the pre-imaginal survival ratio is necessary later, for the construction of the life-table in the next section.

Again, the logit loglinear technique (from SPSS) was used to analyze the data., But, in the cases of the oviposition rate, and the immature survival rate, a model that best describes the data observed had to be constructed first, for each of these variables, so that the true proportions can be predicted from the models.

5.2.3.1. The data

For the oviposition rate experiment: a thrips larva that has been probed by the parasitoid was classified according to 3 factors: (A) the strain of the wasp, (B) the species of the host larva, and (D) the response of the wasp, i.e. whether or not she has deposited an egg into it.

For the pre-imaginal survival experiment: an egg of the parasitoid carried by a thrips larva, was classified according to 3 factors: A) the strain of the wasp, B) the species of the host larva, and D) the response of the parasitoid egg, i.e. whether or not it has succeeded to grow and survive as immature stages, within the host larva, as evidenced by the emergence of an adult parasitoid, This also answers the question about the host larva, i.e. whether or not it is suitable for the development of the parasitoid.

Modeling the odd response ("yes" over "no") of the host/parasitoid: the terms that are involved in this logit multinomial model are first, the constant ($\mu_{(ij)}$) of the equation (Appendix 4.3). The second term is the coefficient for the response ($\lambda^{D}_{(l)}$) of the larva/parasitoid. The third one is the coefficient for the two-ways interaction of response by strain of *C. menes* ($\lambda^{AxD}_{(il)}$). The fourth term is the coefficient for the two-ways interaction of response by thrips species ($\lambda^{BxD}_{(jl)}$). The last term is the three-ways interaction for response by strain by species ($\lambda^{AxBxD}_{(ijl)}$).

5.2.3.2. Interpretation of the analysis

The goodness of fit statistics used (in SPSS) to test the models were the likelihood ratio chi-square, and the Pearson chi-square. If the model fits the data well, the observed significance level for these two statistics is expected to be large. Otherwise, the p-value should be below the 0.05 level of significance.

The comparison of host suitability between strains of *C. menes* or between host species were made in the same ways as for the host resistance and host acceptance parameters in Chapter 4, and like these behavioural parameters, host suitability was rated low,

medium, or high depending on whether the odd for an egg of the parasitoid to survive rather than die, was less, equal, or higher than "1". The level of significance for all tests was set at 0.05.

5.3. Results and discussions

5.3.1. Oviposition rates of *C. menes* on the different species of host

The number of inserted larvae that were involved in the previous experiment is shown in the 2 x 3 ways table (Table 5.1). Altogether, 169 and 364 inserted larvae of *M. sjostedti* and *F. schultzei* respectively, were dissected to check for the presence of the parasitoid egg.

			Strain of *C. menes.*			
			Indian1	Indian2	Local	Total
a)	**Response**	with egg	15	7	52	74 (43.79)
		without egg	40	21	34	95 (56.21)
		Total	55	28	86	169 (100)
b)	**Response**	with egg	129	94	16	239 (65.66)
		without egg	75	45	5	125 (34.34)
		Total	204	139	21	364 (100)

Table 5.1: Results of survey of inserted larvae: observed frequencies (and percent) of inserted *M. sjostedti* (a), and *F. schultzei* (b) larvae with and without egg of the different strains of *C. menes*

The analysis of the oviposition rate indicated that a larva of *F. schultzei* was more likely to receive an egg from the parasitoid, once stung by any of the 3 strains of *C. menes*. The oviposition rates of the three strains on *F. schultzei* were not different from each other, and from that of the local strain on *M. sjostedti*. However, they were significantly higher than the oviposition rates of the two Indian strains on *M. sjostedti* (Table 5.2). These results are consistent with the overall acceptance rates measured in the previous chapter.

The model which excludes the three-ways interactions (response x strain x species) from the full model, was found to fit best the data. The analysis of this model (Appendix 5.1a), indicates that the observed significance levels for the goodness of fit statistics, are quite large; This implies that the model fit the data reasonably well. The plots of residuals (Appendix 5.1 b and c), do not suggest any deficiency in this model.

Based on the model, the predicted oviposition rate of each strain of the parasitoid on the various host species is shown in Table 5.2. Except for the local strain, the expected oviposition rate of all the other strains are very close to the observed data.

Strain of *C. menes*:	Host species	Oviposition rate (%)	
		observed	expected
Indian1	*F. schultzei*	63.24	63.06 a
Indian2	*F. schultzei*	67.63	66.42 a
Local	*F. schultzei*	76.19	85.92 a
Indian1	*M. sjostedti*	27.27	27.94 b
Indian2	*M. sjostedti*	25.00	31.00 b
Local	*M. sjostedti*	60.47	58.09 a

Numbers followed by the same letters are not significantly different (logit loglinear model test)

Table 5.2: Observed and expected oviposition rate (%) of the different strains of *C. menes* on the different species of host larvae

5.3.2. Survival of the immature *C. menes* on the different species of thrips

Altogether a cohort of 559 inserted larvae were surveyed for their acceptance and eventually, for the survival of the parasitoid up to adult stage. The results of the surveys are presented in Tables 5.3 and 5.4. Data could not be available for the local strain on *F. schultzei*. The periodical declines of the local population of *C. menes* in the field, and the low number of female wasp obtained from emerging adults could not satisfy adequate supply of female wasps to do all tests in this work.

Estimation of initial number of eggs. From the oviposition rates measured previously, it was predicted that out of this cohort of 559 inserted larvae, 275 larvae would have actually been carrying an egg of the parasitoid. The detailed results for each strain on the different host species are presented in Table 5.3.

Table 5.3: Estimation of the initial number of eggs in the cohort of inserted larvae

Strain of *C. menes*	Host species	Number of larvae inserted	Oviposition rate*	Number of eggs**
Indian1	*F. schultzei*	129	0.63	**81**
Indian2	*F. schultzei*	117	0.66	**78**
Indian1	*M. sjostedti*	110	0.28	**31**
Indian2	*M. sjostedti*	116	0.31	**36**
Local	*M. sjostedti*	84	0.58	**49**

(*) Estimated from the model
(**) Estimated from the oviposition rate

The final number of adults emerged: The 275 larvae with eggs of the parasitoid (estimated above from the oviposition rate) represented the actual number of eggs of the different strains, that were followed for their development and survival up to the adult stage. From these 275 eggs of the parasitoid, only 75 had given emergence to an

adult parasitoid. The details are presented in the two-ways table (Table 5.4) showing their frequencies according to their responses, i.e. survived or dead.

The analysis of the model (Appendix 5.2a) shows that the model that excludes the three-ways interaction does not fit better the data than the full model. Thus the observed immature survival rates, i.e. estimated from the full model (Appendix 5.2b) for the different strains of *C. menes* on the different species of hosts, are considered, and will be used for the life-table study in the next experiment. They are shown in Table 5.5.

Table 5.4: Results of survey of the cohort of the parasitoid eggs: observed frequencies of survivors and dead immature of the different strains of *C. menes* in *M. sjostedti* (a), and *F. schultzei* (b) hosts

			Strain of *C. menes*.			
			Indian1	Indian2	Local	Total
a)	**Response**	dead	20	34	46	100
		survived	11	2	3	16
		Total	31	36	49	116
b)	**Response**	dead	65	45	-	110
		survived	16	33	-	49
		Total	81	78		159

Table 5.5: Estimation of the immature survival rates of the different strains of *C. menes* on the different species of thrips

Strain of *C. menes*	Host species	Estimated egg number	Observed number of adults emerged	Estimated Immature survival (π_o)
Indian1	*F. schultzei*	81	16	**0.20** bc
Indian2	*F. schultzei*	78	33	**0.42** a
Indian1	*M. sjostedti*	31	11	**0.36** ab
Indian2	*M. sjostedti*	36	2	**0.06** d
Local	*M. sjostedti*	49	3	**0.07** cd

Numbers followed by the same letters are not significantly different (logit loglinear model test)

5.3.2.1. Comparison between host species.

The analysis (Appendix 5.3) showed that the immature survival of the Indian2 strain increased significantly when *F. schultzei* was offered as host, as compared to *M. sjostedti*. Thus *F. schultzei* can be considered as better quality host for the Indian2 than *M. sjostedti*. However, the suitability of the two species of host to the Indian1 strain were not significantly different. In other words, both thrips species should be equally good in quality for the Indian1 strain. Thus, as far as the host suitability is concerned, *F. schultzei* had again proven to be a good choice as check for the best host for the Indian2 strain. However, *M. sjostedti* as well as *F. schultzei* could be chosen as check host for the Indian1 strain.

5.3.2.2. Comparison between strains of *C. menes*

On M. sjostedti *host*

With *M. sjostedti* host, the odd survival of the Indian1 strain was over 7 times more than the same odd for the Indian2, and the local strain (Appendix 5.4b). In other

words, *M. sjostedti* was more suitable to the Indian1 strain than it was to the Indian2 strain, and to the local strain to which this species is supposed to be associated in the field (Fig. 5). In fact, a medium host suitability, which is the highest that was recorded in this experiment, was obtained with *M. sjostedti* for the development of the Indian1 strain (Appendix 5.4a). Thus with respect to the ability to survive in *M. sjostedti,* the Indian1 strain should be more adapted than the other strains of *C. menes,* for the biological control of *M. sjostedti.* There was no difference in *M. sjostedti* suitability, between the local strain and the Indian2 strain. Both strains had a relatively poor survival rate in this thrips species.

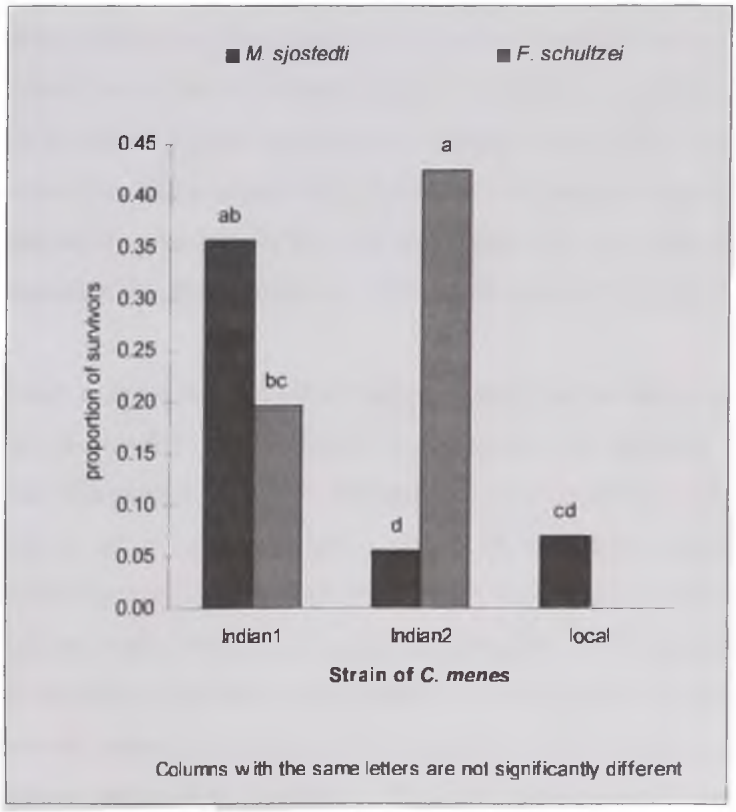


Figure 5: Survival rate of the immature stages of the different strains of *C. menes*, on the two different species of host larvae

On the check host

The results (Fig.5) indicate that *F. schultzei* was more suitable to the Indian2 and Indian1 strains, than *M. sjostedti* was to the local strain. The difference in the check hosts suitability between the Indian1 strain and the local strain was not significant, but it was at the limit. The 95% Confidence Interval of the difference laid between -0.01 and 2.41 (Appendix 5.5b). With *F. schultzei* again, the survival of the Indian2 strain was higher than that of the Indian1 strain. The table of analysis (Appendix 5.5b) shows that the odd of the Indian2 strain to survive rather than die in this host was almost three times as much as the same odd for the Indian1 strain.

The higher suitability of *F. schultzei* to the Indian2 strain compared to the Indian1, is not surprising. When they were reared on *F. schultzei* in the laboratory, the Indian2 strain "yielded" more than the Indian1 strain. Thus these two Indian strains are again different with respect to their survival in *F. schultzei* host larvae. By comparing the survival of the two Indian strains with that of the local strain in their respective check hosts (which are *F. schultzei*, and *M. sjostedti* respectively), this study may provide the first explanation of the low performance of the local strain of *C. menes* on *M. sjostedti*.

It is important to point out that, when rearing the thrips in the laboratory we observed a higher larval mortality on *M. sjostedti* as compared to *F. schultzei*. This additional factor of the host mortality at the larval stage must have caused the premature death of the parasitoid in *M. sjostedti* larvae, which is no longer attributable to an immunological reaction from the host. Therefore, it is not unlikely that the suitability of *M. sjostedti* was under-estimated. The absolute suitability of *M. sjostedti* to *C. menes* could be higher than what was actually measured in this experiment, should the rearing of this thrips be improved to reduce larval mortality. Therefore, the results obtained in this experiment may not be conclusive. Also, the question about the physiological compatibility of *M. sjostedti* host and the parasitoid, may still remain to be answered. The potentials of all the strains of *C. menes* to survive in *M. sjostedti* need to be confirmed, as they may be overshadowed by the problem of the host larval mortality.

5.4. Conclusion

This study has indicated that the oviposition rate of this parasitoid was very low. About half of larvae are released without egg deposition after being probed by *C. menes*. In the second half in which the parasitoid has oviposited, at least 50% of the parasitoid egg dies inside the host before reaching the adult stage. The question whether the parasitoid death was caused by the host physiological resistance, i.e. the host immunity, or by a premature death of the host larvae can be raised. It is obvious that parasitoid mortality due to host immunity is the adequate indication of the host suitability. But this experiment was not designed to distinguish between these two possible causes of the parasitoid mortality.

This experiment also revealed the unsuitability of *M. sjostedti* to the local strain of *C. menes*, which could be an explanation for the low field infestation rate in Benin. The relatively high suitability of *M. sjostedti* to the Indian1 strain focuses attention on this strain. How could its physiological compatibility with *M. sjostedti* compensate for its behavioural incompatibility to make it a good biological control agent against this pest?

Chapter 6

COMPARISON OF DEMOGRAPHIC PARAMETERS BETWEEN AFRICAN AND ASIAN POPULATIONS OF *CERANISUS MENES* (HYMENOPTERA: EULOPHIDAE).

6.1. Introduction

The growth and development of insect parasitoids is often influenced by the host species, from which they develop, (Salt, 1940; Corrigan and Lashomb, 1990). This is due to the nutritional value of the food they obtain from these hosts, as well as the host physiological growth. The survival of the immature stages of the parasitoid studied in the previous chapter, is one of the biological features of the parasitoid that is related to the quality of the host as food. The length of time required to complete the development of the parasitoid in the host, is another correlate of the host quality. Also, the adult longevity, size, and the population sex ratio, all of which determine the fitness of the emerging adult parasitoid, are associated with the quality of the food obtained from the host (Abdel-rahman, 1974; Bellows, 1985; Bai *et al.*, 1992) All these different biological characteristics of the parasitoid can affect the ability of *C. menes* to have a normal development and maintain itself on the different thrips species used as host.

As mentioned in the previous chapter, the physiological compatibility between the host thrips and *C. menes* is a prerequisite before any of the Asian strains of the parasitoid could be considered as candidate for the control of the cowpea thrips. Thus, once the immature *C. menes* has overcome the physiological resistance of the host larva to survive, the physiological compatibility with the host should continue to be checked through the developmental time, and the fitness of the progenies produced from that host.

Once *C. menes* is able to complete development in a particular species of thrips, the demographic parameters of the parasitoid on that host are the next important factors

which will finally determine the performance of the parasitoid as a good biological control agent against the thrips.

The aim of this last experiment is therefore to determine and compare these demographic parameters among the different populations of *C. menes* when the different species of thrips are used as host.

The biological parameters that will be focused on are:

1) The mean developmental time (MDT).

2) The intrinsic rate of natural increase (r_m).

3) The net reproductive rate (R_0).

4) The generation time (T_g).

5) The population sex ratio.

6) The adult longevity.

7) The total fecundity.

6.2. Materials and methods

6.2.1. The insect materials and rearing procedure

The pre-imaginal survival of the local strain on *F. schultzei* had not been determined in Chapter 5. So this strain of the parasitoid was studied only in *M. sjostedti* host, while the two Indian strains were studied in both *F. schultzei* and *M. sjostedti* host. For the collection and rearing of the insects, the same materials and methods as in Chapter 3 were used.

6.2.2. Experimental procedure

Experimental technique and climatic conditions: The age specific life and fertility table method (Southwood, 1978) was used to evaluate most of these parameters. The

experiments were conducted in a controlled environmental chamber (Percivals) in which the photoperiod was set at 16 hours per day, the average temperature at 25°C ± 1°C, and the relative humidity fluctuated between 70%, and 80%.

Experimental set-up: For the fertility studies, freshly emerged adult females of each strain of the parasitoid were followed individually during their entire life-span, then their daily production of offspring recorded and sexed.

A mixture of one and two days old thrips larvae (at least 50 individuals) were offered in an oviposition/rearing unit, to a newly emerged female parasitoid (at day "d_0") that had been placed together with males for at least 12 hours before, to assure insemination of the female wasp.

Every successive day (d), each surviving female was offered a new batch of thrips larvae until death of the adult parasitoid. The presumed parasitized larvae in each oviposition/feeding unit were then kept in the incubation chamber (Percivals), and monitored every other day as explained in Chapter 3, until pupation of thrips or parasitoid. The parasitoid pupae were then transferred in a pupation unit, and checked daily until emergence of the filial parasitoid. Following emergence, all adult offspring were stored in vials without thrips larvae, but with honey to feed on. The vial was kept in the incubator, then each adult parasitoid was checked daily until death.

Replication: For the different strains of *C. menes* on each species of host larvae, a single cohort of female wasps was followed.

6.2.3. Data collection and statistical analysis

6.2.3.1. The MDT, and adult longevity

The MDT of the parasitoid was measured on the offspring produced by the cohort of female parents. It was estimated from the average duration between the time of inoculation of the thrips larvae with a female parasitoid, and the time of emergence of

each of her adult offspring. The longevity of the adult parasitoid was measured for both female parents and offspring in each cohort, It was estimated from the average duration between the time of emergence, and the time of death of each adult parasitoid.

6.2.3.2. The total fecundity and fertility

The fecundity is the capacity of the parasitoid to produce eggs. The fertility is its capacity to produce female offspring. In this experiment these two parameters were measured respectively by the total adult offspring, and the female adult offspring production. All the eggs content in the ovary of the female parasitoid might not have been laid. And even if they were, they may not all have developed up to adult stage, as it was found in the previous study (Chapter 5). Thus, the parasitoid fecundity and fertility in this study are under-estimated from the adult offspring produced over the lifetime of an average female.

6.2.3.3. The sex ratio

The sex ratio is calculated as the proportion of females over the total progenies produced in a cohort. For the statistical analysis, the numbers of male and female offspring produced by each female wasp of a cohort were considered, and tested against the null hypothesis of 1:1 ratio, using the logit log linear model technique, as in Chapters 4.

6.2.3.4. The net reproductive rate (R_0), the intrinsic rate of natural increase (r_m), and the generation time (T_g)

These parameters are derived from the observed pivotal age (x), the age-specific survival (l_x) and the age specific fertility (m_x) in the life-and-fertility table (Southwood, 1978). In each cohort, their values and their statistics were computed using the programme provided by Hultings *et al.*, (1990).

6.2.3.4.1. Input data for the Hultings' programme

The pivotal age of each female wasp in the cohort (x): The pivotal age of the newly emerged female wasp (x_o) was estimated by the MDT for female. The following days, the pivotal age (x) of the surviving female wasp was obtained simply by adding "x_o" to the age of the adult female wasp (d_x).

The pre-imaginal survivor rate (π_o): It has been estimated in the previous experiment (Chapter 5) for each strain on each thrips host species, and corresponds to the age specific survivorship of freshly emerged female (lx_o).

The daily total male and female progenies produced by each wasp: This was recorded for each female wasp replicate in each cohort. The daily number of male and female offspring produced by a female wasp was recorded during her entire life. The age specific fertility (m_x) of each parasitoid in this cohort was given by the number of female offspring.

6.2.3.4.2. Statistics

In addition to their estimated values, the Hultings' computer programme provides also the standard errors of R_0, and T_g (Hultings *et al.*, 1990).

The intrinsic rate of natural increase (r_m) is obtained without error, as it is an index computed from all the female replicates within a cohort. The jacknife method proposed by Meyer *et al*, (1986), was used to assess its uncertainty. This programme provides in addition to r_m, its jacknifed estimate along with its standard error and 95% Confidence Interval (CI). The Confidence Intervals were used to compare these parameters between the different strains of *C. menes*.

6.3. Results and discussions

In summary, 20 females of each of the local and Indian1 strains but only 4 females of the Indian2 strain were able to be followed, and analyzed on *M. sjostedti* host, whereas on *F. schultzei* host the cohorts of Indian1 and Indian2 strains were represented respectively by 14 and 12 females.

6.3.1. The Mean Developmental Time (MDT) of *C. menes*

None of the 4 females of the Indian2 strain succeeded in parasitizing *M. sjostedti*. The failure of the Indian2 strain to reproduce in *M. sjostedti* host observed in this experiment, did confirm the results obtained in the previous ones, of the low acceptance rate (Chapter 4), and the poor suitability (Chapter 5) of *M. sjostedti* for the Indian2 strain. In all the remaining treatments, the parasitoid had succeeded to complete its development, and the MDT was significantly one day longer for female than for male (Table 6.1). This effect of sex on the developmental time of *C. menes*, common for most hymenopterous parasitoids, has also been previously reported for *C. menes* (Sakimura, 1937a; Murai, 1988, and 1990).

The results show that the developmental time of the parasitoid varied between 17 and 29 days (Fig.6.1). Elsewhere, studies conducted under similar thermal condition, have shown greater variation in the developmental time of *C. menes* (Table 6.2), but they were obtained from different strains of the parasitoid, and/or on different species of host thrips. Most of them (Murai, 1988, 1990; Galazzi *et al.*, 1992; Loomans and Murai (1994) reported a longer developmental time, with a greater variability in the data than was found in this study. This is characteristic of the yellow abdomen type of *C. menes* (Loomans and Murai, 1994). Some of these data were obtained from parthenogenetically reproducing forms of this parasitoid. Few studies found shorter developmental time of *C. menes* 14 days on *T. tabaci* (Sakimura, 1937a) and

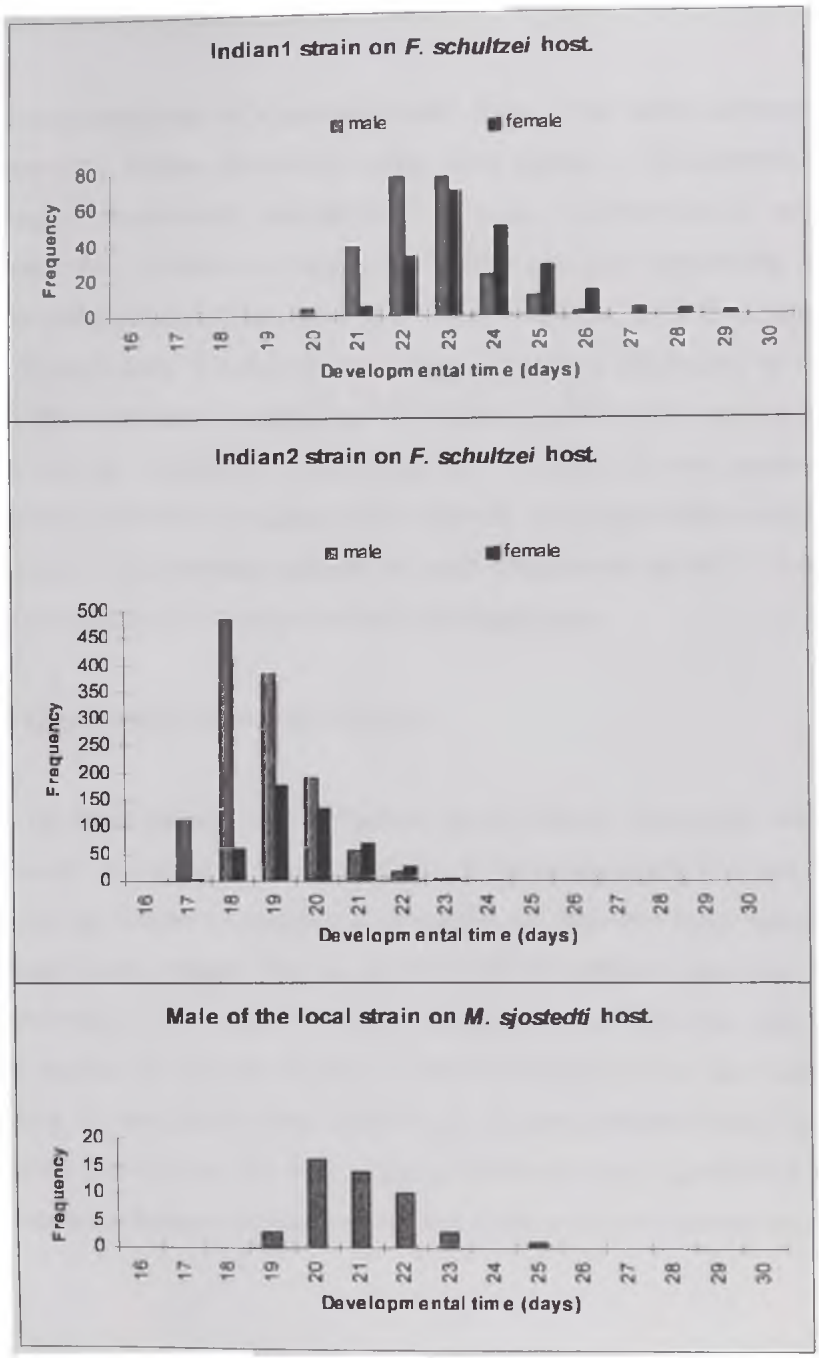


Figure 6.1: The mean developmental time (seconds) frequency graphs of the different strains of *C. menes* on the different host species

respectively 10.8 and 16.3 days on two species of Panchaetothripinae, *Zaniothrips vicini* and *Retithrips syriacus* (Daniel, 1986).

The developmental time of a parthenogenetic form of the brown abdomen type of *C. menes* (the females obviously), using three species of Frankliniella as host: *F. intonsa*, *F. occidentalis*, and mostly *F. schultzei*, was between 23 and 30 days (Loomans, 1991; Loomans and Murai, 1994). With a sexually reproducing form from India, but undefined abdomen colour type, Carl (1971) found a MDT varying between 25 and 28 days using *T. tabaci* as host. These figures are fairly close to the results found in this experiment. Loomans and van Lenteren, (1995) have reported that using Thripine host for the brown abdomen type of *C. menes*, the host species and the geographical origin of the parasitoid, have relatively just a slight effect on the MDT of this parasitoid. This probably explains the small difference in the MDT of the Indian and African strains of *C. menes* observed in this experiment.

6.3.1.1. Comparison between host species

In fact, the developmental time of Indian1 did not change significantly when it was reared on *M. sjostedti* or on *F. schultzei* host. It took respectively 23.5 and 23.7 days on average for females to complete development on these two thrips species (Table 6.1). These results suggest that *M. sjostedti* and *F. schultzei* may have the same nutritional value for the Indian1. It could therefore be concluded that, with regard to the host quality, *M. sjostedti* can be considered equivalent to the check host species *F. schultzei*, for the Indian1 strain. Nevertheless, the developmental time of the Indian1 strain on *M. sjostedti* host has been estimated from only three (3) offspring, one male and two females. Because of this small number, it may not have been well estimated.

Table 6.1: Mean Developmental Time (MDT) (in days) of the different strains of *C. menes*, on the different species of thrips as host

Strain of *C. menes*	Indian1		Indian1		Indian2		Local	
Host species:	*F. schultzei*		*M. sjostedti*		*F. schultzei*		*M. sjostedti*	
	male	female	male	female	male	female	male	female
Sample size (n):	233	207	1	2	1243	478	47	0
MDT (days)	**22.5** d	**23.7** e	**23**	**23.5** abcde	**18.7** a	**19.7** b	**21.0** c	
Sde	0.07	0.10		0.5	0.03	0.05	0.17	

Means followed by the same letters are not significantly different (t-test at $\alpha = 0.05$)

6.3.1.2. Comparison between strain of *C. menes*

On *M. sjostedti* host, the local strain had produced only male offspring. Their average developmental time which was 21.0 days, was not significantly different from that of the two females of the Indian1 which was 23.5 days (Table 6.1). Thus, it was probably not different from the developmental time of the single male of the Indian1 strain on *M. sjostedti*, which was completed in 23 days. This would imply that the Indian1 and the local strains may have the same ability to exploit nutrients from *M. sjostedti* host. For the same reason mentioned above, of the small sample size from which the developmental time of the Indian1 was estimated, these results need to be confirmed.

On their respective check hosts, the results have shown that the MDT of the local strain on *M. sjostedti* was longer than that of the Indian2 strain (18.7 days), but shorter than that of the Indian1 strain (22.5 days) on *F. schultzei* host. The analysis indicate that all these differences were significant (Table 6.1). The first implication of this result is that the two Indian populations were different in MDT. Secondly, considering that a long developmental time of the parasitoid could be an indication of a poor host quality, this results would imply that *M. sjostedti* could not be worse in nutritional value for the local strain, than *F. schultzei* was for the Indian1 strain. On the contrary, it appeared to be a better quality host for the local strain than the check host was for the Indian1 strain. Under such circumstances, this conclusion would contradict the hypothesis formulated in this work, that the biological characteristics of the Asian strain of *C. menes* measured on the check host, are indicating a higher adaptation than those of the local strain measured on *M. sjostedti*. But the quality of the host is not always directly related with the developmental time of the parasitoid. There are cases where the developmental time of a parasitoid remains constant in bad quality host, at the cost of a reduced fitness for the parasitoid (Sequeira & Mackauer, 1992).

Table 6.2: Developmental time at 25 °C, of various strains of *C. menes* reported in the literature

Strain of *C. menes*:			Host species	DT (days)		Ref.:
Origin	Abdomen colour type	Mode of reproduction		Average	Variability: range/Sde	
Germany	?	?	*K. pisivorus*	1 year		Buhl, 1937
Japan	?	Parthenogenetic	*F. intonsa*		30-46	Murai, 1990
Japan	?	Parthenogenetic	*T. tabaci*		30-47	Murai, 1990
Japan	?	Parthenogenetic	*T. hawaiiensis*		30-48	Murai, 1990
France	Yellow	Parthenogenetic	*F. occidentalis*	33.4 days	± 10..3	Loomans, and Murai, 1994
Italy	Yellow	Parthenogenetic	*F. occidentalis*	35.6 days	28-64	Galazzi *et al.*, 1992
Netherlands	Yellow	Parthenogenetic	*F. occidentalis*	36.6 days	± 10..4	Loomans, and van Lenteren (unpublished)
Brazil	Intermediate	Parthenogenetic	*F. occidentalis*	27.5 days	± 1.1	Loomans, and van Lenteren (unpublished)
Italy	Brown	Parthenogenetic	*Frankliniella*	-	23-30	Loomans, 1991
France	Brown	Parthenogenetic	*Frankliniella*	-	23-30	Loomans, 1991
Netherlands	Brown	Parthenogenetic	*Frankliniella*	-	23-30	Loomans, 1991
Spain	Brown	Parthenogenetic	*F. occidentalis*			Loomans, and Murai, 1994
Spain	Brown	Parthenogenetic	*F. occidentalis*	28.4	1.5	Loomans, and Murai, 1994
Japan	?	Sexual	*F. intonsa*	46.9	large	Murai, 1988
India	?	Sexual	*T. tabaci*		25-28	Carl, 1971
Japan	?	Sexual	*T. tabaci*	22.7	narrow	Sakimura, 1937a
India	?	Sexual	*R. syriacus*	10.8		Daniel, 1986
India	?	Sexual	*Z. vicini*	16.3		Daniel, 1986

6.3.2. The reproductive capacity of the different strains of *C. menes*

The results of the fertility tables of the different strains of *C. menes* on the thrips host species tested are shown in Appendix 6.1.

6.3.2.1. Comparison between host species

Again, the comparison of the two host species of thrips on the reproductive capacity of *C. menes* was possible only for the Indian1 strain.

Total Fecundity and fertility

The adult female parasitoid from which offspring production was measured, has been obtained from the stock materials. In other words, they have been reared from one species of thrips, *F. schultzei* for the exotic strains or *M. sjostedti* for the local strain. The data shown in Table 6.4 as the fecundity and fertility of the Indian1 strain on *M. sjostedti* and *F. schultzei* do not evaluate the effect of the host species on the parent wasp fecundity and fertility. The differences in the progenies production observed between the Indian1-*M. sjostedti* and Indian1-*F. schultzei* pairings must be due to the difference in acceptance and suitability when these two species of thrips were presented as host to the Indian1 strain (Chapter 4 and Chapter 5). The effect of the host species on the reproductive capacity of the Indian1 strain remains to be determined.

Adult longevity.

The average longevity of the female offspring of Indian1 reared on *M. sjostedti*. and on *F. schultzei* hosts, as well as that of the female parent of Indian1 (thus on *F. schultzei*) are shown in Table 6.3. The analysis indicated no difference in the longevity of Indian1 strain when it was reared on *M. sjostedti* or *F. schultzei*. The two species of thrips must be again equivalent in their effects on the adult longevity of the Indian1 strain. The longevity of this strain on *M. sjostedti* host was obtained in this experiment,

Table 6.3: Average adult longevity recorded for offspring and parents wasps, in the cohort of the different strains of *C. menes*, with the different species of thrips as host

Strain of *C. menes:*	Indian1			Indian1			Indian2			Local		
Host species:	*F. schultzei*			*M. sjostedti*			*F. schultzei*			*M. sjostedti*		
	offspring		parent	offspring		parent	offspring		parent	offspring		parent
	male	female	female	males	female	female	male	female	female	male	female	female
Sample size:	148	127	14	1	2	20	1950	881	12	39	0	20
Mean Longevity: (days)	**6.78** c	**7.78** b	**8.86** abc	**2.00**	**10.50** abc	**11.15** a	**2.56** e	**3.48** d	**9.50** ab	**0.41** g	-	**6.80** bc
Sde	0.26	0.26	0.92	-	2.50	0.97	0.04	0.09	0.65	0.09	-	0.69

Means followed by the same letters are not significantly different (t-test at $\alpha = 0.05$)

from only 2 individuals. It may not have been well estimated. Therefore the conclusion of this analysis should be considered carefully.

Populations sex ratio. and growth parameters

The results (Tables 6.4a and 6.4b) indicated that the capacity of the Indian1 strain to reproduce was much higher on *F. schultzei* than on *M. sjostedti*. The population growth parameters r_m and R_0, almost null on *M. sjostedti* host, were significantly higher on *F. schultzei* host. This must have been caused first, by the low number of offspring produced (Table 6.4f), and secondly by the low fertility (Table 6.4e) of this strain on *M. sjostedti* host, compared to *F. schultzei* host. The total adult female offspring produced by an average female Indian1 dropped from 25.75 on *F. schultzei* host, to 0.1 on *M. sjostedti* host. There was no difference in the sex ratios of the Indian1 strain when it was reared from the two thrips species. Thus with respect to the population growth parameters, *F. schultzei* was again the most adequate host species for the Indian1 strain.

6.3.2.2. Comparison between strains of *C. menes*

6.3.2.2.1. *M. sjostedti* host

Total progeny production

As mentioned above, the four (4) females in the cohort of the Indian2 strain could not reproduce themselves on *M. sjostedti* host. The studies in the previous two experiments gave several reasons why this result should be expected. First, the ovipositing female of the Indian2 strain had been opposed to the strongest resistance from *M. sjostedti* larvae, and she had the lowest acceptability of this host (Chapter 4). Moreover, her offspring suffered from the highest immature mortality in this host (Chapter 5). This failure by *C. menes* to reproduce in some thrips species has been also observed elsewhere. *C. menes* was mentioned to attack *Haplothrips chinensis*, without

Table 6.4: Life history parameters of the different strains of *C. menes* on the different species of thrips as host

	Strain of *C. menes*:	Indian1	Indian1	Indian2	Local
	Host species:	*F. schultzei*	*M. sjostedti*	*F. schultzei*	*M. sjostedti*
a)	**Intrinsic rate of natural increase (r_m)** (/day)	0.057 b	0 c	0.126 a	0 c
	Sde of jacknifed r_m	0.008	0	0.009	0
b)	**Net reproductive rate (R_0)**	4.49 b	0.04 c	15.61 a	0 c
	Sde	0.93	0.03	2.75	0
c)	**Generation time (T_g)** (days)	26.44	-	21.86	-
d)	**Sex ratio** (proportion of females)	0.47 a*	0.67 a	0.46 a	0
e)	**Total fertility** (/individual)	25.75 a	0.1 b	40.27 a	0
	Sde	4.77	0.07	6.30	
f)	**Total fecundity** (/individual)	54.4 a	0.2 b	86.7 a	3.8 c
	Sde	7.91	0.08	17.45	1.38

(*) sex ratio sig. different from 1:1 ratio (after a logit loglinear model analysis)
Values within a same row followed by the same letters are not significantly different (after t-test at α =0.05).

being able to develop within it (Murai, 1990). Whether or not this host was accepted in the first place remains to be proven.

Unlike the Indian2 strain, the local and Indian1 strains had succeeded to produce at least a second generation of adults in *M. sjostedti*. Again, this must be explained by the more aggressive behaviour of the local strain overcoming host resistance (Chapter 4), and the relatively high survival rate of immature Indian1 strain (Chapter 5). Nevertheless, the progeny productions by these two strains were very low: ten (10) average females of the local strain produced up to forty (40) offspring, while ten (10) of the Indian1 strain could produce only two (2) offspring over their lifetimes.

Fertility

The results (Table 6.4e) showed that when *M. sjostedti* was offered as host, the total fertility of the local strain was zero. In fact, all the 20 female replicates of the cohort of local strain on *M. sjostedti* had produced only male offspring (Appendix 6.1), indicating that their eggs may have not been fertilized. The cause could be a lack of insemination of the female. However, certain female parasitoid, even after mating, can at will fertilize or not the egg being deposited into the host, in response to the environmental conditions. One of them is again, the judgment the ovipositing female wasp makes about the quality of the host. Poor quality hosts receive unfertilized eggs for males production. Thus the "zero" fertility of the local strain on *M. sjostedti* could as well be explained by the decision of the wasp to use it for males, rather than females production.

Beside the lack of egg fertilization, a differential mortality between the two sexes, also related to the poor quality of the host, can be another explanation for the absence of females among the offspring produced by the local strain on *M. sjostedti* host. The fitness of female hymenopteran is known to be more adversely affected by the poor quality of the host than that of males (Charnov, 1979; Charnov *et al.*, 1981; Waage, 1982). All the female offspring of the local strain must have been killed at the immature stage because of poor nutrition received from *M. sjostedti* host.

This would suggest and confirms the results obtained in the previous experiment, that *M. sjostedti* was a poor quality host for the local strain. These explanations are so plausible since the offspring produced by the local from *M. sjostedti* presented all the signs of lack of fitness, characteristics of the poor quality of the host from which the parasitoid was reared. First, a high pupal mortality (87%) was observed in the pupal progenies. Secondly, among the few pupae that evolved up to emergence stage (52 out of 395 pupae), most of them had great difficulty emerging from the pupae. They ended up getting out with wings deformation, and some difficulty of walking. They died soon after emergence. Thirdly, the few that managed to emerge without difficulty and with normal wings, did not live beyond a day (see results below). So the unsuitability of *M. sjostedti* for the local strain was again demonstrated in this experiment through the quality of the offspring produced on this thrips species.

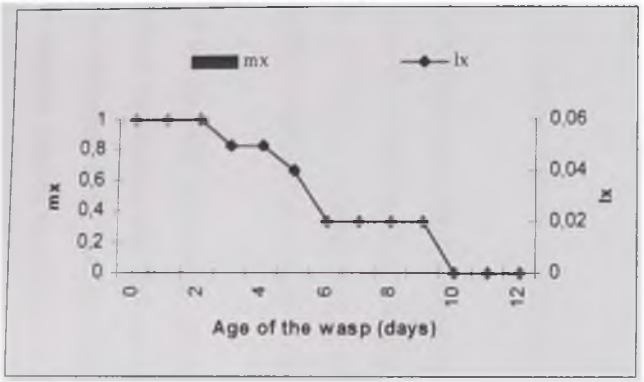
In this same species of host, the Indian1 strain showed some potential, although very little, to produce females in the first generation. Two (2) female offspring were obtained from the whole cohort of 20 wasps. Consequently, the total fertility of an average female was practically null, and not better than that of the local strain (Table 6.4e).

Adult longevity

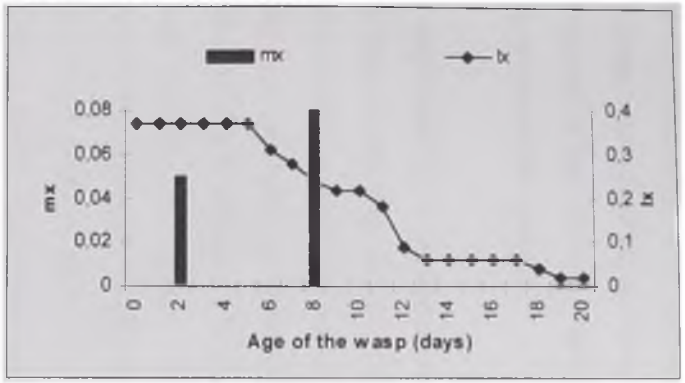
The l_x curves (Fig. 6.2a and 6.2b) showed that the survival of the female parents of the local strain which was already low compared to that of the Indian1 strain at the time of emergence, dropped very soon to "0" by day 10 of emergence, while the survival of the Indian1 strain was reduced just to half at that time. In fact, the average longevity of the Indian1 strain parent (11.2 days) was almost twice as much as that of the local strain parent (6.8 days) (Table 6.3). The female parents of the Indian2 strain had an unusual short longevity when they were offered *M. sjostedti* larvae. They did not live beyond 4 days, and this must have probably contributed in reducing their chance to reproduce on *M. sjostedti*. In this experiment, the parent wasps used in the cohort of *M. sjostedti* host, were obtained from the stock materials, thus reared from different thrips species. The difference in their survivals must be due to some extent, to the difference in the

Figure 6.2: Age specific survivorship(l_x), and fertility (m_x) of the different strains of *C. menes*, on the different species of thrips

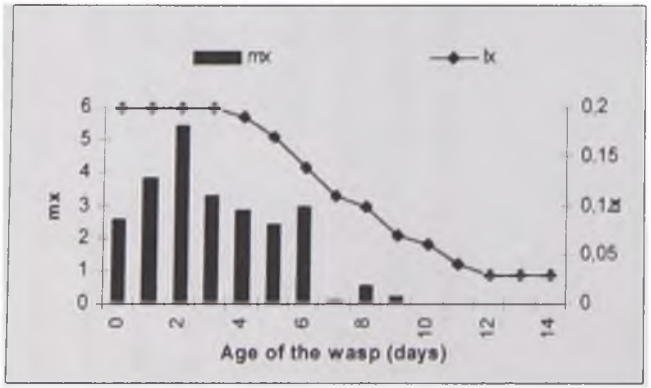
a) Local strain on *M. sjostedti* host



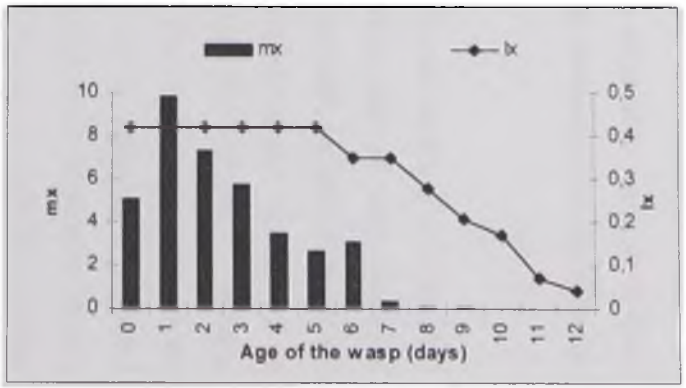
b) Indian1 strain on *M. sjostedti* host



c) Indian1 strain on *F. schultzei* host



d) Indian2 strain on *F. schultzei* host



host species from which they were reared in the laboratory. But also, it is not impossible that they could have been traumatized by the violent defense reactions of this species of thrips when attacking the larvae. So the effect of *M. sjostedti* as food, on the adult longevity of the different strains should be evaluated from the offspring produced in the cohorts of *M. sjostedti*.

When the offspring longevity was compared between the two strains of *C. menes*, the results showed that the offspring of the local strain, which were all males, live for a very short time, about half a day (Table 6.3). From *M. sjostedti*, the Indian1 strain has an average longevity, comparable to that of the adult parents which were reared on *F. schultzei*. The two female offspring they produced lived for 10.5 days on average, but the single male offspring lived just for 2 days. This brief existence of males for the local strain could be a problem for the females to find a mate, especially when males emerged one or two days before females. The result on the female longevity obtained in this experiment is consistent with the longevity of *C. menes* observed in other studies (Table 6.5), which were 10.4 days (Murai, 1990), 10.8 days (Murai and Loomans, 1995), and 12.8 days (Loomans and Murai, 1994). In sum, the local strain of this parasitoid was more adversely affected by *M. sjostedti* host than was the Indian1 strain, with respect to the adult longevity.

Populations growth parameters and sex ratio

As shown in Tables 6.4a and 6.4b, the intrinsic rate of natural increase (r_m), and the net reproductive rate (R_0) of the local and Indian1 strains were null when *M. sjostedti* was offered as host. This was a consequence of the total infertility of the local strain, and the very low fertility of the Indian1 strain on this species of thrips.

The sex ratio of the Indian1 strain on *M. sjostedti* host (2 females to 1 male) appeared to be biased toward the females, but the analysis (Appendix 6.2a) indicated that it was not significantly different from the 1:1 ratio. However, the large standard error obtained in the analysis implies that the value of the sex ratio could not be estimated well, due to the few cases (3 offspring) involved in the sample. Therefore, this result should be interpreted carefully.

The offspring population of the local strain was exclusively composed of males. As discussed earlier, this could be again due to the poor quality of *M. sjostedti* host. The size or the physiology of this thrips species (King, 1989; Bellows, 1985), or even the nutritional state of the host, .i.e. the quality of the food the host itself had received (Harvey *et al.*, 1995), can influence the parasitoid reproductive success. Carl (1971), working with a strain of *C. menes* from India, had also noted a change from a 1:1 sex ratio in field collected sample, to a 1:0 sex ratio, i.e. a production of exclusively males progenies in the laboratory rearing of this parasitoid on *T. tabaci* host. But this was reached gradually after five (5) generations of laboratory culture, whereas in this experiment with the local strain on *M. sjostedti*, it was at the first generation that this phenomenon was observed. The causes must be different.

For biological control, a female-biased sex ratio is considered a positive attribute, by increasing the efficiency of a natural enemy. This experiment showed that, in terms of sex ratio, the Indian1 strain possesses good characteristics -that need however to be confirmed- of a biological control agent against *M. sjostedti*.

6.3.2.2.2. Check hosts

Total progeny production

On *F. schultzei*, the two Indian strains reproduced more successfully than the local strain did on *M. sjostedti* host (Table 6.4f). This is in concordance with the favorable behavioural responses for a successful parasitization, these two strains had demonstrated in all the previous tests, vis-à-vis *F. schultzei* as compared to the local vis-à-vis *M. sjostedti* larvae. The average production by a female wasp was 55 and 86 offspring on *F. schultzei* for Indian1 and Indian2 strain respectively, as compared to just 4 offspring on *M. sjostedti* for the local strain. The total offspring produced by females of the two Indian strains were very low, as compared to the 162 progenies per female *C. menes* reported by Murai (1990) on *F. intonsa* host. It is however not clear whether this value reported by this author refers to the pupal offspring, as it was the case for Loomans and Murai (1994), or to the emerging adult offspring.

Fertility and adult longevity

As observed by Loomans and Murai (1994), also in this experiment the parasitoid did not observe any pre-oviposition period. However, just a single day of post-oviposition period was recorded, while these same authors working with parthenogenetically reproducing strains, had found up to 3-4 days of post-oviposition period. Nevertheless, it was noticed with the sexually reproducing strains studied here, that the female offspring productions also ended 5 and 3 days before death of the female parent for Indian2 and Indian1 strains respectively (Fig. 6.2c and 6.2d). The age specific fertility (m_x) curves of both strains have the same trend (Fig. 6.2c and 6.2d), with a peak at the second and third day of age of the female, respectively. Thus, the maximum production of female offspring can be obtained when the wasps of these two strains are on their second or third days in age.

On *F. schultzei* again, the two Indian strains showed a higher fertility than the local strain had on *M. sjostedti* (Table 6.4e). Among the Indian strains, the total fertility of the Indian2 strain was higher than that of the Indian1 strain. Over lifetime, a female of Indian2 strain had produced on average 40 female offspring, as compared to 26 by a female Indian1 strain. This difference was however not real, suggesting that the two Indian strains might be identical with respect to their fertility on *F. schultzei* host.

As far as the adult longevity of the adult parent is concerned, no difference was found between the three strains of *C. menes*. The average longevity of the female parents were respectively 8.9 and 9.5 days for Indian1 and Indian2 strains on *F. schultzei*, and 6.8 days for the local strain on *M. sjostedti* (Table 6.3). They were not significantly different. As mentioned in Chapter 3, the parent wasps of the Indian strains were reared from *F. schultzei*, whereas most wasps of the local strain used in this experiment were mainly obtained from field-parasitized larvae. The similarity observed in their longevity implies that the adults of the local strain obtained from field-parasitized larvae (which obtained their food from the natural plant for most of their developmental period), were not so badly affected by *M. sjostedti* host, as their offspring which are reared from the laboratory. Further investigations should be

directed on the effect of various nutrition (from different plant host/plant organs) of *M. sjostedti* on the survival of the parasitoid produced from them. This might also help to explain the difference in field parasitism observed on the different host plants of *M. sjostedti* in Benin.

Populations sex ratio, and growth parameter

The reproduction of the Indian strains on *F. schultzei* host was obviously better than that of the local strain on *M. sjostedti* host (Table 6.4a and 6.4b), as a consequence of the lack of fertility of this latter. Between the two Indian strains, the reproduction rates R_0 and r_m of Indian2 (respectively 15.61 and 0.126) were almost by two fold greater than those of the Indian1 strain (respectively 4.49 and 0.057) (Table 6.4a and 6.4b). This explains the higher production obtained from Indian2 than from Indian1 in the laboratory stock culture of these two strains of *C. menes*. This result implies that the two Indian strains are different in their capacity to reproduce in *F. schultzei*.

The intrinsic rate of natural population increase (r_m) of Indian2 strain (0.126), was comparable to those found for the brown abdomen strains from Spain, and Brazil, by Loomans and Murai (1994), and Murai and Loomans (1994) on *F. occidentalis* (Table 6.5). Apart from it, the growth rates of *C. menes* measured for Indian1 in this experiment were by far smaller than the results reported by these authors on the brown abdomen types, but comparable to the growth rate of the yellow abdomen type. In their studies, however, R_0 and r_m were calculated on the basis of the pupal offspring production, and under the assumptions that there were no larval mortality, and that the sex-ratio was 1:1 (Loomans and Murai, 1994). It has been demonstrated in this study, that the pre-imaginal mortality of this parasitoid was far from being negligible. This error must have considerably overestimated the population growth rates measured for *C. menes* in those studies, as suspected by their authors.

Table 6.5: Population parameters (at 25 °C) of various strains of *C. menes* reported in the literature

Strain of *C. menes*: Country of origin	Abdomen colour type	Mode of reproduction	Sex ratio (proportion of female) field	Sex ratio (proportion of female) lab.	Host species	Longevity (days)	Fecundity (offspring/ female)	r_m (/day)	R_0	T_g	Ref.:
Germany	?	?			*K. pisivorus*						Buhl, 1937
Japan	?	Parthenogenetic	0.5	>0.5	*F. intonsa*		162	0.098	63.4		Murai, 1990
Japan	?	Parthenogenetic	0.5		*T. tabaci*	10.4					Murai, 1990
Japan	?	Parthenogenetic	0.5		*T. hawaiiensis*						Murai, 1990
France	Yellow	Parthenogenetic	1	1	*F. occidentalis*	12.8		0.1372	141.8	36.7	Loomans and Murai, 1994
Japan	Yellow	Parthenogenetic	1	1	*F. occidentalis*			0.1175		37.5	Loomans and Murai, 1994
Japan	Yellow	Parthenogenetic	1	1	*F. occidentalis*	10.8			74.2		Murai and Loomans, 1995
Brazil	Intermediate	Parthenogenetic			*F. occidentalis*			0.1276		33.2	Loomans and Murai, 1994
Brazil	Intermediate	Parthenogenetic			*F. occidentalis*				60.4		Murai and Loomans, 1995

Table 6.5 (continued)

Strain of *C. menes*: Country of origin	Abdomen colour type	Mode of reproduction	Sex ratio (proportion of female) field	lab	Host species	Longevity (days)	Fecundity (offspring/ female)	r_m (/day)	R_0	T_g	Ref.:
Spain	Brown	Parthenogenetic	1	1	*F. occidentalis*	12.4		0.1234	49.2	32.2	Loomans and Murai, 1994
Japan	?	Sexual	>0.5		*F. intonsa*						Murai, 1988
India	?	Sexual	0.47	<0.5	*T. tabaci*						Carl, 1971
Japan	?	Sexual	0.6		*T. tabaci*						Sakimura, 1937a
India	?	Sexual	0.6								Daniel, 1986
Indonesia	?	Sexual	0.48								van Heurn, 1923
Thailand	?	Sexual	0.48								Hirose, 1989

The sex ratio measured in this experiment was also different from the 1:1 ratio assumed by the same authors. In fact, the analysis done on the progenies of all female replicates in the cohort (Appendix 6.2a) indicated that the sex ratios of the two Indian strains on *F. schultzei* which were not different from each other, were both significantly male biased: 0.41 and 0.43 were the sex ratio of Indian1 and Indian2 respectively. However, the outcomes of the replicates within each cohort were different. Two of the female parents of the Indian1 strain and one of the Indian2 strain (Appendix 6.1) had exceptionally very low proportions of females among their progenies, causing heterogeneity in the data. Among others, one reason of this heterogeneity could be a mistake when sexing the progenies during the observations. The analysis of the sex ratios computed without these outliers (Appendix 6.2b) did change, but just slightly, the conclusion. It showed that the proportion of females increased slightly, so that the sex ratio of the Indian2 strain, which became 0.46, was no longer different from the 1:1 ratio. However, that of the Indian1 strain (0.47) still remained significantly in favor of males, and not different from that of Indian2 strain. The sex ratios of these two strains of *C. menes* (0.47 and 0..46), were close to the ratios found in field-collected samples of strains of *C. menes* in India (0.47) (Carl, 1971), in Indonesia (0.48) (van Heurn, 1923) and in Thailand (0.48) (Hirose, 1989) (Table 6.5). This observation implies that the species *F. schultzei* may be equivalent, to the native host species of the Asian strains of *C. menes*, in the field. Its choice as a check for the most adequate host species for the Asian strains is once again proven to be a good one. Thus this species of thrips can be a good representative in Africa, of the natural host of the Asian populations of *C. menes* (i.e. *Megalurothrips* spp.).

6.4. Conclusion

This last test failed the Indian1 strain as candidate for the biological control of *M. sjostedti*. It has shown that it would not be able to maintain its population on this species of thrips, because of a low offspring productivity. The two Indian strains have a greater capacity to maintain high level of parasitism on *F. schultzei* than does the local strain on the *M. sjostedti*. But the reason of this lack of fertility on *M. sjostedti* should be clarified before drawing any conclusion from the results obtained in this experiment.

Chapter 7

GENERAL DISCUSSION AND CONCLUSION

The local strain of *C. menes* failed to provide satisfactory control of the cowpea thrips *M. sjostedti* in Benin (West Africa), whilst in the Southeast Asian region, the populations of *C. menes* are thought to keep the Megalurothrips species out of the pest status level. Three (3) questions were raised: 1) Is there any difference between the geographical strains of this parasitoid? 2) Is there any Asian strain that could qualify as a biological control agent against the novel host *M. sjostedti*? 3) Where is the problem of the local strain to control efficiently the cowpea thrips?

In an attempt to answer these questions, the behaviour and some biological characteristics of geographical strains of *C. menes* from Benin, Malaysia, and India have been the object of investigation in this work, to check the compatibility of the parasitoid with *M. sjostedti*. A series of three (3) laboratory experiments simulating the natural chronological sequence of events in building up parasitism were conducted. So for the process of parasitization, the first experiment was concerned with the behaviour of host thrips larvae and *C. menes* after the host has been found by the parasitoid, i.e. the host handling time, the host resistance and host acceptance. The second experiment has investigated the host suitability after it has been accepted by the parasitoid. In the last experiment, the developmental time and life history parameters of the parasitoid were studied, to compare the potential of each strain to maintain and build up a high population growth on the host. To answer the third question about the problem of the local strain, this study has used as control for the most compatible host-parasitoid pairings, *M. usitatus*-Malaysian, or *F. schultzei*-Indian strains to evaluate the compatibility of the pairing *M. sjostedti* -local strain.

Critiques of the methodology and suggestions

Insect behaviour, such as host preference, is usually reported in the literature as qualitative descriptions, which are subjective, therefore, inappropriate for comparison with descriptions from different authors. This work has provided a quantitative method

of evaluating the behavioural parameters of *C. menes*. Thus, these data can be compared with similar data from other studies (e.g. Loomans *et al*, 1991), then compiled as taxonomic characters that can be used for the classification of ecotype of this species of insect. However, some adjustment on the methodology used in this work could improve its accuracy, and practicability in future study.

During the data recording with the "Observer" computer program, it was found difficult to keep up recording the time of on-going actions of the wasp, when simultaneously, inserted larva had to be removed from the Munger cell to check for the presence of the parasitoid egg. This was especially difficult with the two species of Megalurothrips. These larvae usually ran away as soon as they got freed from the ovipositor of the parasitoid, unlike *F. schultzei* and *F. occidentalis* which tolerated a few seconds of paralysis (Daniel, 1986; Loomans 1991). This has affected the precision of the timing of the insertion component of the host handling time. So it would be more judicious in future similar studies, to subdivide this experiment on the behaviour into two separate experiments. In the first one, the "Observer" can be used exclusively for counting, and timing the behavioural events to record data for the host handling time. In this exercise there would be no need to remove inserted larvae to check for host acceptance. The second part of the experiment can be designed to record data for host resistance and host acceptance. In this one, emphasis would be directed on counting the events rather than timing them.

The second suggestion is to cut short the observation time at the beginning of the host-parasitoid interaction, for the evaluation of host resistance. The results of the first experiment revealed that host resistance occurred mostly at the beginning of the host parasitoid interaction. Therefore, whenever this parameter needs to be evaluated in a future study, the observation can be limited at the first two phases, i.e. the antenning and attack of the host-parasitoid interaction, and still provide a reasonable estimate of the overall host resistance for this parasitoid. This would save considerable amount of time, considering that these first two phases take relatively a short time in the host-parasitoid interaction.

The third suggestion would be to eliminate the estimation of host resistance in the behaviour study. In fact, the results on host acceptance and host resistance obtained for the different strains on the different categories of host larvae, seemed to indicate a positive correlation between the ability of the parasitoid to overcome host resistance and the acceptance of that host. In fact, the aggressive behaviour of *C. menes* could also be governed by the same chemical cues which, according to some authors (Arthur *et al*, 1969, 1972; Hegdekar and Arthur, 1973 Strand and Vinson 1983a, 1983b), allow the wasp to decide whether or not to accept the host. Thus, it is probably the acceptability of a host that determines its resistance. Consequently, once the host acceptance parameter is determined, the evaluation of host resistance may be superfluous in the assessment of behavioural compatibility with a novel parasitoid.

Moreover, the estimation of host acceptance could be oversimplified. The oviposition rate measured in the second experiment (i.e. from the insertion step), is consistent with the overall acceptance rate measured in the first experiment (i.e. from the whole interaction). This implies that the oviposition rate (i.e. the acceptance rate measured from inserted larvae) can be used as an approximation of the overall acceptance of this parasitoid for a quick evaluation of behavioural compatibility.

Finally, the suitability of *M. sjostedti* for the development of the parasitoid might not have been well estimated in this work. The normal development of a koinobiont parasitoid depends largely on that of the host (Mackauer, 1986; Godfray, 1994) This rule may apply as well at the lower trophic level, i.e. for the host plant-insect association. Throughout this work, the high mortality observed on *M. sjostedti* larvae, has been suspected to be caused by a problem of nutrition of this thrips species from the laboratory rearing method (host plant type, degradation of food substrate etc..). Likewise, malnutrition must have turned the surviving larvae into poor quality hosts, unable to provide the parasitoid with the adequate nutrients for its development. This must have engendered in turn, a nutritional problem for the parasitoid, as evidenced by the high pupal mortality recorded in the last experiment for both the local and the Indian1 strains. There is a need to improve the *M. sjostedti* rearing method in the laboratory so that the accurate evaluation of its suitability could be achieved. This requires a systematic study of the nutritional needs of *M. sjostedti*.

Consistency of the biological parameters

This work was a laboratory simulation of the natural sequence of events by which the parasitoid utilizes hosts, i.e. its behavioural acceptance of the host, its ability to develop into the host, then to build-up and maintain its population on the host. A model has been created to evaluate the behavioural parameters at the first step of this parasitization process. Therefore, consistency of results on the behaviour measured from the model in the first experiment, and those of the biological parameters measured in the last two (2) experiments, could be an indication of the validity of the model.

Host acceptance and host suitability

The results on host suitability (chapter 5) were consistent with the behavioural response of the parasitoid (chapter 4). It is usually assumed that host suitability is highly correlated with the host quality. Together, they determine the behavioural response of the parasitoid, which receives this information through host kairomones. That information could be about the suitability of the thrips hosts for the survival of the parasitoid offspring. Studies on the behaviour of some parasitoids on species of Drosophila have given evidence that there is a high correlation between the host acceptance by a female parasitoid, and the host suitability for the development of its offspring (van Alphen and Jansen, 1982; van Alphen and Vet, 1986; Driessen *et al.*, 1991). In this work, most of the hosts that were accepted by any strain of the parasitoid (chapter 4), were effectively found suitable host for the development of that parasitoid (chapter 5), and vice-versa. For instance, the Indian1 strain and *F. schultzei* were compatible in behaviour, and in physiology. On the contrary, the Indian2 strain and *M. sjostedti* were incompatible both in behaviour and in physiology.

Host kairomones can also inform the ovipositing wasp about the risk for her own survival. In this study, *M. sjostedti* have been observed to be very aggressive against the offensive wasp. A spectacular reaction of the wasp retreating was sometimes observed with the Asian strains: after contacting the larva, especially the old ones: she

promptly jumped backward a distance away from the larva, as if she was struck by an electric shock, leaving her staggering for a long time before recovering. Afterward, the wasp preened for a long time before resuming search. Vet (1983) has shown that after a female of *Leptopilina clavipes*, parasitoid of *Drosophila* spp was given oviposition experience with host larva feeding on yeast, she became more attracted to the odour of yeast than the odour of decaying fungi, which in nature was the preferred odour to call for oviposition. Many other authors have also demonstrated this ability of some parasitoids to learn to associate a new stimulus from the environment, with the response that is best for their adaptation to this environment (Arthur, 1971; Lewis and Tumlinson, 1988; Lewis and Takuso, 1990). From the shocking experience described above, a female of the Asian strain of *C. menes* may have experienced when she first contacted *M. sjostedti* larva, the parasitoid had probably learned to avoid them in the subsequent contacts, reason why *M. sjostedti* larvae were frequently rejected soon after the first antennal contact (Fig. 4.10). The results in the suitability test (chapter 5) suggested that the non preference of *M. sjostedti* for oviposition by the Indian1 strain (chapter 4) could be due to the higher death risk the wasp would be exposed to, when attacking this strongly resistant thrips species, but not to its poor quality as host for immature growth. Other studies have also shown that a female parasitoid can decide to reject a host, not because of its poor quality for her offspring development, but just because of the danger it represents for her own survival due to the host aggressive defense reactions (Iwasa *et al.*, 1984). Thus the rejection of *M. sjostedti* by the Indian1 strain could be by fear of the ovipositing wasp for its own life.

The behavioural acceptance of a host by *C. menes* does not always imply its suitability. *M. sjostedti* was poorly suitable despite its high acceptance rate by the local strain. It is possible that the poor quality of *M. sjostedti* to the local strain was predictable at the time of oviposition; but its acceptance by the parasitoid was just for the production of male progenies, as discussed earlier (chapter 6), to justify the lack of fertility of the local strain. This would imply the unsuitability of *M. sjostedti* to the local strain, as a species. If this was the case, there should be another thrips species on which the population of the local strain is maintained in the field.

In practice however, some parasitoids may be uncertain about the quality of the host, at the time of oviposition. As a result, the host acceptance is no longer related to the host suitability. This is another explanation of the unexpected behaviour of the local strain, and also that of the Indian1 strain vis-à-vis *M. sjostedti*. In this case, two possible causes of this abnormal response to unsuitable host are suggested by Godfray (1994): The first one is that the poor quality of *M. sjostedti* was not yet fixed at the time of oviposition, thus not predictable by the parasitoid. Accordingly, *M. sjostedti* host larva must have been accepted by the local strain for the production of both sexes. It was demonstrated that the host diet has a significant effect upon the development of the wasp *Ventura canescens* (Harvey *et al.*, 1995). The problem of malnutrition mentioned earlier to explain the abnormal thrips larval mortality could be the cause of a decline in quality of the host larvae, subsequent to the oviposition of the parasitoid. In this case, the expected primary sex ratio of the offspring produced from this host should be 1:1. As the food quality deteriorated, differential mortality on the sexes may have allowed only male offspring of the local strain to survive up to the adult stage. Females are known to be more adversely affected by the poor quality of the host than males (Charnov, 1979; Charnov *et al.*, 1981; Waage, 1982). If this second hypothesis was true, it implies that *M. sjostedti* species could be a suitable host; but the biological potential of the local, and probably those of the exotic strains as well, could not be evaluated precisely in the laboratory, due to the difficulty of rearing the host. These two hypotheses can be verified by studying the primary sex ratio of the progenies produced by the local strain on *M. sjostedti*. This could be done for instance, by distinguishing male from female eggs laid into *M. sjostedti* larvae by the local strain.

The other cause of the unexpected behaviour of the local strain of *C. menes*, is that the quality of *M. sjostedti* was not accurately assessed by the parasitoid, leading to the high host acceptance rate observed in this work. This inability of certain parasitoids to discriminate poor quality hosts was also reported by van Alphen and Drijver (1982). They found that a strain of *Asobara tabida* from Holland readily accepted the population of *Drosophila* spp from Southern Europe, which was a poor quality host for it. Likewise, the Indian1 strain of *C. menes* must have been unable to recognize

M. sjostedti as a bad quality host, as a consequence of imprecision on the wasp assessment of the host quality.

Host acceptance, suitability, and demographic parameters

The results of the previous two tests, i.e. the host suitability (chapter 5), as well as the behavioural responses of the parasitoid vis-à-vis the two species of thrips (chapter 4) were confirmed by the results obtained on the life history notes of the three (3) populations of *C. menes*, the local and the two Indian strains in the last test (chapter 6). The physiological and behavioural incompatibility of *M. sjostedti* with the Indian2 strain are concordant with the failure of this strain to reproduce on this host.

In the last test (chapter 6), the local strain produced numerous pupae on *M. sjostedti*. This was a sign that a large number of eggs must have been produced, as the result of the high acceptance rate of this thrips species measured in chapter 4. However, the important pupal mortality and the lack of fitness of the emerging adult progenies produced from *M. sjostedti* (chapter 6) confirmed the unsuitability of this host found in the second test (chapter 5) for this strain.

On the contrary, with the high rejection rate of *M. sjostedti* (chapter 4), very few eggs must be expected to be produced by the Indian1 in the cohort of *M. sjostedti*. This was reflected in the last experiment (chapter 6): the offspring production of the Indian1 strain was too few to allow growth of its population on this thrips species. The rate of reproduction was consequently, very low (R_0<1). However the Indian1 strain had produced healthy offspring, with a balanced sex ratio, confirming thereby, the suitability of *M. sjostedti* (chapter 5).

Thus, the results on the population parameters measured in the last test were also consistent with the behaviour of the parasitoid observed in the previous experiments. The model that has been used to measure the behavioural parameters of *C. menes* must be valid.

The effects of host age on the behaviour of *C. menes*

This study has indicated that the host handling time of *C. menes* increased slightly with the age of the thrips larvae, but without any detrimental effect on the efficiency of this parasitoid. Thus, any of the three (3) age groups of larvae studied in this work can be used for rearing without risk of wasting this parasitoid time allocation.

However, it confirmed results found in other studies that the one-day-old larvae were less resistant, which explained their being handled faster than older larvae. This made them more easily available to *C. menes* for parasitization. As opposed to host resistance, the host acceptance decreased in fact, with the age of the larvae. Low resistance and high acceptance rates of young hosts could increase chance of success of the parasitization. This advantage on the one and two days old host larvae, should be taken into consideration when choosing larvae for rearing *C. menes*.

The differences between the strains of *C. menes*

This investigation has shown that there were in fact biological differences among the four (4) strains of *C. menes* when reared on *M. sjostedti*. All of them had the same handling time of *M. sjostedti* larvae. In fact, this parameter is supposed to remain constant within the species (Hassell, 1978).

The local population of *C. menes* was different from the Southeast Asian ones. Among all the populations of *C. menes* tested, it had the highest acceptance rate of this host. It resembled the Malaysian strain in their ability to overcome *M. sjostedti* host resistance. It resembled the Indian2 strain in their poor physiological compatibility with *M. sjostedti*, but was completely different from the Indian1 in all these aspects. The mean developmental time of the local strain on *M. sjostedti* was shorter than that of the Indian1 strain. The difference may not be significant, but the result needs to be confirmed because it was based on observation of a single individual of the Indian1 strain. This study has also shown that under the condition in which *M. sjostedti* has been cultured in the laboratory, the Indian1 strain has better ability to exploit nutrients from larvae of this species than does the local strain. Its pupal mortality observed on

the last experiment was lower, and its female offspring survival higher than for the local strain. Just like different species of parasitoid, the different geographical strains of *C. menes* must also differ in nutrients requirement, or in their ability to regulate their host physiology for efficient exploitation of nutrients from it.

There is also difference among the Asian strains. The Malaysian was different from the two Indian strains. It had a higher ability to overcome *M. sjostedti* resistance, although a much lower acceptance rate of this host. Unfortunately, the suitability of *M. sjostedti* could not be tested with the Malaysian strain.

The two Indian strains showed also some differences. When *M. sjostedti* was offered as host, they both had a low acceptance rate of this thrips species, coupled with a poor ability to overcome its physical resistance (chapter 4). However, the two strains must differ in their ability to exploit host nutrients for normal development. *M. sjostedti* was more suitable to Indian1 than to Indian2. Consequently, the Indian2 strain did not produce any offspring on *M. sjostedti*, whereas the Indian1 strain managed to produce few, but healthy progenies on *M. sjostedti*. The two strains differed also on *F. schultzei* host. They both have the same immature survival in this species of thrips (chapter 5). However the Indian2 strain benefited over the Indian1 strain the advantage of being less affected by *F. schultzei* resistance, and of having a higher acceptance rate of *F. schultzei* than the Indian1 strain. Moreover, the longevity of the Indian2 strain was slightly more than that of the Indian1 strain. As a result, the Indian2 strain has a higher rate of reproduction than the Indian1 strain.

The Indian1 was clearly stepping out of the other Asian populations of *C. menes*, by being physiologically more compatible with *M. sjostedti*. The difference was particularly surprising with the Indian2 strain. They were two sympatric populations of *C. menes*; collected from the same host plant, in association with same thrips species. The trait about the colour of the female abdomen on which their separation was previously based on, was finally not fixed. As stated earlier (chapter 3), the Indian1 population on which the experiment had been conducted, was coming from a single individual reared for several generations in the laboratory. Therefore the natural population from which it came, must have been subjected to a genetic bottle-neck

effect. Consequently, the genetic make-up of the resulting population studied in this work, would be quite different from that of the mother population from India, to which this study refers. By chance it has ended up being more physiologically adapted to *M. sjostedti* than did the Indian2 population. There is no evidence yet, that the natural populations of Indian1 and that of the Indian2 strains are actually different. However, the laboratory populations of indian1 and of Indian2 appeared different in their physiological requirement.

The study of the host parasitoid system that constitute the different geographical populations of *C. menes* and *M. sjostedti* host, has perhaps provided data which permits to test the hypothesis of the foreign origin of *M. sjostedti* as suggested by Tamò *et al.*, (1997). There is a constant race for adaptation between interacting organisms that evolve together, like host and parasitoid. The survival of the parasitoid for instance, implies its building strategies that would allow it to better exploit a host, or to counteract the host defense reactions (physical and physiological). Like in the process of biotypes formation, the change in the parasitoid starts with change in its behaviour, followed later on, by physiological, and biochemical changes, whenever its population is subjected to novel selective pressure from the environment. In the case of the African and Asian strains of *C. menes*, the different species of thrips locally available as host, should be one of the factors responsible for the genetic divergence between the two geographical populations.

This investigation has shown that the local strain of *C. menes* had behavioural characteristics that were better adapted for a successful parasitization of *M. sjostedti*, but lacked physiological compatibility with this host. This behavioural adaptation of the local strain to *M. sjostedti* was obviously the consequence of the relative long period of association of the African Megalurothrips -*M. sjostedti*- with the African strain of *C. menes*, compared to the Asian population of the parasitoid to which it had been associated just for the time of this study. However, this association of the local strain-*M. sjostedti* must be just in a recent past, since physiological adaptation is not yet achieved. On the contrary, there was no behavioural adaptation of the Asian strains to *M. sjostedti*. Physiological compatibility with *M. sjostedti* was also lacking, but not completely in the Asian population of this parasitoid. The single subject that generated

the laboratory population of the Indian1 strain has proved it. Thus, because the potential for physiological compatibility still exists in the Asian population, *M. sjostedti* must have sometimes, co-evolved with the Asian *C. menes* for a longer period than it is actually doing with the African *C. menes*.

Any Asian strain as candidate for the biological control of *M. sjostedti* ?

Despite its low level of parasitism observed on *M. sjostedti* in Benin, it was revealed that at the host selection phase, the local strain showed behaviour patterns more compatible for a successful parasitization of *M. sjostedti* than any of the exotic strains. The host handling time is not a factor that could affect the parasitization success of any of the strains of *C. menes*. The ratio host handling time over longevity was about 0.00002 for all the strains. With this small ratio, they are expected to be equally efficient in host handling time (Hassell, 1978), irrespective of the species of the host larvae. Thus in future studies, this parameter should be excluded in the evaluation for efficiency of this parasitoid. Likewise, the small difference in *M. sjostedti* resistance between strains must not be so important to produce a significant difference on the parasitization of *M. sjostedti*. With a medium resistance, the Malaysian strain was very well reared on *M. usitatus*. Thus with that same magnitude of resistance from *M. sjostedti*, the Indian strains should not have any problem to succeed in parasitization of *M. sjostedti* larvae. Thus as far as host resistance is concerned, all the four strains should be equally capable to parasitize *M. sjostedti* larvae. At the host acceptance, the local strain had shown the highest acceptance rate of *M. sjostedti*. It was by far, followed by the two Indian strains for which the acceptance of *M. sjostedti* was very weak. And this thrips species was totally rejected by the Malaysian strain.

Surprisingly, the second experiment of this work has shown that the suitability of *M. sjostedti* for the development of the parasitoid was highest with Indian1 strain. It was found to be very poor for the local strain as well as for the Indian2 strain. According to Wiedenmann and Smith (1997), physiological compatibility should be given more consideration than behavioural compatibility when selecting novel parasitoid for biological control. Does it means that the Indian1 strain should not be excluded despite its inadequate behaviour? Their argument was that there must be a

potential for parasitoid of closely related hosts, for overcoming the resistance of the novel host. *M. sjostedti* may be very closely related to Asian thrips, still, the Indian1 strain has not been able to overcome *M. sjostedti* defense reactions successfully. Hokkanen and Pimentel (1989) discussing the feasibility of biological control in the New Association Approach, have stated that host resistance is generally the major cause of failure of novel parasitoid. The lack of adaptation of the parasitoid to the unfamiliar defense mechanism of the novel host is believed to be the main cause.

In fact, studies have shown the existence of genetic variations in behavioural response among geographic strains of the Pteromalid *Tomicobia tibialis* Ashmead, vis-à-vis their host *Ips pini* Say (Lanier et *al.,* 1972) This variation in behaviour was due to a difference in their sensibility to the host kairomones, and this has consequently resulted in a variability observed in their field infestation rates. Thus, if the lack of adaptation of the Indian1 strain to *M. sjostedti* has also a genetic basis, then there is little chance that this behaviour could be reversed to improve the acceptance of this thrips species by the Indian1 strain. Although parasitoids use the same chemical cues for host location as for host acceptance (Godfray, 1994), associative learning (i.e. the ability to change behaviour due to experience) of a new stimulus discussed earlier can be developed in a parasitoid for host location, but not for host acceptance. Just like Lanier and co-workers in their study with *T. tibialis* cited above, Mollema (1991) has also demonstrated that recognition of the host chemical cues by different geographical strains of *A. tabida* that call for oviposition, was a heritable character which could only be transferred from mother to daughter. For this reason, it is unlikely that the Indian1 strain of *C. menes* which could not recognize the good quality host of *M. sjostedti*, could be trained for a better acceptance of the cowpea thrips. Nevertheless, the possibility to manipulate Asian populations of *C. menes*, for example by breeding it with the local strain to produce individuals that are more adapted to *M. sjostedti* should be investigated.

This study showed clearly that despite the good acceptance rate of *M. sjostedti* by the local strain, and the high suitability of this thrips species to the Indian1 strain, the populations of these strains of the parasitoid would be doomed to extinction if this species of thrips was targeted as host. In conclusion, none of the strains of *C. menes*,

including the local one, would be able to parasitize successfully *M. sjostedti* because of behavioural and/or physiological incompatibility.

Limitations of the local strain of *C. menes* in the parasitization of *M. sjostedti*

It was confirmed in this investigation that there was no problem at any level of the parasitization process, for the Asian strains to parasitize their respective check hosts. *F. schultzei* was the best thrips species which was compatible with the two Indian strains in every aspect of their biology. On this host, the two Indian strains show the same sex ratios as the natural field populations of *C. menes* in Asia. This is particularly important since deviation from the target host species, *M. sjostedti*, could happen once the Indian strains would be released in the West African region.

By contrasting the local strain on *M. sjostedti* with the Asian strains on their check hosts, this study has provided a possible explanation for the unsuccessful parasitization of *M. sjostedti* by the local observed in the laboratory, and its low field parasitism in Benin. The host handling time cannot be a factor affecting the efficiency of the local strain of *C. menes* on *M. sjostedti*. The handling time of *M. sjostedti* by the local did not differ significantly from that of the check host by any of the Asian strains. In terms of their ability to overcome resistance of their associated host, and also in their acceptance rates, the local strain was not as good as the two Indian strains, but was equivalent to the Malaysian strain. There was also similarity between the Malaysian and the local strains, in their acceptance behaviour vis-à-vis their respective native hosts, *M. usitatus* and *M. sjostedti*. This implies that physiological incompatibility was most likely the reason why the local strain was unable to sustain a growth of its population on *M. sjostedti*, as well as the Asian strains do on their native hosts. The local strain and *M. sjostedti* was the most compatible host-parasitoid pairings with respect to their behavioural host acceptance and resistance. The parasitoid produced a large number of offspring on this species of thrips; but because of the unsuitability of this host, there was a high pupal mortality, and the progenies that survived were biologically unfit to allow reproduction.

Thus, this work has demonstrated that host unsuitability resulting in a severe immature mortality as suspected by Tamò and co-workers (1997) was in fact the major cause of the failure of the parasitization, and the low field parasitism of the cowpea thrips observed in Benin. This raises the question about the host species/condition upon which the local population was maintained in the field. For instance, the correct identification of the host thrips must be established.

Conclusion

There is a great diversity of strains of *C. menes* with different geographical origins, female abdomen colours, and modes of reproduction, and a variety of hosts have been tested with them. This work has provided the first report comparing the biology of *C. menes*, under the following combination of characteristics: the populations being compared were originating from distant parts of the World which are Benin in Africa, India and Malaysia in Southeast Asia. They were all of the bisexual form with brown abdomen. And they were tested using as support host insect *F. schultzei*, a factitious host, *M. sjostedti* and *M. usitatus* the suspected native hosts for the African and Asian strains respectively, and as support host plant, cowpea, also factitious host plant for the Asian populations of *C. menes*. Therefore, it has provided data which permitted the testing of taxonomic prediction about the diversity of the complex of *C. menes*. This study of host-parasitoid system was also a first step to help understand the problem of co-evolution of the species *M. sjostedti* and *C. menes*. Finally, it has helped determine the potential and limitation of each population to parasitize the African cowpea thrips, *M. sjostedti*.

This work showed clearly that none of the geographical strains of *C. menes* can parasitize successfully *M. sjostedti* reared from cowpea plant. Therefore, none of the Southeast Asian populations can be selected as candidate for the biological control of the cowpea thrips. However, it has provided an important taxonomic information. Particularly, it showed that the African and Asian strains of *C. menes* are different from each other in certain aspects of their biology. Thus they must be different biotypes of *C. menes*. However, the difference between the original populations of the two Indian strains need to be confirmed. Finally, the unsuitability of *M. sjostedti*, as evidenced by

a low survival of immature as well as adult parasitoid, and by a strongly male biased sex ratio, was probably the cause of the poor performance of the local strain to control the cowpea thrips in Benin.

It is obvious that *C. menes* would thrive better in natural conditions, when it is free to choose a host thrips species and host plant among all available in the natural environment. It would be interesting to investigate on what happens to the parasitization process at the ecological selection phase in the field, i.e. before the host selection phase that was studied in this work. Especially, the host plant finding by the wasp searching for hosts, needs be studied. It is also possible that *C. menes* can exploit *M. sjostedti* only under certain situations. The effect of the host plant upon which *M. sjostedti* feeds, on the development of *C. menes* is another area of research to elucidate the problem of inefficiency of the local strain to control *M. sjostedti* on cowpea crop. The existence of a different thrips species upon which the local population of *C. menes* is maintained in the ecosystem of Benin, is another eventuality to be taken into consideration. At last, it is important to note that *F. schultzei* could be a potential host for the Asian strains of this parasitoid once introduced in the West African sub-region.

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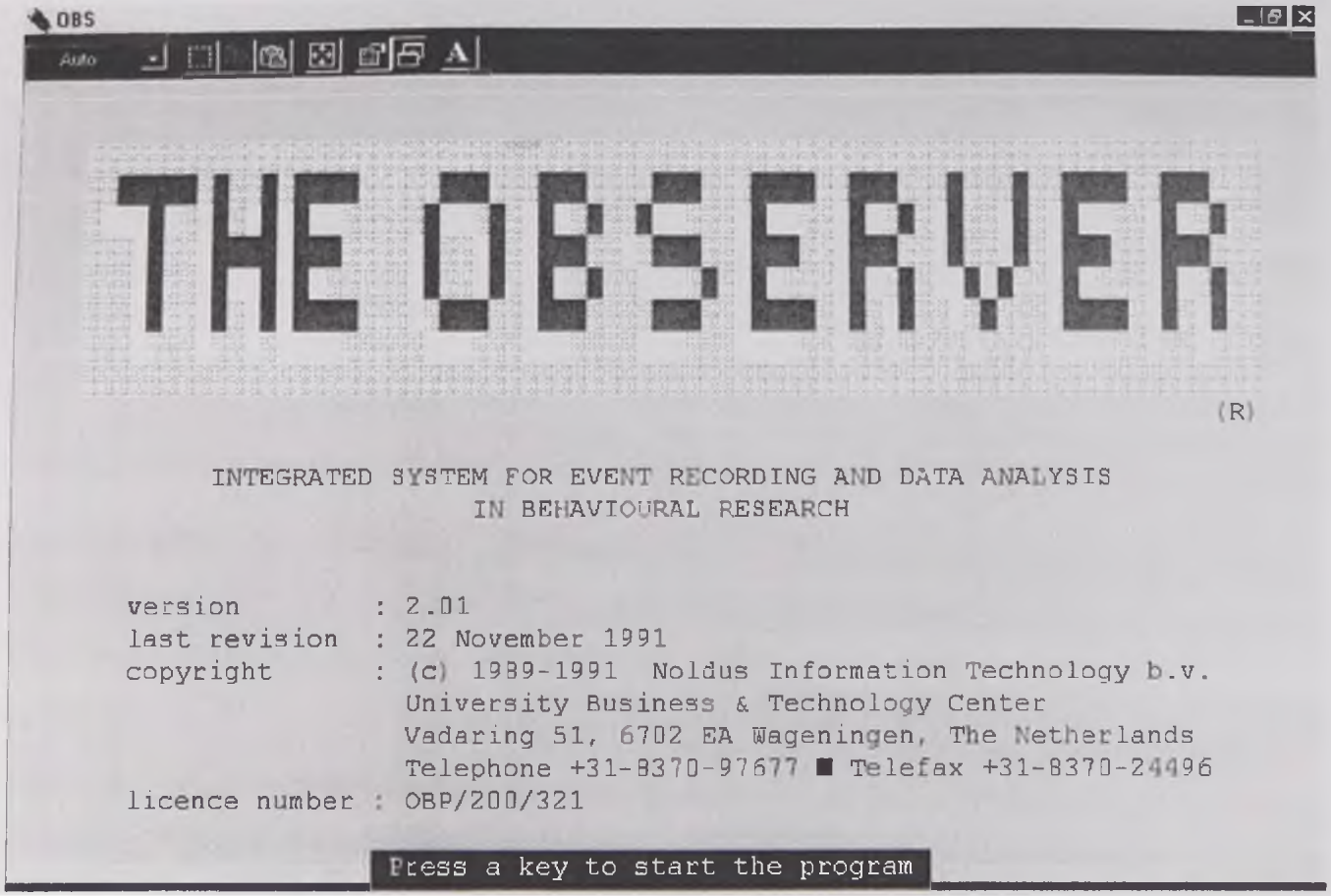
APPENDICES

APPENDIX 4.1: Summary of the experimental set-up for the behavioural study

TREATMENTS	*C. menes* strain	Malaysian						Indian1						Indian2						Local					
	'Host species	*M. sjostedti*			*M. usitatus*			*M. sjostedti*			*F. schultzei*			*M. sjostedti*			*F. schultzei*			*M. sjostedti*			*F. schultzei*		
	Host age (days)	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
NUMBER OF REPLICATIONS (# females)		6	5	5	4	5	6	12	9	10	10	10	10	10	9	7	8	10	5	10	10	10	10	9	8
DURATION OF OBSERVATION per wasp(mn)		60	60	60	60	60	60	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30

APPENDIX 4.2: Opening Screen of the Observer



APPENDIX 4.3: The full loglinear model equation (a) and the equivalent logit model equations (b) for the effect of strain (b1) the effect of host species (b2), and the interaction effect of strain and host species (b3) on the oviposition response of the parasitoid

a) $f(ijl) = \mu + \lambda^{D}_{(l)} D + \lambda^{A}_{(i)} A + \lambda^{B}_{(j)} B + \lambda^{AxB}_{(ij)} AxD + \lambda^{BxD}_{(jl)} BxD + \lambda^{AxBxD}_{(ijl)} AxBxD$

b1)

$\lambda^{D}_{(yes)}$ = Ln [f(*x*, yes) / f(*x*, no)]
$\lambda^{AxD}_{(i)}$ = Ln {[f(*i*, yes) / f(*i*, no)] / [f(*x*, yes) / f(*x*, no)]}

b2)

$\lambda^{D}_{(yes)}$ = Ln [f(*y*, yes) / f(*y*, no)]
$\lambda^{BxD}_{(j)}$ = Ln {[f(*j*, yes) / f(*j*, no)]/[f(*y*, yes) / f(*y*, no)]}

b3)
$\lambda^{D}_{(yes)}$ = Ln f(*x*, *y*, yes)/ Ln f(*x*, *y*, no)
$\lambda^{AxBxD}_{(ij)}$ = Ln {[f(*i*, *j*, yes) / f(*i*, *j*, no)] / [f(*x*, *y*, yes) / f(*x*, *y*, no)]}

where:

$\lambda^{D}_{(yes)}$ is the lambda parameter for the odd response on the reference strain/species
$\lambda^{AxD}_{(i)}$ is the lambda parameter for the odd response of strain (*i*)
$\lambda^{BxD}_{(j)}$ is the lambda parameter for the odd response on species (*j*)
$\lambda^{AxBxD}_{(ij)}$ is the lambda parameter for the odd response of strain (*i*) on host species (*j*)

f(*x*, yes) =frequency of "yes" responses by the reference strain "*x*"
f(*x*, no) =frequency of "no" responses by the reference strain "*x*"
f(*i*, yes) =frequency of "yes" responses by strain "*i*"
f(*i*, no) =frequency of "no" responses by strain "*i*"

f(*y*, yes) =frequency of "yes" responses on the reference host species "*y*"
f(*y*, no) =frequency of "no" responses on the reference host species "*y*"
f(*j*, yes) =frequency of "yes" responses on host species "*j*"
f(*j*, no) =frequency of "no" responses on host species "*j*"

f(*x*, *y*, yes) =frequency of "yes" responses on the reference species "*y*" by the reference strain "*x*"
f(*x*, *y*, no) =frequency of "no" responses on the reference species "*y*" by the reference strain "*x*"
f(*i*, *j*, yes) =frequency of "yes" responses on species "*j*", by strain "*i*"
f(*i*, *j*, no) =frequency of "no" responses on species "*j*", by strain "*i*"

APPENDIX 4.4: Example of an "Observer" data file

These data are recorded during the interaction of a female wasp of *C. menes* with a *F. schultzei* thrips larvae. "CF" is the configuration file linked to this file for the data recording; "CO" are comments, and "CB", questions answered before begining the observation; "QA" are questions answered after. Numeric data in the left column indicate the time at which the events in the right colum occur.

```
**********************************************************************************
@CF,CERANISU.CNF                                549.6    nt
@CO,wasp age= 0h; mated, host age=2d, sp=F. schut.  571.3    ss
  0.0    wa                                     605.1    pr
  0.0    nt                                     729.0    wa
  8.7    en                                     852.2    en
  9.2    at                                     853.0    at
 10.1    in                                     853.3    in
224.8    ss                                     853.3    ??
224.8    hf                                     876.2    wa
281.4    wa                                     876.2    nt
281.4    nt                                     894.0    ss
282.2    en                                     894.8    pr
283.2    at                                     944.2    wa
283.4    in                                     947.2    en
283.4    ov                                     947.9    at
312.5    wa                                     948.2    in
312.5    nt                                     948.2    es
330.7    en                                     949.8    wa
332.1    at                                     949.8    nt
332.4    in                                    1179.2    en
332.4    re                                    1180.4    at
349.1    wa                                    1180.6    in
349.1    nt                                    1180.6    re
352.3    ss                                    1192.1    wa
352.9    pr                                    1192.1    nt
459.8    wa                                    1206.6    ss
484.7    en                                    1207.0    pr
485.2    at                                    1214.0    wa
486.3    in                                    1315.1    en
486.3    ov                                    1316.0    at
502.2    wa                                    1316.0    ex
502.2    nt                                    1316.5    wa
511.4    en                                    1319.5    ss
511.6    at                                    1320.7    pr
512.0    in                                    1601.6    wa
512.0    ov                                    1708.1    ss
525.9    wa                                    1800.0    {eo}
525.9    nt                                   @DT,09-03-1997,14:41:44
536.1    ss                                   @QB,7,Indian2,0h, F. schut.,2d,25°,27°,no
538.3    wa                                   @QA,khady,active
539.1    en                                   @NO, {en}
539.9    at
540.1    in                                   @QA,khady,active
540.1    ov                                   @NO,{en}
549.6    wa
**********************************************************************************
```

APPENDIX 4.5: Example of an "Observer" sequence file

These are data obtained from the same observation as in the data file in Appendix 4.4. It contains the same information, except that the numeric data in the left column indicate the time at which the combinations of events in the right column occur.

****

@CF,CERANISU.CNF
@CO,wasp age= 0h; mated, host age=2d, sp=*F. schut.*

0.0	wa, nt
8.7	en, nt
9.2	at, nt
10.1	in, nt
224.8	ss, nt
224.8	ss, hf
281.4	wa, hf
281.4	wa, nt
282.2	en, nt
283.2	at, nt
283.4	in, nt
283.4	in, ov
312.5	wa, ov
312.5	wa, nt
330.7	en, nt
332.1	at, nt
332.4	in, nt
332.4	in, re
349.1	wa, re
349.1	wa, nt
352.3	ss, nt
352.9	pr, nt
459.8	wa, nt
484.7	en, nt
485.2	at, nt
486.3	in, nt
486.3	in, ov
502.2	wa, ov
502.2	wa, nt
511.4	en, nt
511.6	at, nt
512.0	in, nt
512.0	in, ov
525.9	wa, ov
525.9	wa, nt
536.1	ss, nt
538.3	wa, nt
539.1	en, nt
539.9	at, nt
540.1	in, nt
540.1	in, ov
549.6	wa, ov
549.6	wa, nt
571.3	ss, nt
605.1	pr, nt
729.0	wa, nt
852.2	en, nt
853.0	at, nt
853.3	in, nt
853.3	in, ??
876.2	wa, ??
876.2	wa, nt
894.0	ss, nt
894.8	pr, nt
944.2	wa, nt
947.2	en, nt
947.9	at, nt
948.2	in, nt
948.2	in, nt, es
949.8	wa, nt
1179.2	en, nt
1180.4	at, nt
1180.6	in, nt
1180.6	in, re
1192.1	wa, re
1192.1	wa, nt
1206.6	ss, nt
1207.0	pr, nt
1214.0	wa, nt
1315.1	en, nt
1316.0	at, nt
1316.0	at, nt, ex
1316.5	wa, nt
1319.5	ss, nt
1320.7	pr, nt
1601.6	wa, nt
1708.1	ss, nt
1800.0	{eo}

@DT,09-03-1997,14:41:44
@QB,7,Indian2,0h, *F. schut.*,2d,25°,27°,no
@QA,khady,active
@NO, {en}

****

APPENDIX 4.6: Example of an "Observer" report file

This is the Observer Report file of the same observation as in the data file in Appendix 4.4, and the sequence file in Appendix 4.5. It analyses the information shown in these two files. First, it shows information about the data file being analyzed (A), then the settings of the configuration file to which it is linked (B), the information given about the data before, and after the observation (C), and finally the result of the analysis for single events (D) and combination of events (E): the frequency (N), total, mean, and S.E of the duration of the single and combination of events.

****

THE OBSERVER 2.0

REPORT FILE: ND27.REP

****

(A)

Data file analyzed	: ND27.ODF
Linked configuration file	: CERANISU.CNF
Data file comment	: wasp age= 0h; mated, host age=2d, sp=*F. schut.*
Date of analysis	: 04-15-1998
Analysis comment	: Behaviour of Indian2 on *F. schultzei*

****

(B)

EVENT RECORDER CONFIGURATION

Computer used as event recorder	: IBM PC or compatible
Maximum time per observation	: 30 minutes
Data storage optimization	: Speed
Disk checking during event recording	: No
Auditory feedback during event recording	: Yes

Number of event classes: 3

Class	Events	Exclusive
1 parasite action	6	Yes
2 wasp reactions	5	Yes
3 larval reactions	3	No

Events in class 1: parasite action

Event	Key	Label	Dur/Freq
1 walking	w	wa	Duration
2 encounter	e	en	Duration
3 inserting	t	in	Duration
4 attack	r	at	Duration
5 standing still	q	ss	Duration
6 preening	6	pr	Duration

Events in class 2: wasp reactions

Event	Key	Label	Dur/Freq
1 nothing	8	nt	Duration
2 retreat	5	re	Duration
3 host feeding	u	hf	Duration
4 oviposition	9	ov	Duration
5 missing		??	Duration

Events in class 3: larval reactions

Event	Key	Label	Dur/Freq
1 escape	d	es	Frequency
2 excretion	f	ex	Frequency
3 RAS		rs	Frequency

****

(C)

Date	: 09-03-1997
Start of observation	: 14:41:44 h
Total duration of observation	: 1800 sec
Observation no	: 7
Ceranisus strain	: Indian2
Ceranisus age (hours)	: 0h
thrips species	: *F. schult.*
larvae thrips size (age)	: 2d
rearing conditions	: 25°C
Observation env. condit.	: 27°C
experienced wasps	: no
user's name	: khady
comments	: active

(D)

FREQUENCIES AND DURATION, LUMPED PER EVENT
(for events with frequency > 0)

EVENT	N	DURATION (TOTAL)	DURATION (MEAN)	DURATION (SD)
(parasite action)				
walking	17	696.2	40.95	62.80
encounter	10	8.0	0.80	0.35
inserting	9	335.8	37.31	66.98
attack	10	4.4	0.44	0.31
standing still	8	187.5	23.44	34.65
preening	5	568.1	113.62	104.43

(wasp reactions)				
nothing	9	1623.9	180.43	203.56
retreat	2	28.2	14.10	3.68
host feeding	1	56.6	56.60	0.00
oviposition	4	68.4	17.10	8.43
missing	1	22.9	22.90	0.00
(larval reactions)				
escape	1	-		
excretion	1			

(E)

FREQUENCIES AND DURATION, FOR COMBINATIONS OF EVENTS
(for combinations with frequency > 0)

ORDER OF NESTING: parasite action * wasp reactions

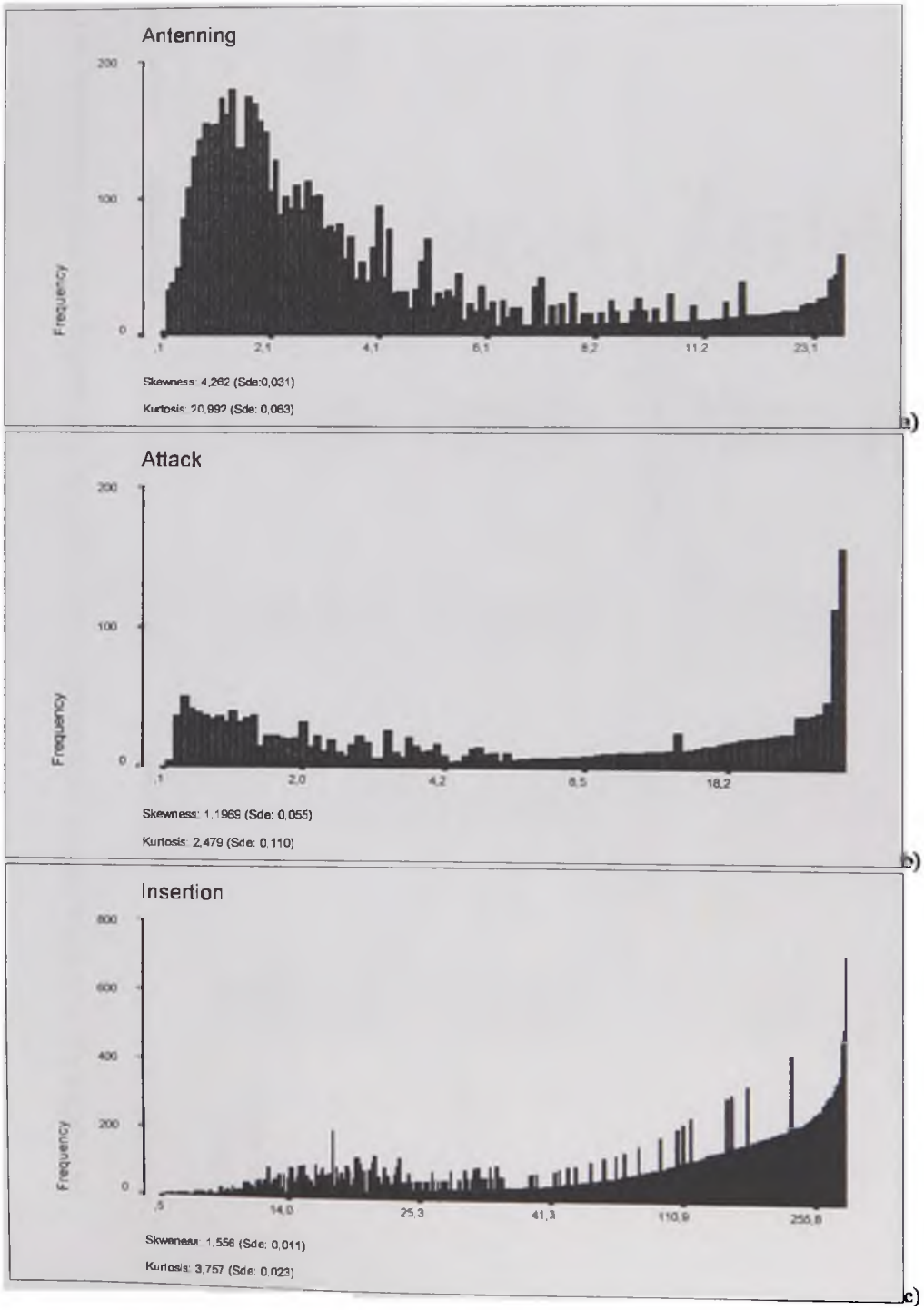
LEVEL 1 PARASITE ACTIONS	LEVEL 2 WASP REACTIONS	NON-NESTED EVENT	N	DURATION (TOTAL)	DURATION (MEAN)	DURATION (SD)
walking	nothing		17	696.2	40.95	62.80
	retreat		2	0.0	0.00	0.00
	host feeding	-	1	0.0	0.00	0.00
	oviposition	-	4	0.0	0.00	0.00
	missing	-	1	0.0	0.00	0.00
encounter	nothing	-	10	8.0	0.80	0.35
inserting	nothing	-	9	216.3	24.03	71.50
		escape	1	-	-	-
	retreat		2	28.2	14.10	3.68
	oviposition		4	68.4	17.10	8.43
	missing	-	1	22.9	22.90	0.00
attack	nothing		10	4.4	0.44	0.31
		excretion	1			-
standing still	nothing	-	8	130.9	16.36	32.63
	host feeding	-	1	56.6	56.60	0.00
preening	nothing	-	5	568.1	113.62	104.43

****

****

APPENDIX 4.7: Frequency distributions of the antenning (a), attack (b). and insertion components of the host handling time by *C. menes,* during the interaction with the thrips larvae

(Y axis is the frequency of the component which duration (sec.) are on the X axis)



APPENDIX 4.8: Descriptive statistics of the different components of the host handling time (HHT) (in seconds) by *C. menes*

		Antenning	Attack	Insertion	Host feeding	TOTAL HHT
					-	
Without host feeding:	Mean:	1.8	1.7	27.2	-	30.9
	Mode:	0.7	0.2	17.6	-	-
	Median:	1.2	0.5	19.4	-	-
	Min.:	0.0	0.0	1.5	-	20.9
	Max.:	58	157.2	264.0	-	59.9
	Size (n):	3472	1162	564	-	-
With host feeding:	Mean:	1.8	1.7	196.6	280.6	477.4
	Mode:	0.7	0.2	120.4	470.4	-
	Median:	1.2	0.5	171.3	207.9	-
	Min.:	0.0	0.0	5.2	3.2	-
	Max.:	58.0	157.2	1428.4	1446.0	1155.3
	Size (n):	3472	1162	132	126	

	Whole insertion	Insertion preceding:		
		Oviposition	Retreat	Host feeding
Mean:	51.3	26.6	28.0	196.6
Mode:	17.6	17.6	12.1	120.4
Median:	21.6	19.6	19.2	171.3
Min.:	0.5	2.4	1.5	5.2
Max.:	711.9	264.0	202.4	1428,4
Size (n):	891	325	239	132

APPENDIX 4.9: Table of analysis of resistance of the different species of thrips against *C. menes*: magnitude of the host resistance (a), and their comparison between species (b).

	Parameter: Host species	Estimate	SE	Z-value	Asymptotic 95% CI: Lower	Asymptotic 95% CI: Upper	Sig.*	Odd value	Score of resistance
a)		(log odd)							
	M. sjostedti	-0.0315	0.0424	-0.74	-0.11	0.05	ns	0.97	medium
	M. usitatus	-0.1116	0.1182	-0.94	-0.34	0.12	ns	0.89	medium
	F. schultzei	-0.9381	0.0747	-12.56	-1.08	-0.79	s	0.39	weak
b)		(log odd ratio)							
	M. sjostedti vs *M. usitatus*	0.0801	0.1256	0.64	-0.17	0.33	ns	1.08	
	M. usitatus vs *F. schultzei*	0.8265	0.1398	5.91	0.55	1.10	s	2.29	
	M. sjostedti vs *F. schultzei*	0.9066	0.0859	10.56	0.74	1.07	s	2.48	

(*): s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 4.10: Table of analysis of resistance of the different species of thrips against the different strains of *C. menes*: magnitude of the host resistance (a), and their comparison between species within a strain (b).

	Parameter:		Estimate	SE	Z-value	Asymptotic 95% CI		Sig.*	Odd value	Score of resistance
	Strain of *C. menes:*	Host species:				Lower	Upper			
a)			(log odd)							
	Malaysian	*M. usitatus*	-0.1116	0.1182	-0.94	-0.34	0.12	ns	0.89	medium
	Malaysian	*M. sjostedti*	-0.1427	0.0764	-1.87	-0.29	7.14E-03	ns	0.87	medium
	Indian1	*F. schultzei*	-0.9029	0.105	-8.6	-1.11	-0.7	s	0.41	weak
	Indian1	*M. sjostedti*	0.128	0.0755	1.69	-0.02	0.28	ns	1.14	medium
	Indian2	*F. schultzei*	-1.7835	0.1957	-9.11	-2.17	-1.4	s	0.17	weak
	Indian2	*M. sjostedti*	0.1393	0.0907	1.54	-0.04	0.32	ns	1.15	medium
	Local	*F. schultzei*	-0.4321	0.1335	-3.24	-0.69	-0.17	s	0.65	weak
	Local	*M. sjostedti*	-0.3802	0.1095	-3.47	-0.59	-0.17	s	0.68	weak
b)			(log odd ratio)							
	Malaysian	*M. sjostedti* vs *M. usitatus*	-0.0311	0.1408	-0.22	-0.31	0.24	ns	0.97	
	Indian1	*M. sjostedti* vs *F. schultzei*	1.0309	0.1293	7.97	0.78	1.28	s	2.80	
	Indian2	*M. sjostedti* vs *F. schultzei*	1.9228	0.2157	8.92	1.5	2.35	s	6.84	
	Local	*M. sjostedti* vs *F. schultzei*	0.0519	0.1727	0.3	-0.29	0.39	ns	1.05	

(*): s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 4.11: Table of analysis of resistance of hosts of the different age groups of larvae against *C. menes*: magnitude of the host resistance (a), and their comparison between host ages (b)

	Parameter: Host age (days)	Estimate	SE	Z-value	Asymptotic 95% CI		Sig.*	Odd value	Score of resistance
					Lower	Upper			
a)	1	(log odd)							
	2	-0.7326	0.0615	-11.91	-0.85	-0.61	s	0.48	weak
	3	-0.067	0.0579	-1.16	-0.18	0.05	ns	0.94	medium
		0.0482	0.0634	0.76	-0.08	0.17	ns	1.05	medium
b)		(log odd ratio)							
	1 vs 3	-0.7807	0.0883	-8.84	-0.95	-0.61	s	0.46	
	2 vs 3	-0.1151	0.0858	-1.34	-0.28	0.05	ns	0.89	
	2 vs 1	0.6656	0.0845	7.88	0.5	0.83	s	1.95	

(*): s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 4.12: Table of analysis of resistance of *M. sjostedti* larvae against the different strains of *C. menes*: magnitude of the host resistance (a), and their comparison between strains of the parasitoid (b).

	Parameter / Strain of *C. menes*:	Estimate	SE	Z-value	Asymptotic 95% CI		Sig.*	Odd value	Score of resistance
					Lower	Upper			
		(log odd)							
a)	Malaysian	-0.1427	0.0764	-1.87	-0.29	7.14E-03	ns	0.87	medium
	Indian1	0.128	0.0755	1.69	-0.02	0.28	ns	1.14	medium
	Indian2	0.1393	0.0907	1.54	-0.04	0.32	ns	1.15	medium
	Local	-0.3802	0.1095	-3.47	-0.59	-0.17	s	0.68	weak
		(log odd ratio)							
b)	Malaysian vs Local	0.2376	0.1335	1.78	-0.02	0.5	ns	1.27	
	Indian1 vs Local	0.5083	0.133	3.82	0.25	0.77	s	1.66	
	Indian2 vs Local	0.5195	0.1421	3.66	0.24	0.8	s	1.68	
	Indian1 vs Malaysian	0.2707	0.1075	2.52	0.06	0.48	s	1.31	
	Indian2 vs Malaysian	0.282	0.1186	2.38	0.05	0.51	s	1.33	
	Indian2 vs Indian1	0.0113	0.118	0.1	-0.22	0.24	ns	1.01	

(*): s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 4.13: Table of analysis of resistance of larvae of the check host species against the different strains of *C. menes*: magnitude of host resistance (a), and their comparison between strains of the parasitoid (b).

	Parameter: / Strain of *C. menes*:			Estimate	SE	Z-value	Asymptotic 95% CI		Sig.*	Odd value	Score of resistance
							Lower	Upper			
				(log odd)							
a)	Malaysian			-0.1116	0.1182	-0.94	-0.34	0.12	ns	0.89	medium
	Indian1			-0.9029	0.105	-8.6	-1.11	-0.7	s	0.41	weak
	Indian2			-1.7835	0.1957	-9.11	-2.17	-1.4	s	0.17	weak
	Local			-0.3802	0.1095	-3.47	-0.59	-0.17	s	0.68	weak
				(log odd ratio)							
b)	Malaysian	vs	Local	0.2686	0.1611	1.67	-0.05	0.58	ns	1.31	
	Local	vs	Indian1	0.5226	0.1517	3.45	0.23	0.82	s	1.69	
	Local	vs	Indian2	1.4033	0.2242	6.26	0.96	1.84	s	4.07	
	Malaysian	vs	Indian1	0.7913	0.1581	5	0.48	1.1	s	2.21	
	Malaysian	vs	Indian2	1.6719	0.2286	7.31	1.22	2.12	s	5.32	
	Indian1	vs	Indian2	0.8807	0.2221	3.97	0.45	1.32	s	2.41	

(*): s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 4.14: Table of analysis of acceptance by *C. menes*, of host from the different age groups of larvae: magnitude of the host acceptance (a), and their comparison between host ages (b).

	Parameter / Host age (days)	Estimate	SE	Z-value	Asymptotic 95% CI		Sig.*	Odd value	Score of acceptance
					Lower	Upper			
		(log odd)							
a)	1	-1.2786	0.0849	-15.07	-1.44	-1.11	s	0.28	low
	2	-1.4283	0.1019	-14.02	-1.63	-1.23	s	0.24	low
	3	-1.953	0.1374	-14.22	-2.22	-1.68	s	0.14	low
		(log odd ratio)							
b)	1 vs 3	0.6744	0.1615	4.18	0.36	0.99	s	1.96	
	2 vs 3	0.5247	0.171	3.07	0.19	0.86	s	1.69	
	2 vs 1	0.1497	0.1326	1.13	-0.11	0.41	ns	1.16	

(*): s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 4.15: Table of analysis of acceptance by *C. menes* of the different species of thrips: magnitude of the host acceptance (a), their comparison between species (b), and between host species within strain (c)

	Parameter		Estimate	SE	Z-value	Asymptotic 95% CI		Odd value	Sig.*	Score of resistance
	Strain of *C. menes:*	Host species:				Lower	Upper			
			(log odd)							
a)		*M. usitatus*	-0.9464	0.1807	-5.24	-1.3	-0.59	0.39	s	low
		M. sjostedti	-2.6367	0.1191	-22.13	-2.87	-2.4	0.07	s	low
		F. schultzei	-0.5092	0.0818	-6.23	-0.67	-0.35	0.60	s	low
			(log odd ratio)							
b)		*M. usitatus* vs *M. sjostedti*	1.6903	0.2165	7.81	1.27	2.11	5.42	s	
		F. schultzei vs *M. sjostedti*	2.1275	0.1445	14.72	1.84	2.41	8.39	s	
		F. schultzei vs *M. usitatus*	0.4373	0.1984	2.2	0.05	0.83	1.55	s	
			(log odd ratio)							
c)	Malaysian	*M. usitatus* vs *M. sjostedti*	4.5548	0.8379	5.44	2.91	6.2	95.09	s	
	Indian1	*F. schultzei* vs *M. sjostedti*	2.6508	0.2843	9.32	2.09	3.21	14.17	s	
	Indian2	*F. schultzei* vs *M. sjostedti*	3.458	0.3998	8.65	2.67	4.24	31.75	s	
	Local	*M. sjostedti* vs *F. schultzei*	0.964	0.3067	-3.14	0.36	1.57	2.62	s	

(*): s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 4.16: Table of analysis of acceptance of *M.* sjostedti host by the different strains of *C. menes*: magnitude of host acceptance (a), and their comparison between strains of the parasitoid (b)

	Parameter: Strain of *C. menes*:		Estimate	SE	Z-value	Asymptotic 95% CI		Sig.*	Odd value	Score of acceptance
						Lower	Upper			
a)			(log odd)							
	Malaysian		-5.5013	0.8182	-6.72	-7.1	-3.9		0.00	low
	Indian1		-3.0101	0.2602	-11.57	-3.52	-2.5	s	0.05	low
	Indian2		-3.381	0.3713	-9.11	-4.11	-2.65	s	0.03	low
	Local		-1.0729	0.1599	-6.71	-1.39	-0.76	s	0.34	low
b)			(log odd ratio)							
Local	vs	Malaysian	4.4284	0.8336	5.31	2.79	6.06	s	83.80	
Local	vs	Indian1	1.9373	0.3054	6.34	1.34	2.54	s	6.94	
Local	vs	Indian2	2.3081	0.4043	5.71	1.52	3.1	s	10.06	
Indian1	vs	Malaysian	2.4911	0.8585	2.9	0.81	4.17	s	12.07	
Indian2	vs	Malaysian	2.1203	0.8985	2.36	0.36	3.88	s	8.33	
Indian1	vs	Indian2	0.3709	0.4534	0.82	-0.52	1.26	ns	1.45	

(*):
s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 4.17: Table of analysis of acceptance of the check host by the different strains of *C. menes*: magnitude of host acceptance (a), and their comparison between strains of the parasitoid (b)

	Parameter			Estimate	SE	Z-value	Asymptotic 95% CI		Sig.*	Odd	Score of
	Strains of *C. menes*:						Lower	Upper		value	acceptance
				(log odd)							
a)	Malaysian			-0.9464	0.1807	-5.24	-1.3	-0.59	s	0.39	low
	Indian1			-0.3594	0.1145	-3.14	-0.58	-0.13	s	0.70	low
	Indian2			0.077	0.1484	0.52	-0.21	0.37	ns	1.08	medium
	Local			-1.0729	0.1599	-6.71	-1.39	-0.76	s	0.34	low
b)				(log odd ratio)							
	Malaysian	vs	Local	0.1265	0.2413	0.52	-0.35	0.6	ns	1.13	
	Indian1	vs	Local	0.7135	0.1967	3.63	0.33	1.1	s	2.04	
	Indian2	vs	Local	1.1498	0.2181	5.27	0.72	1.58	s	3.16	
	Indian1	vs	Malaysian	0.587	0.214	2.74	0.17	1.01	s	1.80	
	Indian2	vs	Malaysian	1.0234	0.2338	4.38	0.57	1.48	s	2.78	
	Indian2	vs	Indian1	0.4363	0.1874	2.33	0.07	0.8	s	1.55	

(*):
s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 4.18: Table of analysis of acceptance of *F. schultzei* host by the local strain of *C. menes*: magnitude of host acceptance (a), and its comparison with the two Indian strains of *C. menes* (b)

	Parameter: Strains of *C. menes*:			Estimate	SE	Z-value	Asymptotic 95% CI		Sig.*	Odd value	Score of acceptance
							Lower	Upper			
				(log odd)							
a)	Local			-2.0369	0.2617	-7.78	-2.55	-1.52	s	0.13	low
				(log odd ratio)							
b)	Indian1	vs	Local	1.6775	0.2857	5.87	1.12	2.24	s	5.35	
	Indian2	vs	Local	2.1138	0.3009	7.03	1.52	2.7	s	8.28	

(*):
s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 4.19: Frequency of larvae encountered by some female wasps of the parasitoid, during the 30 minutes of searching time

Wasp #	Strain of *C. menes*					
	Indian1			Local		
	Host age (days)			Host age (days)		
	1	2	3	1	2	3
1	18	30	33	20	10	20
2	25	36	18	21	10	8
3	24	32	25	13	11	13
4	5	26	33	19	11	2
5	12	22	28	12	20	24
6	23	23	33	4	15	24
7	12	50	37	7	6	6
8	18	28	2	22	14	2
9	14	38	4	8	14	3
10	13	-	10	9	9	10
11	22	-	-	-	-	-
12	21	-	-	-	-	-

APPENDIX 5.1: Analysis of the model without the three-ways interaction, for the oviposition rate of the different strains of *C. menes*, in the different host species

Model: Multinomial Logit
Design: Constant + RESPONSE + RESPONSE*SPECIES + RESPONSE*STRAIN

a) **Goodness-of-fit Statistics**

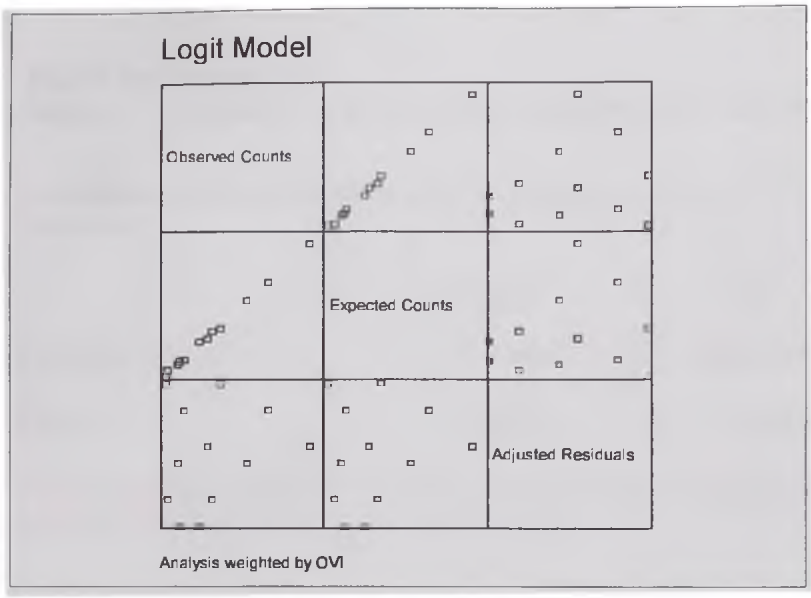
	Chi-Square	DF	Sig.
Likelihood Ratio	2,2045	2	0,3321
Pearson	2,4194	2	0,2983

b) **Table Information**

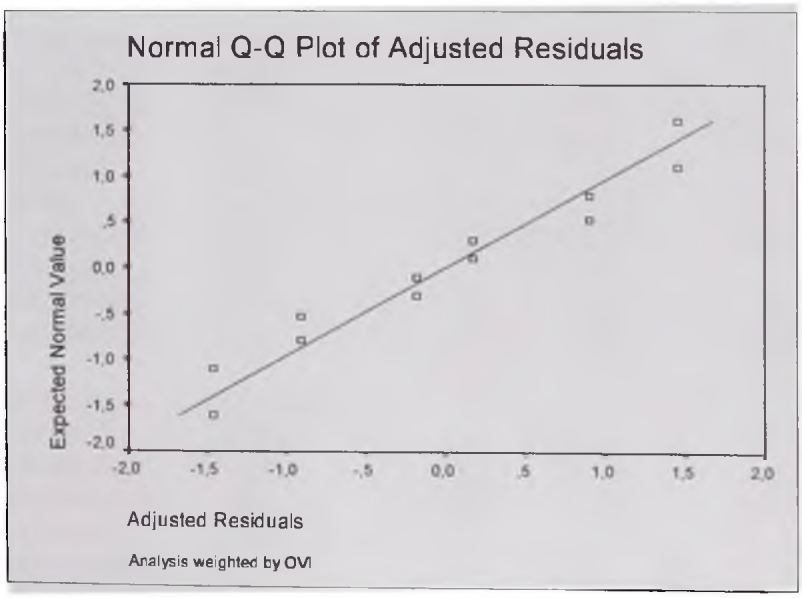
Factor	Value	Observed Count	Observed %	Expected Count	Expected %
STRAIN	Indian1				
SPECIES	*M. sjostedti*				
RESPONSE	yes	15	27.27	15.36	**27.94**
RESPONSE	no	40	72.73	39.64	72.06
SPECIES	*F. schultzei*				
RESPONSE	yes	129	63.24	128.64	**63.06**
RESPONSE	no	75	36.76	75.36	36.94
STRAIN	Indian2				
SPECIES	*M. sjostedti*				
RESPONSE	yes	7	25	8.68	**31**
RESPONSE	no	21	75	19.32	69
SPECIES	*F. schultzei*				
RESPONSE	yes	94	67.63	92.32	**66.42**
RESPONSE	no	45	32.37	46.68	33.58
STRAIN	Local				
SPECIES	*M. sjostedti*				
RESPONSE	yes	52	60.47	49.96	**58.09**
RESPONSE	no	34	39.53	36.04	41.91
SPECIES	*F. schultzei*				
RESPONSE	yes	16	76.19	18.04	**85.92**
RESPONSE	no	5	23.81	2.96	14.08

The bolded values are the estimated oviposition rate (in percent) of the parasitoid

c) Plots of the adjusted residuals for the model equation



d) The normal probability plots of the adjusted residuals



(It appears consistent with normality)

APPENDIX 5.2: Analysis of the model for the immature survival rate of the different strains of *C. menes*, on the different host species

Model: Multinomial Logit
Design: Constant + RESPONSE + RESPONSE*SPECIES + RESPONSE*STRAIN

a) **Goodness-of-fit Statistics** (for the model with only the two-ways interactions)

	Chi-Square	DF	Sig.
Likelihood Ratio	18.6094	2	9.00E-05*
Pearson	18.3346	2	0.0001*

(*)The observed significance levels are too low. The model with only two ways-interaction does not fit better than the full model.

b) **Table Information** (for the full model)

		Observed		Expected	
Factor	Value	Count	%	Count	%
SPECIES	*M. sjostedti*				
STRAIN	Indian1				
RESPONSE	Survivor	11.5	36.24	11.5	**36.24**
RESPONSE	Dead	20.23	63.76	20.23	63.76
STRAIN	Indian2				
RESPONSE	Survivor	2.5	6.76	2.5	**6.76**
RESPONSE	Dead	34.46	93.24	34.46	93.24
STRAIN	Local				
RESPONSE	Survivor	3.5	7.03	3.5	**7.03**
RESPONSE	Dead	46.3	92.97	46.3	92.97
SPECIES	*F. schultzei*				
STRAIN	Indian1				
RESPONSE	Survivor	16.5	20.04	16.5	**20.04**
RESPONSE	Dead	65.85	79.96	65.85	79.96
STRAIN	Indian2				
RESPONSE	Survivor	33.5	42.56	33.5	**42.56**
RESPONSE	Dead	45.21	57.44	45.21	57.44
STRAIN	Local				
RESPONSE	Survivor	0.5	50	0.5	50
RESPONSE	Dead	0.5	50	0.5	50

The bolded values are the estimated survival rate (in percent) of the immature parasitoid

APPENDIX 5.3: Table of analysis of the suitability of *M. sjostedti* and of *F. schultzei* to the two Indian strain of *C. menes*

Parameter				Estimate	SE	Z-value	Asymptotic 95% CI		Odd value	Sig.*
Strain of *C. menes*	Host species						Lower	Upper		
				(log odd ratio)						
Indian1	*M. sjostedti*	vs	*F. schultzei*	0.819	0.4606	1.78	-0.08	1.72	2.27	ns
Indian2	*M. sjostedti*	vs	*F. schultzei*	-2.3237	0.6935	-3.35	-3.68	-0.96	0.10	s

(*):
s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 5.4: Table of analysis of the suitability of *M. sjostedti* to the different strains of *C. menes*

Parameter: / Strain of *C. menes*:			Estimate	SE	Z-value	Asymptotic 95% CI		Odd value	Sig.*	Score of host suitability
						Lower	Upper			
a)			(log odd)							
Local			-2.5823	0.5544	-4.66	-3.67	-1.5	0.08	s	low
Indian1			-0.565	0.3693	-1.53	-1.29	0.16	0.57	ns	medium
Indian2			-2.6235	0.655	-4.01	-3.91	-1.34	0.07	s	low
b)			(log odd ratio)							
Indian1	vs	Local	2.0173	0.6661	3.03	0.71	3.32	7.52	s	
Indian2	vs	Local	-0.0412	0.8581	-0.05	-1.72	1.64	0.96	ns	
Indian1	vs	Indian2	2.0585	0.7519	2.74	0.58	3.53	7.83	s	

(*):
s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 5.5: Table of analysis of the suitability of the check hosts to the different strains of *C. menes*

Parameter: / Strain of *C. menes*:			Estimate	SE	Z-value	Asymptotic 95% CI Lower	Asymptotic 95% CI Upper	Sig.*	Odd value	Score of host suitability
a)			(log odd)							
Local			-2.5823	0.5544	-4.66	-3.67	-1.5	s	0.08	low
Indian1			-1.384	0.2753	-5.03	-1.92	-0.84	s	0.25	low
Indian2			-0.2998	0.228	-1.32	-0.75	0.15	ns	0.74	medium
b)			(log odd ratio)							
Indian1	vs	Local	1.1983	0.619	1.94	-0.01	2.41	ns	3.31	
Indian2	vs	Local	2.2825	0.5994	3.81	1.11	3.46	s	9.80	
Indian2	vs	Indian1	1.0842	0.3574	3.03	0.38	1.78	s	2.96	

(*):
s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"

APPENDIX 6.1: Results of the life and fertility tables of the different strains of *C. menes* on the different host species

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Strain of *C. menes* : Local
Host species : *M. sjostedti*
Number of wasps in the cohort : 20

Pivotal age	Age specific fertility	Age specific survival	Average daily production:	
(x)	(m_x)	(l_x)	# males	%females
22	0	0.06	0.05	0
23	0	0.06	0.7	0
24	0	0.06	0.58	0
25	0	0.05	0.44	0
26	0	0.05	0.27	0
27	0	0.04	0.33	0
28	0	0.02	0.75	0
29	0	0.02	0	0
30	0	0.02	0.17	0
31	0	0.02	0	0
32	0	0.01	0	0
33	0	0	0	0
34	0	0	0	0

Strain of *C. menes* : Indian1
Host species : *F. schultzei*
Number of wasps in the cohort : 14

Pivotal age	Age specific fertility	Age specific survival	Average daily production:	
(x)	(m_x)	(l_x)	# males	%females
23.7	2.57	0.2	3	46.15
24.7	3.86	0.2	3.86	50
25.7	5.43	0.2	5	52.05
26.7	3.29	0.2	5.07	39.32
27.7	2.85	0.19	3.23	46.84
28.7	2.42	0.17	3.67	39.73
29.7	3	0.14	3.8	44.12
30.7	0.13	0.11	2.88	4.17
31.7	0.57	0.1	3.71	13.33
32.7	0.2	0.07	3.6	5.26
33.7	0	0.06	4.75	0
34.7	0	0.04	0.33	0
35.7	0	0.03	1	0
36.7	0	0.03	0.5	0
37.7	0	0.03	0	0

Strain of *C. menes* : Indian1
Host species : *M. sjostedti*
Number of wasps in the cohort : 20

Pivotal age	Age specific fertility	Age specific survival	Average daily production:	
(x)	(m_x)	(l_x)	# males	%females
23.5	0	0.37	0.05	0
24.5	0	0.37	0	0
25.5	0.05	0.37	0	100
26.5	0	0.37	0	0
27.5	0	0.37	0	0
28.5	0	0.37	0	0
29.5	0	0.31	0	0
30.5	0	0.28	0	0
31.5	0.08	0.24	0	100
32.5	0	0.22	0	0
33.5	0	0.22	0	0
34.5	0	0.18	0	0
35.5	0	0.09	0	0
36.5	0	0.06	0	0
37.5	0	0.06	0	0
38.5	0	0.06	0	0
39.5	0	0.06	0	0
40.5	0	0.06	0	0
41.5	0	0.04	0	0
42.5	0	0.02	0	0
43.5	0	0.02	0	0

Strain of *C. menes* : Indian1
Host species : *F. schultzei*
Number of wasps in the cohort : 14

Pivotal age	Age specific fertility	Age specific survival	Average daily production:	
(x)	(m_x)	(l_x)	# males	%females
23.7	2.57	0.2	3	46.15
24.7	3.86	0.2	3.86	50
25.7	5.43	0.2	5	52.05
26.7	3.29	0.2	5.07	39.32
27.7	2.85	0.19	3.23	46.84
28.7	2.42	0.17	3.67	39.73
29.7	3	0.14	3.8	44.12
30.7	0.13	0.11	2.88	4.17
31.7	0.57	0.1	3.71	13.33
32.7	0.2	0.07	3.6	5.26
33.7	0	0.06	4.75	0

34.7	0	0.04	0.33	0
35.7	0	0.03	1	0
36.7	0	0.03	0.5	0
37.7	0	0.03	0	0

Strain of *C. menes* : Indian2
Host species : *F. schultzei*
Number of wasps in the cohort : 12

Pivotal age (x)	Age specific fertility (m_x)	Age specific survival (l_x)	Average daily production: # males	Average daily production: %females
19.7	5.08	0.42	6.33	44.53
20.7	9.83	0.42	3.42	74.21
21.7	7.33	0.42	4.5	61.97
22.7	5.75	0.42	5.5	51.11
23.7	3.5	0.42	3.25	51.85
24.7	2.67	0.42	4.67	36.36
25.7	3.1	0.35	6.9	31
26.7	0.3	0.35	4.2	6.67
27.7	0.13	0.28	8.88	1.39
28.7	0.17	0.21	6.83	2.38
29.7	0	0.17	4.4	0
30.7	0	0.07	3.5	0
31.7	0	0.04	0	0

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APPENDIX 6.2: Table of analysis of the population sex ratios for the two Indian strains of *C. menes* on the different host species: a) With all females in the cohort, and b) Without outliers females.

Parameter				Estimate	SE		Z-value	Asymptotic 95% CI		Odd value	Sig*.
Strain of *C. menes:*	Host species:	Strain of *C. menes:*	Host species:					Lower	Upper		
a)				log(female/male)						(#males to 1 female)	Ho: 1:1ratio.
Indian1	- *M. sjostedti*			0.5108	1.0328	**	0.49	-1.51	2.54	1.7	ns
Indian1	- *F. schultzei*			-0.3616	0.0734		-4.92	-0.51	-0.22	0.7	s
Indian2	- *F. schultzei*			-0.2693	0.0629		-4.28	-0.39	-0.15	0.8	s
b)				(log odd ratio)							Ho:equal sex ratios.
Indian1	- *M. sjostedti*	vs Indian1	- *F. schultzei*	0.8724	1.0354		0.84	-1.16	2.9	2.4	ns
Indian1	- *F. schultzei*	vs Indian2	- *F. schultzei*	-0.0923	0.0967		-0.95	-0.28	0.1	0.9	ns
Indian1	- *M. sjostedti*	vs Indian2	- *F. schultzei*	0.7801	1.0347		0.75	-1.25	2.81	2.2	ns

(*):
s = odd value significantly different from "1" at $\alpha = 0.05$ (after a loglinear model test)
ns = odd value not significantly different from "1"
(**): Sde is very large (> estimate), thus the value of the sex ratio cannot be estimated well from the data because of the small sample size