# ASPECTS OF THE BIOLOGY OF *ANAGRUS* SPP. (HYMENOPTERA: MYMARIDAE), WITH SPECIAL REFERENCE TO HOST-PARASITOID RELATIONSHIPS

BY

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## ABSTRACT

Several aspects of the biology of two new species of *Anagrus* (being described by Dr. I. Walker (in press)) were studied in the laboratory.

Populations of *Anagrus* spp. were established from field collection of parasitized overwintering eggs of *Cicadella viridis* (L.) (Homoptera: Cicadellidae). Two host species were used in the experiments, they were *C. viridis* (L.) and the Delphacid *Dicranotopis hamata* (Boheman).

The morphology of the adult stages of *Anagrus* is described and detailed observations were made on copulation, parthenogenesis and emergence. The development of the immature stages was followed and described.

Experiments were set up to compare the oviposition behaviour of the parasitoids on the two host species and the effect of these on the physiology, developmental period and reproductive capacity of the parasitoids was studied and compared. Ecological aspects of host parasitoid interactions were investigated. Experiments were set up to compare the extent of intraspecific competition between the larvae. The functional response was determined for the two species and studies were made on interference and interspecific competition.

TABLE OF CONTENTS

## GENERAL INTRODUCTION

The species of Mymaridae are of minute size, generally of 0.2-1.5 mm in length; they have exceptionally long antenna and the long, narrow wings are fringed with long hairs.

So far as known the larvae of all the members of the family are internal parasitoids of eggs of other insects, particularly the Homoptera, but also the Odonata, Heteroptera, Lepidoptera, Coleoptera, Neuroptera and Corrodentia (Clausen, 1940).

Important contributions towards the understanding of the particularly difficult systematics of the family were made by Debauche (1948) and Kryger (1950). Anneke and Doutt (1961) recorded 130 genera and about 1100 cosmopolitan species. Peck's (1963) catalogue includes a comprehensive bibliography on Mymaridae.

The possibility of using Mymaridae as agents of biological control have fostered several studies on the biology and ecology of these parasitoids. In an attempt to control the sugar cane leafhopper, *Perkinsiella saccaricida* Kirk., a number of Mymarids were introduced into Hawaii from Australia in 1904 (Perkins, 1905). By the end of 1905, the Mymarid *Paranagrus optabilis* Perkins was recovered from the field and it became abundant and widespread in 1907. The introduction in 1927 of the Mirid bug *Tytthus mundulus* (Bredd), predator of the leafhopper eggs, together with the effect of *P. optabilis*, brought the population of *P. saccharicida* under control (De Bach, 1974).

An account of the work done on a Mymarid parasitoid of the eucalyptus snout beetle *Gonipterus scutellatus* Gyll. in South Africa is given by Mossop (1929). The parasitoid *Anaphoidea nitens* Girault was introduced

from Australia in order to control the beetle. From 1926 to 1933, over half a million parasitoids were mass produced and released in hundreds of plantations. By 1936, complete control had occurred everywhere (Tooke, 1955). It is significant that it is the only case of complete biological control attributed to an egg parasitoid acting alone (De Bach, 1974).

In California, the leafhopper *Dikrella cruentata* (Gillette) breeds throughout the year in the leaves of wild *Rubus* spp. and its eggs are parasitised by *Anagrus epos* Girault. In the summer, *A. epos* has a numerical response to eggs of its alternative host, the grape leafhopper, *Erythroneura elegantula* Osborn, a serious pest of grapes. Doutt and Nakata (1973) showed that when the *Rubus* spp infested by *D. cruentata* were near a vineyard, the early dispersion of *A. epos* from the over-wintering *Rubus* sites into the vineyard produces a substantial reduction in the sizes of the first two broods of leafhoppers. This reduction is an important element in the pest management programs of vineyards in California and any practice disruptive to this particular host/parasitoid system should be avoided.

*Anaphes flavipes* (Foerster) was introduced into the United States from France in an attempt to control *Oulema melanopus* (L.) the cereal leaf beetle (Anderson and Paschke, 1968, 1969, 1970a & b), but it failed to achieve total control of the pest.

In order to evaluate the importance of *Anaphes nipponicus* Kuwayama against the rice leaf beetle, *Lema oryzae* Kuwayama, in Japan, some experiments on its liberation were conducted during the period 1931 to 1934, but the parasitoid failed to become established (Kuwayama, 1935).

Otake (1967, 1968, 1969, 1970a & b, 1976) studied the biology and ecology of *Anagrus* nr *flaveolus* Waterhouse, a parasitoid of the small

brown planthopper, *Laodelphax striatellus* (Fallen), an important pest of rice, vector of the rice stripe virus. Whilst the aquatic habit of the adults of *Anagrus fuscus* (Foerster), *Caraphractus cinctus* (Walker) and *Prestwichia aquatica* Lubock has attracted the attention of several authors (Henriksen, 1918-1919, 1922; Rimsky-Korsakov, 1916; Enock, 1898).

The most important recent work on the biology of Mymaridae has been that of Jackson (1958a and b, 1961, 1963, 1966, 1969) working on *C. cinctus* (Walker), a parasitoid of the eggs of the Dytiscidae.

In Europe, different species of the genus *Anagrus*, parasitoids of leafhopper eggs have been studied by Bakkendorf (1925, 1933-1934), Ganin (1869), Maillet (1960), Olmi (1970), Pierre (1906), Raatikainen (1967) and Witsack (1973), who published an extensive study on the biology and field ecology of *Anagrus* spp in East Germany.

Mymarids belonging to the genus *Anagrus* have been studied in England by Enock (1914), Hassan (1939), Ison (1959) and Mac Gill (1934). Whalley (1956, 1958, 1969) in North Wales studied the biology and ecology of *Anagrus* spp parasitising Homoptera associated with *Juncus*. Studies of the biology and population ecology of several species of leafhoppers have been carried out in Silwood Park, Berkshire, England and parasitism by *Anagrus* spp is reported by May (1971), Morcos (1953), Rothschild (1962, 1967) and Tay (1972).

Walker (in press) describes four new species of *Anagrus* bred from leafhopper eggs collected in Silwood Park. The present study, based on two of these species, aimed to gather more information on their general biology and on the host-parasitoid relationships, for as the above review shows, the bionomics of this family are not thoroughly understood. Furthermore particular attention was paid to the quantification of some

of the various parameters of their biology, (responses to host density, interference between adult parasitoid females, etc.) that have been shown in the studies of May, Hassell and others (May, 1976) to be of great significance in the dynamics of host-parasitoid relationships. Hitherto quantitative data has not been available for parasitoids as small as *Anagrus*.

A second theoretical problem on what it was hoped this study might throw some light is the competitive interactions between closely allied species.

# CHAPTER I

## BIOLOGY OF *ANAGRUS* SPP

### i. Introduction

In this chapter several aspects of the biology of *Anagrus* sp B and C were studied. In each section the relevant information already published is compared with the results obtained from the present study. In this way an attempt is made to present a comprehensive study of the biology of these interesting egg parasitoids as a background to the intensive studies on features of their dynamics and interactions.

### ii. Material and methods

#### 1. Material

##### a) Host material from the field

Stems of *Juncus effussus* L. bearing overwintering eggs of *Cicadella viridis* (L.) and *Miellerianella fairmairei* (Perris) were collected in the field from September until February.

##### b) Host oviposition sites

Ovipositing females lay their eggs through a slit into the pith of the *Juncus* stem leaving a characteristic scar on the surface of the stem.

Eggs are usually inserted at right angles to the stem main axis and show no internal sign of their presence. Occasionally *C. viridis* eggs are deposited just beneath the epidermis and form a distinct swelling.

*Cicadella viridis* lay rows of four to nineteen eggs with a mean of around ten. The female leaves a longitudinal scar varying between 4-12 mm. Oviposition scars are more frequent in the basal portion of the *Juncus* stem. A pale, white, waxy substance, which generally appears round the slit, renders the oviposition sites distinguishable. The egg rows of

*Muellerianella fairmairei* (Perris) are smaller than those of *C. viridis*, with five to twenty eggs in small rows, 1-3 mm in length. The tip of the eggs may be seen if the oviposition scar is carefully examined and they can be counted. The outside of the slit is partially covered by a hardened secretion produced by the female.

The majority of the oviposition sites are found within 25 cm of the ground, with *C. viridis* being most frequent in the lower portions, often covered by the leaf sheath, and the delphacids most frequent in the upper portion of the *Juncus* stem (Morcos, 1953; Whalley, 1956; Rothschild, 1967; Tay, 1972).

2. Methods

a) Collection and storage of hosts from the field

*Juncus* stems with *C. viridis* and *M. fairmairei* oviposition scars were collected periodically during the winter months.

Bundles of approximately a hundred thoroughly washed stems were wrapped with wet paper towel, placed in a tightly closed plastic bag and kept in the refrigerator at 1-3$^{o}$ C. In order to reduce the incidence of mould developing on the stems, the paper towel, which was renewed fortnightly, was wetted with a 0.8 gr. $L^{-1}$ solution of Nipasept.

b) Collection and storage of parasitoids from the field

Overwintering eggs of *C. viridis* were the main source of *Anagrus* sp B and *Anagrus* sp C; less frequently, overwintering eggs of *M. fairmairei* may yield a few *Anagrus* sp B larvae.

The parasitoid larvae can be seen through the chorion of the host egg, becoming bright orange in colour when they mature.

Eggs parasitised by the mymarids can be kept in the refrigerator for several weeks, the development of *Anagrus* larva is retarded accordingly.

c) Production of hosts in the laboratory

Cultures of *M. fairmairei* and *Dicranotopis hamata* (Boh.) were kept in a C.T. room at 20°C and 16 hours day conditions. Muslin-covered cages (50 x 40 x 40 cm) with four to five pots of *Holcus mollis* L. were used for mass culturing. Plastic flower pots 13 cm in diameter, containing oat seedlings or *Holcus* grass, and covered by a plastic cylinder were used as oviposition chambers.

*M. fairmairei* and *D. hamata* oviposit and bred abundantly in *H. mollis*. Oats seedlings can be used to advantage as host plant for *D. hamata* because the eggs are easily detected inside the leaf blade. A continuous supply of suitable hosts was secured by changing the grass every three days and replacing the dead adults in the oviposition chambers.

Provided the grass was continuously watered, host eggs remained suitable for several weeks for mass culture of the parasitoid, when kept in a 5°C cabinet.

d) Production of parasitoids in the laboratory

Newly emerged parasitoids were placed inside breeding cages with abundance of host eggs. The breeding cages used throughout the study were made out of glass tubes (9 x 3 cm) fitted with a bottom layer of 1.3% agar and a strip of moist filter paper. The tube was closed with a cotton stopper.

In order to prevent the development of mould, Nipasept was added to the simmering agar (0.5 gr. $L^{-1}$) and Nipasept solution was used to wet the filter paper.

*Juncus* stems from the field bearing overwintering *C. viridis* eggs were opened before use in order to make sure that the host eggs were not parasitized.

After the death of the ovipositing *Anagrus* females, host eggs were removed from the stem or piece of grass, and placed on the filter paper. A pair of fine tweezers were used to remove the eggs from the plant tissue and a fine cammel hair brush was used for further manipulation.

Careful handling and the correct amount of moisture in the filter paper are critical for a successful rearing of the parasitoid.

Parasitoid cultures were reared at 20°C unless otherwise stated.

e) Dissection and measurement of the parasitoids

Fresh specimens were dissected in 10% Ringer's solution using a very fine entomological pin mounted on a wooden handle.

Parasitized *C. viridis* eggs were cut open at one end and the contents squeezed out of the chorion. The *Anagrus* larvae was then transferred into a small tube with 70° alcohol or kept 24 hours in Dubosq-Brasil or Carnoy's fluid and then transferred to 70° alcohol.

A binocular dissecting microscope provided with substage illumination and 12.5 x, 50 x and 100 x magnification was used throughout the study. All the measurements were made with a x 10 micrometer eye piece fitted to a binocular dissecting microscope and 5 x and 10 x objective.

f) Preservation of parasitoid specimens

A record of the field collection and the laboratory experiments was entered in a log book. Each culture tube was successively numbered and these numbers used to identify the resultant progeny.

Adult specimens were preserved in 70° alcohol or mounted permanentely in polyvinyl-lactophenol.

g) Graphical methods

Drawings of specimens mounted in polyvinyl-lactophenol were made with the aid of a camera lucida attached to a binocular Wield microscope.

iii. Morphology of the adult

1. Introduction

The genus *Anagrus* was originally described by Halliday (1833); an english translation of the original latin description was published by Kryger (1950). A more detailed account of the morphology of the genus was given by Debauche (1948) and Anneke and Doutt (1961) included a key for the known genera.

Mac Gill (1934), in her paper on the biology of *A. atomus* Hal. shows a very schematic view of the male genitalia. Whilst in his monograph on belgian Mymaridae, Debauche (1948) gives a lateral view of the parameres. The validity of using the shape of the parameres is discussed by Whalley (1956) and Viggiani (1970) emphasized the taxanomic value of the male genitalia in *Anagrus* and gave a detailed account of its morphology.

In the original description of *Anagrus* sp B and sp C, Walker (in press) showed the parameres of both species.

An account of the morphology of the female reproductive organs of *Caraphractus cinctus* Walker is given by Jackson (1969) and King and Copland (1969) were concerned with the structure of the female reproductive system in the Mymaridae and its relationship with other families in Chalcidoidea.

Walker (in press) considered the length of the ovipositor as a good taxinomic character.

*Anagrus* sp B and sp C were described by Walker (in press) from adults which developed in overwintering *Cicadella viridis* (L.) eggs collected in Silwood Park.

The adults of both species are morphologically and physiologically affected by the host species (see Section III). Therefore, a detailed description of adults bred from overwintering *C. viridis* eggs (collected in Silwood Park) and reared in the laboratory from *Dicranotopis hamata* (Boh.) eggs is given below.

2. Description of the adult

*Anagrus* sp B

The colour of the females bred from *C. viridis* overwintering eggs is pale brown, but the antennal flagelum, head, pronotum and mesonotum, legs, dorsal portion of the abdomen and distal portion of the ovipositor sheath are a darker brown.

Dorsally, the head is almost rectangular, its width is 1.5 times its length, with prominent dark brown eyes. The ocelli are dark red-brown arranged in a obtuse-angle triangle.

The antennae of the female (Fig. 3) are filiform, 9-jointed, slightly shorter than the body, with a long scape, broader in the apical third; pedicel pear shaped about half as long as the scape. The third subsegment is very short, shorter than the pedicel. with the apical end almost oblique. The subsegments of the flagellum are subcylindrical, with the apical diameter wider than the basal. The subsegment IV has no sensory groove, subsegments V and VI have only one sensory groove, subsegments VII and VIII have two sensory grooves each and subsegment IX has five sensory grooves. The terminal subsegment or club of the antenna is ovoid, with the enlarged portion towards the apical end. The

subsegments IV to IX are covered with short setae and are brown coloured, darker than the glabrous subsegments I-III.

The mandibles are three-toothed, with the apical teeth brown and the two basal ones dark brown to black.

The thorax is long and narrow, almost parallel-sided, and twice as long as the head. Pronotum and mesonotum are brown coloured but darker than the posterior part of the thorax.

The forewing (Fig. 1) has an anterior margin which is almost rectilinear; the posterior margin is slightly concave, expanded beneath the marginal vein and at the apex, which is round. The wing membrane is light brown, with short bristles evenly distributed throughout the entire surface. The marginal setae increase in length towards the apical end, with the longer ones in subapical position and they are 1.5 times longer than the breadth of the wing.

The hind wings are narrower and more pedunculated than the forewing. The setae on the posterior margin are longer than the ones on the anterior margin. The wing shows only one vein, which reinforces the peduncule and bears three hook-shaped and three stout, conical setae at the apical end. These setae are attached to the posterior margin of the forewing, maintaining the wings coupled when in flight.

A five-toothed strigil present in the distal end of the anterior tibia, opposed to a row of fine setae forming a comb-like structure in the first tarsal joint is used to clean the antennae. The meso and metathoracic tibia have a simple apical spur. The tarsi are 4-jointed.

The abdomen is pale brown, 1.5 times longer than the thorax and 1.2

times longer than the ovipositor, slender and tapering toward the end (Fig. 4). The urotergites of the segments III to IX and the female genital plates are brown.

The ovipositor is well developed, slightly exserted and exceeds the length of the abdomen when not i use.

The male *Anagrus* sp B is approximately the same size as the female.

The pattern of coloration is basically the same but darker than that of the female.

Except for the genitalia, the form of the antenna is the most striking difference between the sexes.

The antennae of the male (Fig. 2) are filiform, 13-jointed, longer than the body. The scape and pedicel are similar in shape to those of the female only slightly shorter. The subsegment III is longer than the pedicel but shorter than IV with four sensory grooves. The subsegments IV-XII are subequal, cylindrical, with five sensory grooves on each. The basal part of the subsegments is tappered; the sensory groove runs lengthwise and occupies the distal 6/7 of the length of the subsegment. The prominent sensory grooves give the subsegment a ridged appearance. The last subsegment, bearing five sensory grooves, is similar in length to the previous ones, but tappered toward the apex, which is rounded.

The host has a marked effect on *Anagrus* sp B. When the species is bred from *D. hamata* (Boh.), the size and coloration is affected (see also Chapter III). In alcohol-preserved specimens, the coloration of the adults is lighter than specimens bred from *C. viridis* (L.) but the pattern of coloration is the same. When specimens bred from *D. hamata* are mounted in polyvinyl-lactophenol, the eyes and ocelli of the male are red-brown,

Figure 1. Forewing of *Anagrus* sp. B.

Figure 2. Antenna of the male of *Anagrus* sp. B., showing subsegments I to IV and XI to XIII.

Figure 3. Antenna of the female of *Anagrus* sp. B.

Figure 4. Ovipositor of *Anagrus* sp. B.

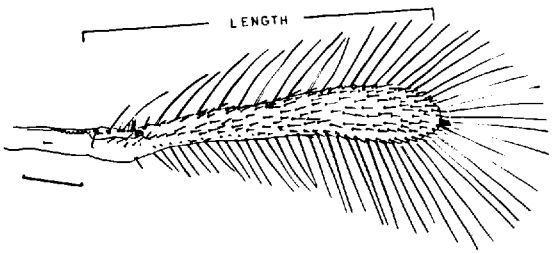
Figure 5. Ovipositor of *Anagrus* sp. C.

Figure 6. Antenna of the female of *Anagrus* sp. C.

Figure 7. Forewing of *Anagrus* sp. C.

Figure 8. Antenna of the male of *Anagrus* sp. B showing subsegments I to IV and XI to XIII.

Scale 100 μ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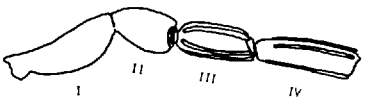
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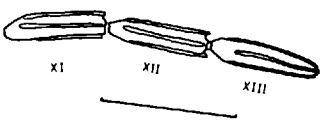
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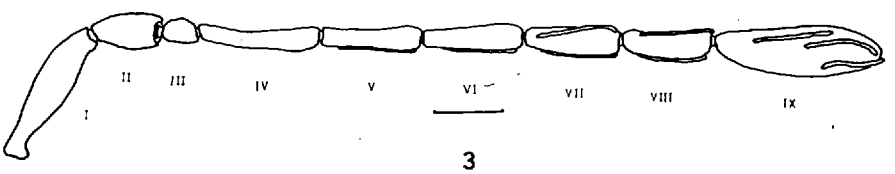
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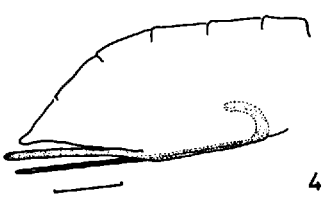

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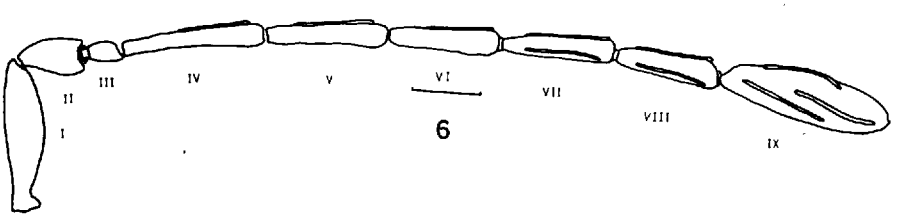
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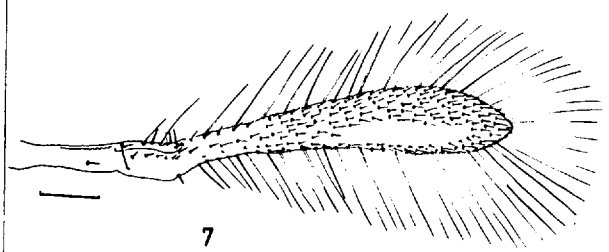

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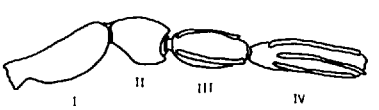
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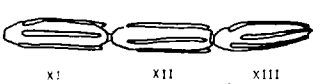
XI
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the overall coloration is paler and the areas which were pale brown, now look pale orange brown. The coloration of the female is now orange brown, with head, pronotum, mesonotum and antennal subsegments III-IX dark orange-brown.

Measurements of the length of the hind tibia, forewing, antenna and the number of sensory grooves on each antennal subsegment of male and female *Anagrus* sp B and sp C., and female ovipositor of both species bred from *D. hamata* are shown in Tables 1 and 2. A t-test was used to compare these measurements, the t-value is also given in the Tables.

*Anagrus* sp. C

When bred from *C. viridis* eggs, the adults of *Anagrus* sp. B and sp. C are very similar. The features in which sp. C differs from sp. B as described above are ennumerated below.

The coloration of *Anagrus* sp. C female is pale orange to yellow brown with some darker areas.

The ocelli are red brown, situated on a brown coloured sclerite, which contrasts with the paler vertex. The eyes are dark red brown.

The antenna of *Anagrus* sp. C females (Fig. 6) is longer than that of *Anagrus* sp. B. The length of subsegments II-IX is significantly different (p 0.05) but the length of subsegment I is similar in both species. The antennal subsegment IV has one sensory groove in *Anagrus* sp. C and none in *Anagrus* sp. B. This feature, together with the remarkable differences in size of the antennal subsegments IV-IX, can be used to advantage in the differentiation of both species.

The forewing has its disc only partially covered by bristles. A bare patch, which appeared constantly in our material, is illustrated in Fig. 7.

Table 1. Measurements of *Anagrus* sp. B and sp. C females bred from *D. hamata**.

| Length of | *Anagrus* sp. B (n = 10) | | | |
|---|---|---|---|---|
| | Mean | SD | Range | Number of sensory grooves |
| TIBIA III | 0.238 | 0.011 | 0.220 -0.260 | |
| FOREWING | 0.544 | 0.023 | 0.500 -0.560 | |
| OVIPOSITOR | 0.337 | 0.031 | 0.310 -0.400 | |
| Antennal subsegment | | | | |
| I | 0.086 | 0.004 | 0.080 -0.090 | - |
| II | 0.043 | 0.003 | 0.040 -0.045 | - |
| III | 0.032 | 0.002 | 0.030 -0.035 | - |
| IV | 0.072 | 0.003 | 0.070 -0.080 | - |
| V | 0.065 | 0.004 | 0.060 -0.070 | 1 |
| VI | 0.062 | 0.003 | 0.060 -0.065 | 1 |
| VII | 0.062 | 0.002 | 0.060 -0.065 | 2 |
| VIII | 0.061 | 0.002 | 0.060 -0.065 | 2 |
| IX | 0.111 | 0.002 | 0.110 -0.115 | 5 |
| TOTAL LENGTH | 0.594 | | | |

* measurements in mm.

Table 1. Continued

| Length of | *Anagrus* sp. C (n = 9) | | | | t-value | Probability p< |
|---|---|---|---|---|---|---|
| | Mean | SD | Range | Number of sensory grooves | | |
| TIBIA III | 0.253 | 0.007 | 0.240 −0.260 | | 3.484 | 0.001 |
| FOREWING | 0.583 | 0.017 | 0.570 −0.610 | | 4.268 | 0.001 |
| OVIPOSITOR | 0.508 | 0.019 | 0.480 −0.530 | | 14.010 | 0.001 |
| Antennal subsegment | | | | | | |
| I | 0.089 | 0.003 | 0.085 −0.090 | - | 2.092 | N.S. |
| II | 0.047 | 0.003 | 0.045 −0.050 | - | 3.137 | 0.05 |
| III | 0.028 | 0.003 | 0.025 −0.030 | - | 2.807 | 0.05 |
| IV | 0.090 | 0.003 | 0.085 −0.095 | 1 | 13.443 | 0.001 |
| V | 0.079 | 0.002 | 0.075 −0.080 | 1 | 9.877 | 0.001 |
| VI | 0.071 | 0.002 | 0.070 −0.075 | 1 | 8.222 | 0.001 |
| VII | 0.071 | 0.002 | 0.070 −0.075 | 2 | 9.400 | 0.001 |
| VIII | 0.068 | 0.003 | 0.065 −0.070 | 2 | 8.256 | 0.001 |
| IX | 0.118 | 0.003 | 0.115 −0.120 | 5 | 7.392 | 0.001 |
| TOTAL LENGTH | 0.661 | | | | | |

Table 2. Measurements of *Anagrus* sp. B and sp. C males bred from *D. hamata**.

| Length of | *Anagrus* sp. B (n = 10) | | | |
|---|---|---|---|---|
| | Mean | SD | Range | Number of sensory grooves |
| TIBIA III | 0.236 | 0.001 | 0.220 -0.260 | |
| FOREWING | 0.559 | 0.020 | 0.520 -0.600 | |
| Antennal subsegment | | | | |
| I | 0.070 | 0.003 | 0.070 -0.080 | - |
| II | 0.043 | 0.004 | 0.040 -0.050 | - |
| III | 0.052 | 0.003 | 0.040 -0.050 | 4 |
| IV | 0.069 | 0.002 | 0.065 -0.070 | 5 |
| V | 0.069 | 0.002 | 0.065 -0.070 | 5 |
| VI | 0.069 | 0.002 | 0.065 -0.070 | 5 |
| VII | 0.069 | 0.002 | 0.065 -0.070 | 5 |
| VIII | 0.069 | 0.002 | 0.065 -0.070 | 5 |
| IX | 0.068 | 0.003 | 0.060 -0.070 | 5 |
| X | 0.068 | 0.004 | 0.060 -0.075 | 5 |
| XI | 0.067 | 0.003 | 0.060 -0.070 | 5 |
| XII | 0.068 | 0.004 | 0.060 -0.070 | 5 |
| XIII | 0.074 | 0.004 | 0.070 -0.080 | 5 |
| TOTAL LENGTH | 0.855 | | | |

* measurements in mm.

Table 2. Continued

| Length of | *Anagrus* sp. C (n = 10) | | | | t-value | Probability p< |
|---|---|---|---|---|---|---|
| | Mean | SD | Range | Number of sensory grooves | | |
| TIBIA III | 0.256 | 0.007 | 0.240 -0.260 | | 4.629 | 0.001 |
| FOREWING | 0.595 | 0.013 | 0.580 -0.610 | | 4.674 | 0.001 |
| Antennal subsegment | | | | | | |
| I | 0.079 | 0.003 | 0.070 -0.080 | - | 5.657 | 0.001 |
| II | 0.041 | 0.002 | 0.040 -0.045 | - | 1.395 | N.S. |
| III | 0.050 | 0.002 | 0.045 -0.050 | 4 | 2.611 | 0.05 |
| IV | 0.076 | 0.004 | 0.070 -0.080 | 5 | 4.472 | 0.001 |
| V | 0.074 | 0.003 | 0.070 -0.080 | 5 | 4.160 | 0.001 |
| VI | 0.074 | 0.004 | 0.070 -0.080 | 5 | 3.536 | 0.01 |
| VII | 0.072 | 0.002 | 0.070 -0.075 | 5 | 2.464 | 0.05 |
| VIII | 0.071 | 0.002 | 0.070 -0.075 | 5 | 2.121 | 0.05 |
| IX | 0.071 | 0.002 | 0.070 -0.075 | 5 | 2.324 | 0.05 |
| X | 0.071 | 0.002 | 0.070 -0.075 | 5 | 2.450 | 0.05 |
| XI | 0.071 | 0.002 | 0.070 -0.075 | 5 | 2.458 | 0.05 |
| XII | 0.071 | 0.002 | 0.070 -0.075 | 5 | 2.449 | 0.05 |
| XIII | 0.071 | 0.002 | 0.070 -0.075 | 5 | 2.151 | 0.05 |
| TOTAL LENGTH | 0.892 | | | | | |

The length of the forewing of female *Anagrus* sp. C is significantly longer than that of *Anagrus* sp. B ($p<0.001$).

The metathoracic tibia of *Anagrus* sp. C is significantly longer than that of *Anagrus* sp. B ($p<0.01$).

The urotergites of segments III and IV, the distal end of the abdomen and the genital plates are pale brown.

The well developed ovipositor exceeds the tip of the abdomen by 1/5 of the ovipositor length and is 1.2 times longer than the abdomen (Fig. 5). The tip of the ovipositor sheath is pale brown to brown-coloured and darker than the basal portion.

*Anagrus* sp. C males are similar in size and pattern of coloration to the female. They are orange brown-coloured with the urotegites dark orange brown, giving the abdomen a slightly stripped appearance.

The antenna of *Anagrus* sp. C males is longer than that of *Anagrus* sp. B. The length of the antennal subsegments I and III to XIII of *Anagrus* sp. C are significantly different from those of *Anagrus* sp. B, with the exception of subsegment II, which length is similar in both species (Table 2). The distribution of the sensory grooves of the male antenna is similar in both species.

The forewing and metathoracic tibia of *Anagrus* sp. C is significantly longer than those of *Anagrus* sp. B ($p<0.001$).

The coloration of adults *Anagrus* sp. C bred from *D. hamata* is similar to those bred from *C. viridis*, but there are changes in size (Chapter III).

3. The male genitalia

The male genitalia of *Anagrus* sp. B and sp. C were studied.

When both species are bred from *D. hamata* eggs, (Fig. 9, 10, 12) the male genitalia were smaller than in specimens bred from *C. viridis* (Fig. 11, 13, 14).

The anterodorsal opening of the phalobase is subrectangular in both species. In *Anagrus* sp. B the size of the genitalia, excluding the aedeagus, is 1.5 times the length of the opening. Whilst in *Anagrus* sp. C the size of the genitalia, excluding the aedeagus, is twice the size of the opening.

The genitalia in *Anagrus* sp. B (Fig. 9-11) is shorter and broader than that of *Anagrus* sp. C (Fig. 12-14) and this broader appearance is enhanced by the outward bend of the arms of the parameres in sp. B. Laterally the margins of the arms of the parameres are almost parallel in *Anagrus* sp. C tappering slowly towards the apical end, in marked contrast with the faster tappering in sp. B.

Both species have crotchet-shaped parameres, with two subequal terminal sclerites ("digiti volsellare" of Viggiani, 1970) in *Anagrus* sp. B, and with basal terminal sclerite stouter than the apical one in sp. C.

4. The female genitalia

The ovipositor of *Anagrus* sp. B and sp. C bred from *C. viridis* are shown in Fig. 4 and 5. In both species the length of the ovipositor depends on the host species they were bred from (Chapter III).

When the parasitoids are bred from *D. hamata*, the ovipositor of *Anagrus* sp. C is significantly longer than that of *Anagrus* sp. B ($p<0.001$) (Table 1).

In the present study, the length of the ovipositor is used to differentiate both species and also as an estimate of the female size.

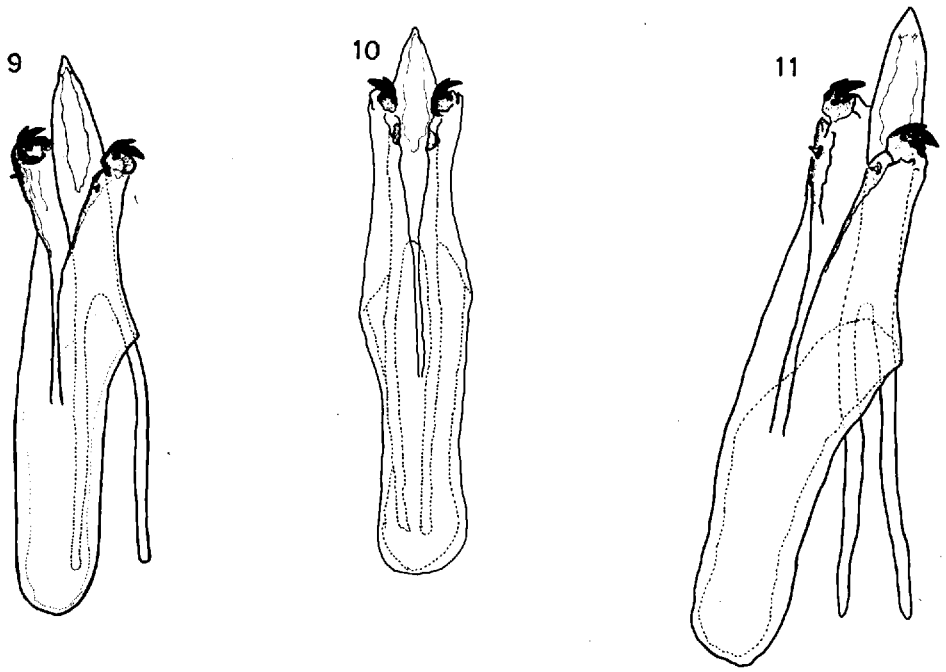
Figure 9 and 10. Male genitalia of *Anagrus* sp. B, bred from *D. hamata*.

Figure 11. Male genitalia of *Anagrus* sp. B, bred from *C. viridis*.

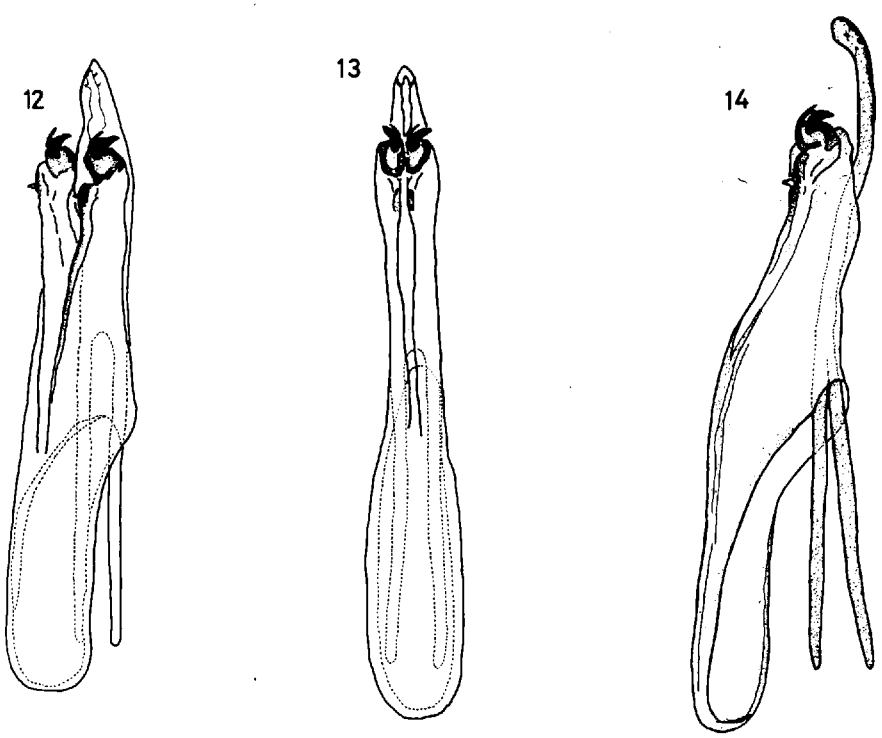
Figure 12. Male genitalia of *Anagrus* sp. C, bred from *D. hamata*.

Figure 13 and 14. Male genitalia of *Anagrus* sp. C, bred from *C. viridis*.

Scale 50 μ




50µ



iv. Biology of *Anagrus* spp. - Laboratory experiments

1. Emergence of the adult parasitoid

The emergence of the adult mymarids have been recorded by several authors, e.g. Mossop (1929) and Tooke (1955) for *Anaphoidea nitens* Girault; Saterthwait (1931) for *Anaphoidea calendra* Gahan; Kuwayama (1935) for *Anaphes nipponicus* Kuwayama; Jackson (1961) for *Caraphractus cinctus* Walker; Balduf (1928) for *Polynema striaticorne* Girault; Anderson and Paschke (1968, 1969, 1970[a][b]) for *Anaphes flavipes* (Foerster) and Ison (1959), Mac Gill (1934), May (1971), Morcos (1953), Olmi (1969), Pickles (1932), Raatikainen (1962, 1967), Rothschild (1962, 1967), Whalley (1969) and Witsack (1973) for several species of *Anagrus*.

The adult emerges by biting its way through the chorion of the host, leaving a round hole in the plant material in which the host egg was laid.

The distribution of hosts within the plant had a marked influence on emergence. When the host eggs were laid inside the leaf of spring cereals, e.g. *Javesella pellucida* (F.) in Denmark, the adults *A. atomus* made their way from the host egg onto the surface of the leaf; but, if the eggs were laid in the stem, the adults which burrowed towards the inside of the stem emerge into the cavity where they remained for some time before making there way through the stem wall and sometimes even through the leaf sheath, in order to escape to the surface (Raatikainen, 1962, 1967).

Sometimes the host eggs are enclosed in a capsule, like in *Gonipterus* spp., and the adults of *Anaphoidea nitens* had to chew their way through the tough capsule or they may utilize the hole beneath the capsule made by *Gonipterus* larvae that escaped parasitism (Tooke, 1955).

The emergence hole of the parasitoid is either at one or other end of the host egg (when there is one parasitoid in the egg) or in any position, but close to where the parasitoid head was (when there are many parasitoids in the egg as with *C. viridis*) (Whalley, 1969).

The emergence of *Anagrus* sp. B and C was studied in the laboratory and as many as four holes were found in a *C. viridis* in which five *Anagrus* sp. C had developed.

In the laboratory, Raatikainen (1962, 1967) and Witsack (1973) showed that emergence was definitely most frequent in the morning and no emergence was observed at night, while Witsack (1973) recorded a circadian rhythm of emergence with slight proterandry.

Under field conditions, 97.6% of the *Anaphes flavipes* adults emerged before 6 a.m. and males tended to emerge before the females (Anderson and Paschke, 1968, 1969, 1970a).

Seven *Anagrus* sp. C females were allowed to oviposit in *C. viridis* eggs, and the time of emergence of the resultant progeny was recorded. The removal of the host eggs from the *Juncus* stem made easy the recording of the pattern of emergence of the adults.

The results showed that 98% of the emergence took place before 12 hr and no emergences were recorded between 18:00 hr to 3:00 hr. Males tended to emerge before the females (Fig. 15 and Appendix, Table 1).

Jackson (1961) reported that when both sexes of *C. cinctus* were present in an egg of *Agabus*, it was the male that cut the emergence hole, and if two or more males were present they may work together to enlarge the same hole. This is not the case with *Anagrus* sp. B and *Anagrus* sp. C where each individual bores its own hole, unless there are several para-

sitoids and some may use a hole already open by another adult.

In *Anaphes nipponicus* Kuwayama, the emergence takes place in the host egg and the newly emerged adult remains in it for a day. Then the adult makes a round hole and goes away. The time of escaping is restricted to early morning, 76.6% of the adults emerging between 24:00 and 5:00 hr (Kuwayama, 1935).

Movement within the host egg 24 hours prior to emergence was recorded in *Anagrus* sp. B and *Anagrus* sp. C but never to the extent reported by Kuwayama (1935). The adults freed the antennae and legs but the body never changed position within the host egg.

The newly emerged adults are very active, moving rapidly and they were seen drinking droplets of moisture condensed on the surface of the stems. As soon as the adult leaves the host egg, it starts to walk around, stopping to clean the wings using the metathoracic legs and the antennae with the strigil on the prothoracic legs (May, 1971).

The meconium is shed after emergence.

The adults will jump backwards when disturbed and even feigned death, recovering quickly after a while. They have been observed flying in the laboratory, when about to fly, they will raise their wings over the body and spring into the air.

2. Copulation

Copulation has been observed in the Mymaridae by several authors including Anderson and Paschke (1968, 1969), Bakkendorf (1933-1934), Jackson (1958, 1961, 1966), Mossop (1929), Saterthwait (1931), Tooke (1955), and Enock (1898), Henriksen (1922) and Rimsky-Korsakov

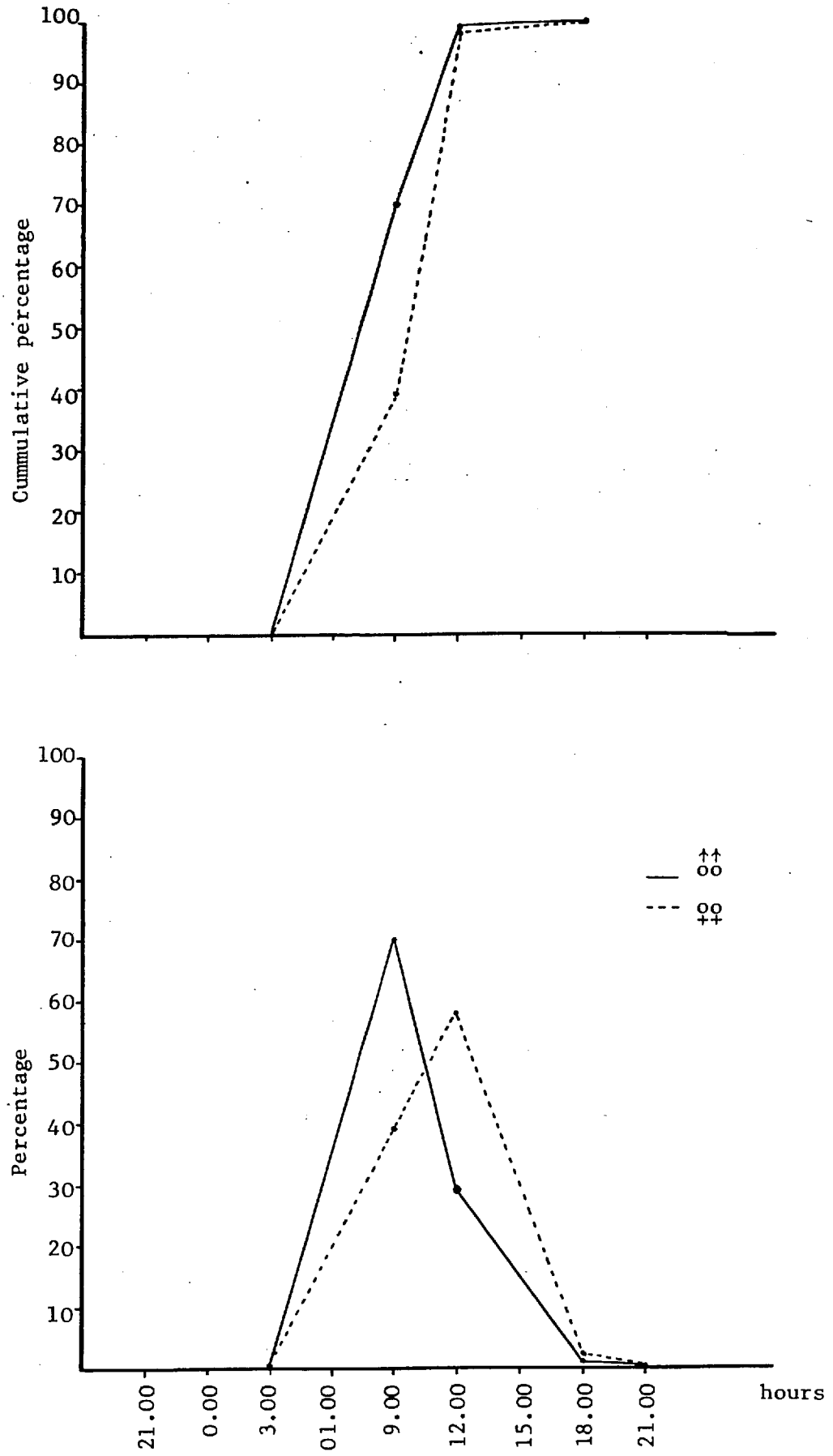



Figure 15. Pattern of emergence of adult *Anagrus* sp. C from *C. viridis*.

(in Clausen, 1940) recorded it in the aquatic species *Prestwichia aquatica* (Lubb.).

Records of copulation in *Anagrus* spp. are more abundant in the literature (Bakkendorf (1925), Ison (1959), Maillet (1960), Raatikainen (1967), Rothschild (1962, 1967) and Witsack (1973)).

Walker (in press) observed copulation in laboratory reared specimens of *Anagrus* sp. Y attacking eggs of various delphacids in *Holcus* grass, *Anagrus* sp. A parasitising *Stenocranus minutus* (Fab.) (Hom.:Delphacidae) and *Anagrus* sp. B and C reared from *C. viridis* eggs. She confirmed the observations of Witsack (1973) on the copulation behaviour of *A. incarnatus* Hal. parasitising the delphacids *Anakelisia fasciata* (Kirsch) and *S. minutus*

Enock (1898) watched the mating of *P. aquatica* in the eggs of the Dytiscidae in which they had developed and prior to the emergence of any of the individuals of the group. Rimsky-Korsakov (in Clausen, 1940) stated that one male may mate with all the females present in the host egg. Henriksen (1922) however, was unable to verify this habit and saw no indication of mating activity, for all the individuals remained quiescent until one had made an emergence hole, whereupon they escaped one by one.

The males tend to emerge first and wait upon the host eggs for the females to come out and then mate with one female after another (Jackson, 1961, 1966).

Adults were capable of copulation immediately after emergence (Tooke, 1955; Bakkendorf, 1925; Raatikainen, 1967; Rothschild, 1962, 1967; and Witsack, 1973) but Anderson and Paschke (1968) failed to observe

mating sooner than 45 min. after emergence.

Copulation was observed in adults of *Anagrus* sp. B and sp. C reared in the laboratory from *C. viridis* eggs.

The males, which usually emerged first (Fig. 15) remained in the vicinity of the egg waiting for another imago to emerge. They do this even when only males are present in the egg.

The reaction to movement within the host eggs is instantaneous and several males may cluster on top of the egg from which an adult is about to emerge. The male or males will mate with the female as soon as it emerged, but if a male emerges, the male pursues the newly emerged male until they lose interest in each other. This male homosexual behaviour has been recorded by Jackson (1961) and Walker (in press).

When the males are within range of a virgin female, they show a very definite behaviour. They raise their wings perpendicularly to their body and start moving quickly towards the female with the tip of the abdomen bent forwards and the wings vibrating continuously with very fast, short strokes. The virgin female willing to copulate, stops her movement and remains motionless. The male makes contact with the female, walks forward with the ventral surface of its abdomen brought forwards, facing upwards and clings to the female's wings and body with the first pair of legs. The male then slides under the female until the male's genitalia reaches the female's genital opening situated at the base of the abdomen and copulation takes place. Both partners remain immobile during copulation until the female walks away.

Balduf (1928) observed the copulation behaviour of *Polynema striaticorne* and suggested that the long antennae of the male served to stroke the female's head during copulation, but in both species of *Anagrus*

the male antennae were held straight and no stroking movements were noticed.

The males of *P. striaticorne* are strongly aggressive and Balduf (1928) reported that three individuals made simultaneous efforts to copulate with a single female, this probably being a common phenomenon in view of the numerical predominance of males over females in this species.

Anderson and Paschke (1968) observed as many as six males of *Anaphes flavipes* (Foerster) attempting to copulate with the same female.

In the laboratory, *Anagrus* sp. B and sp. C displayed this behaviour. In one occasion, fourteen *Anagrus* sp. C males were recorded attempting to copulate with a female that was already engaged in copulation with another male. The males formed a cluster on top of the copulating pair but all activity ceased instantly when the female walked away.

Copulation was recorded to last from 15-20 sec. in *A. incarnatus* Hal. (Rothschild, 1962, 1967) and up to 2 min. in *Anaphes flavipes* (Anderson and Paschke, 1968). Balduf (1928) recorded one pair of *P. striaticorne* who remained in copula for 5 minutes. A mean copulation time of 35.6 sec. (range 17-47 sec.; n = 7) was estimated by Witsack (1973) for adults of *A. incarnatus* emerged from *Anakelisia fasciata*.

In the laboratory the copulation time of 175 females of *Anagrus* sp. C was measured and the sex of the progeny was noted. For females producing females in their progeny, the shortest copulation time recorded was 24 sec. and the longest was 2 min. 9 sec. The mean was estimated as 63 sec. (SD = 26; n = 175).

The copulation time for 20 *Anagrus* sp. B females was also recorded and the mean was estimated as 1 min. 36 sec. (SD = 46; n = 20). The

shortest copulation time was 40 sec. and the longest was 2 min. 59 sec. in the case of females producing females among their progenies.

A single mating is sufficient to allow fertilized eggs to be laid throughout the life of the female, but occasionally a double mating is observed; 10 out of 175 in *Anagrus* sp. C but none in *Anagrus* sp. B. The double matings in *Anagrus* sp. C occurred when a female failed to move away quickly from the male and the same male, or occasionally a different one, succeeded in mounting the female again.

Tooke (1955) observed that a single *Anaphoidea nitens* male could copulate with several females during its lifetime, whilst females could mate with several different males.

No attempt was made to determine the mating frequency of both species of *Anagrus*. However, Anderson and Paschke (1969) recorded a mean of 3.5 times (range 0-7) for 13 males of *Anaphes flavipes* and said that differences in size of the male and consequently parasitoid vigor may account for much of the variation showed by these observations.

Walker (in press) noted that newly emerged females of *Anagrus* sp. A, sp. B, sp. C and sp. Y were readily mated by males of the same species but she failed to record pairings between sexes of different species.

3. Parthenogenesis

In Hymenoptera, females are generally produced from fertilised eggs and are diploid, whilst males develop from unfertilised eggs (arrhenotokous parthenogenesis), and are haploid (Askew, 1971). In Mymaridae, beside species with arrhenotokous parthenogenesis, there are also species where males are exceedingly rare or absent altogether and females develop parthenogenetically.

Arrhenotokous parthenogenesis was reported by Anderson and Paschke (1968, 1969) in *Anaphes flavipes* (Förster); Stoner and Surber (1969) in *Anaphes ovijentatus* (Crosby and Leonard); Mossop (1929) in Patasson (*Anaphoidea*) *nitens* (Gir.) and Jackson (1966) in *Caraphractus cinctus* Walker; and Enock (1914), Otake (1969), Raatikainen (1967), Tay (1972), Whalley (1969) and Witsack (1973) for several species of *Anagrus*.

All the species of *Alaptus* studied by New (1969) exhibit parthenogenesis. Males of *A. richardsi* Hinks were unknown, and this species appears to be thelytokous; the bisexual species examined (*A. pallidicornis* Foerster; *A. fusculus* Haliday in Walker, and *A. minimus* Hal.) are all amphitokous.

Clausen (1940) said that unisexual reproduction is the normal habit of *Anagrus atomus* Hal., *Anagrus frequens* Perkins, *Paranagrus optabilis* Perkins, *P. perforator* Perkins and *Polynema euchariformis* Hal. and males have been found occasionally, however, in each of these species with exception of the last. Mac Gill (1934) showed that the female of *Anagrus atomus* can reproduce parthenogenetically at any rate for the greater part of the year. For two years she failed to obtain males from the material collected and though in 1933 three male insects were bred from leafhoppers, none of these were seen to copulate.

Walker (in press) observed that unfertilised females produced only males in *Anagrus* sp. A, sp. B and sp. C, but in *Anagrus* sp. D reproduction was at least in part parthenogenetic, producing only females and few males, while *Anagrus* sp. E was said to have reproduced predominantly - if not entirely - parthenogenetically, and the occurrence of males in nature is doubtful.

Jackson (1966) observed that unmated females lay readily, even about an hour after emergence.

Several unmated *Anagrus* sp. B and sp. C females were allowed to oviposit and in all cases the progeny obtained were males. This technique was used to maintain a continuous supply of males for the copulation test.

4. Characteristics of the progeny produced by fertilized and virgin females

In many hymenopterous species, copulation is a prerequisite of normal oviposition, but there are species that oviposit readily before mating.

In *Trichogramma*, *Microbracon* and *Macrocentrus* females may be less fecund after mating than before (Flanders, 1946) and Lund (1938) found this to be the case in *Trichogramma evanescens* West.

Arrhenotokous parthenogenesis was reported in Mymaridae by several authors (see page 38) and Otake (1969) found that although there was a wide variation in fecundity, the difference between parthenogenetic and gametogenetic reproduction was not significant. Accordingly an experiment was set up to assess the effect of copulation on the size and quality of the progeny of virgin and fertilised females.

a) Material and methods

Parasitised *C. viridis* eggs containing three female pupae of *Anagrus* sp. C were selected and placed individually in breeding cages until the emergence of the adults. When all three females in the host emerged, a female was allowed to copulate, another was kept virgin and the third female was dissected and the number of eggs present in the ovary was

recorded. Copulation time was also recorded for each mated female (Appendix Table 2).

Twenty four pairs of females, treated as described, were allowed to lay in twenty *C. viridis* (L.) eggs which were changed daily until the death of each female. The females were then dissected and the number of eggs left in the ovaries was recorded. The experiment started at 12 noon and the host eggs were changed at the same time each day. The number of days the female was seen alive was used as a measure of longevity. Number of early second instar larva present in the host gave an estimate of number of eggs oviposited and the presence of female pupae in the progeny showed that the mated females were impregnated.

All the mated females produced male and female progeny but only males were produced from virgin females.

The results are shown in Appendix Table 2.

The mated females oviposited an average of 45.21 eggs (SD = 22.683; n = 24) and the virgin females oviposited an average of 33.25 eggs (SD = 21.698; n = 24) (see Table 3).

A paired t-test showed that the difference between the size of the progeny of mated and virgin females was significant ($p < 0.05$).

5. Fertility and fecundity

Fertility is the number of viable eggs laid by a female. Fecundity is the measure of the total egg production. In those insects where all the eggs are mature on emergence the total potential fecundity may be estimated by examining the ovaries (Southwood, 1966).

Lacking extensive data on actual fecundity of ichneumonids, ovariole

numbers is the best indicator of egg production (Price, 1973). In both Ichneumonidae and Tachinidae (Diptera), Price (1974) showed that fecundity is closely correlated with the ovariole number ($r^2 = 0.97$).

According to King and Copland (1969), the Mymarids have a polytrophic ovariole and in *Caraphractus cinctus* Jackson (1969) found that this polytrophic mature was only evident by studying the ovarian development in the early pupal stage. The total number of ovarioles depended upon the size of the insect and each ovariole contained from two to three eggs (Jackson, 1966).

In a newly emerged individual each ovariole contains a mature egg and very few immature eggs (King and Copland, 1969). This type of ovigenesis, termed proovigenesis by Flanders (1950), ensures the production of a large number of eggs during the short life of the female (Jackson, 1969; King and Copland, 1969).

Bakkendorf (1925) squeezed *A. incarnatus* females under water and counted 30 eggs in a female emerged from homopteroid eggs in *Cirsium oleraceum* L., and about 50 eggs in a female collected in the field. The same test was used by Stoner and Surber (1969) to assess the number of eggs in *Anaphes ovijentatus* (Crosby and Leonard) with females of varied age. A mean of 47.7 eggs/female was estimated (n = 57, s = 10.6). When only newly emerged females were used, the results of three replicates were more consistent 48.4 (n = 50; s = 5.7), 48.5 (n = 81, s = 5.8) and 49.2 (n = 100, s = 5.9) eggs/female respectively.

Kuwayama (1935) reported that dissected *Anaphes nipponicus* Kuwayama females had a mean of 23.6 eggs/female (n = 33, range 4-51) and concluded that a large female has more eggs.

The fecundity of *C. cinctus* was estimated by Jackson (1961) as the number of eggs oviposited plus the eggs left in the ovaries. Two females were dissected after oviposition and a total of 144 and 150 eggs each was recorded.

Several virgin *Anagrus* sp. B and sp. C females, bred out *C. viridis* and *D. hamata*, were dissected during the present study and the number of eggs present in the ovaries was recorded (see Chapter III). In both species the fan-shaped ovaries were composed of a variable number of ovarioles, each of them containing one mature egg.

Using the data shown in Appendix Table 2, the fecundity of *Anagrus* sp. C was estimated. The values are shown in Table 3.

The fecundity of mated and virgin females is given by the number of eggs oviposited by the female plus the number of eggs left in the ovaries.

A paired "t" test showed that the estimated fecundity of mated and virgin females do not differ significantly.

When fecundity was estimated by counting the eggs in the ovaries of newly emerged virgin females, and compared with the estimated fecundity of mated and virgin females respectively, a paired "t" showed that these values differ significantly ($p<0.05$).

Mortality in the early stages of development account for the difference.

Therefore, fecundity is best estimated by dissecting newly emerged virgin females.

A wide range of fertility has been reported for the Mymaridae by several authors. Jackson (1958b, 1961) showed that the large females of

Table 3. Fecundity and fertility of *Anagrus* sp. C females.

| Females were | FECUNDITY | | FERTILITY | |
|---|---|---|---|---|
| | Mean number of eggs | SD | Mean number of eggs | SD |
| mated | 65.9 | 9.78 | 45.2 | 22.68 |
| virgin | 64.8 | 10.01 | 33.3 | 21.70 |
| dissected | 71.3 | 7.28 | | |

*C. cinctus* were capable of laying over 100 eggs whilst *Anaphoidea nitens* laid an average of 25.3 eggs (n = 8, range 13-36) in 10 egg-capsules of the host, *Gonipterus scutellatus* Gyll (Tooke, 1955).

Anderson and Paschke (1968, 1969, 1970a) estimated the fertility of *Anaphes flavipes* (Förster) parasitising eggs of the beetle *Oulema melanopus* (L.) as the number of *Oulema* eggs capable of being parasitised by a single parasitoid and as the actual number of *Anaphes* ova deposited per host egg. The average number of eggs parasitised per female was 11.9 (SD = 1.9; n = 777) and the average number of parasites produced by these females was 19 (SD = 3.1) (Anderson and Paschke, 1970$^{a}_{b}$).

New (1969) showed that *Alaptus pallidicornis* Foerster females, parasitising three species of psocids, laid an average of 56, 61 and 62 eggs.

Three females *A. atomus* produced progeny varying in numbers between 28 to 42 (Raatikainen, 1972) and in *Anagrus* nr. *flaveolus* Waterhouse, Otake (1969) reported an average fertility of 22.9 individuals in the progeny (range 0-38). Tay (1972) carried out an absolute estimate of the fertility of *A. atomus*. A pair of newly emerged parasitoids were allowed to parasitise 20 *C. viridis* eggs, which were dissected after a week and the larvae counted. The mean number of eggs laid per female was 29.95 (SD = 1.24; n = 20, range 14-36). It has to be noted that this species is considered by Walker (in press) as similar to her *Anagrus* sp. C.

The fertility values for mated and virgin *Anagrus* sp. C females, shown in Table 1, were already discussed (page 27-28).

The host species from which the adult female had emerged and the number of parasitoids developing in the host, had a marked effect on the fecundity and fertility of the parasitoid (see Chapter III).

6. Oviposition

In Mymaridae, the females appear to be fully mature as soon as they emerge from the host and if suitable eggs are available oviposition begin almost immediately.

Oviposition was observed as soon as one hour after emergence (Anderson and Paschke, 1969; Jackson, 1966; Mac Gill, 1934; New, 1969; Witsack, 1973) and was most active during the first two days of the female's life (Mossop, 1928; Raatikainen, 1967).

One *Anagrus* nr. *flaveolus* Waterhouse female was able to lay as many as 28 eggs in a 24 hour period but those that lived longer, even up to 7-8 days, laid few extra eggs and ceased reproduction after 2-3 days (Otake, 1969). Jackson (1966) reported a female *C. cinctus* which laid 68 eggs in 8 hours.

An estimate of the number of eggs oviposited daily by mated and virgin *Anagrus* sp. C females and the longevity of each female - expressed as number of days the female was seen alive - is shown in Appendix Table 2.

The daily rate of oviposition of each group of females, expressed as percentage of the total number of eggs laid by all the females, is shown in Fig. 16 together with the data for female survival.

During the first 48 hours all the mated and virgin females survived and were capable of laying 94 and 85% of their total number of eggs. In the next 24 hrs, the female population was reduced by almost 50% and a few more eggs were laid.

In another experiment, four mated and five virgin *Anagrus* sp. C females were allowed to lay in twenty *C. viridis* eggs. The experiment

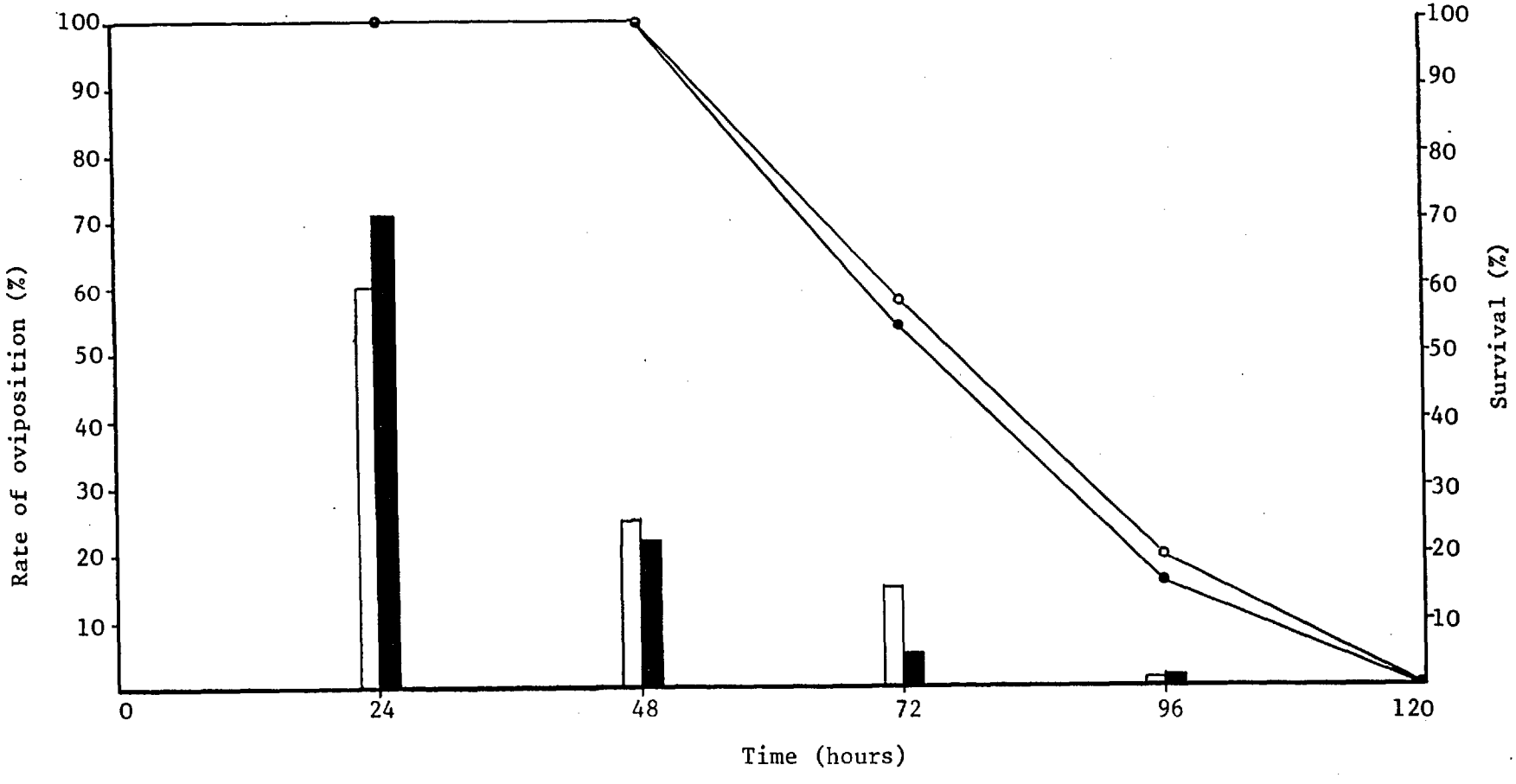



Figure 16. Rate of oviposition and survival of virgin (□) and mated (■) *Anagrus* sp. C females.

started at 12 noon and the host eggs were changed every six hours until the death of the female. The number of eggs laid was recorded (Appendix Table 3) and is shown in Fig. 17. The newly emerged females were 0-6 hours old when the experiment started, so it can be said that mated and virgin females laid 64 and 62% of their eggs between 6-12 hours after emergence.

7. Development of the immature stages

a) The egg stage

There is little variation in egg form within the family (Clausen, 1940).

The main body of the egg is ellipsoidal, ovoid or spindle-shaped, with a slender tapering peduncule ranging in length from one-tenth of the egg body in *Anaphoidea nitens* (Clark, 1941; Tooke, 1955), *Caraphractus cinctus* (Jackson, 1961), *Anaphes nipponicus* (Kuwayama, 1935) and *Anaphes flavipes* (Anderson and Paschke, 1969) to equal its length in *Polynema striaticorne* (Balduf, 1928).

The ovarian eggs of several species of *Anagrus* were described by Bakkendorf (1925), Dumbleton (1934), Ison (1959), Mac Gill (1934), May (1971), Tay (1972) and Witsack (1973).

A very comprehensive study of the egg and larval morphology of *Polynema* sp. was reported by Ganin (1869) but was stated by Bakkendorf (1925) to be *Anagrus*, probably *A. incarnatus* Hal., though Henriksen (1919) believed it to be *A. subfuscus* Foerster.

The ovarian egg is stalked, the body being elongate-ovoid to ovoid, varying in length from 0.06 mm in *A. atomus* (Mac Gill, 1934) to 0.3 to 0.4 mm in *A. incarnatus* (May, 1972) and the peduncule about one-third to one-half the total length.

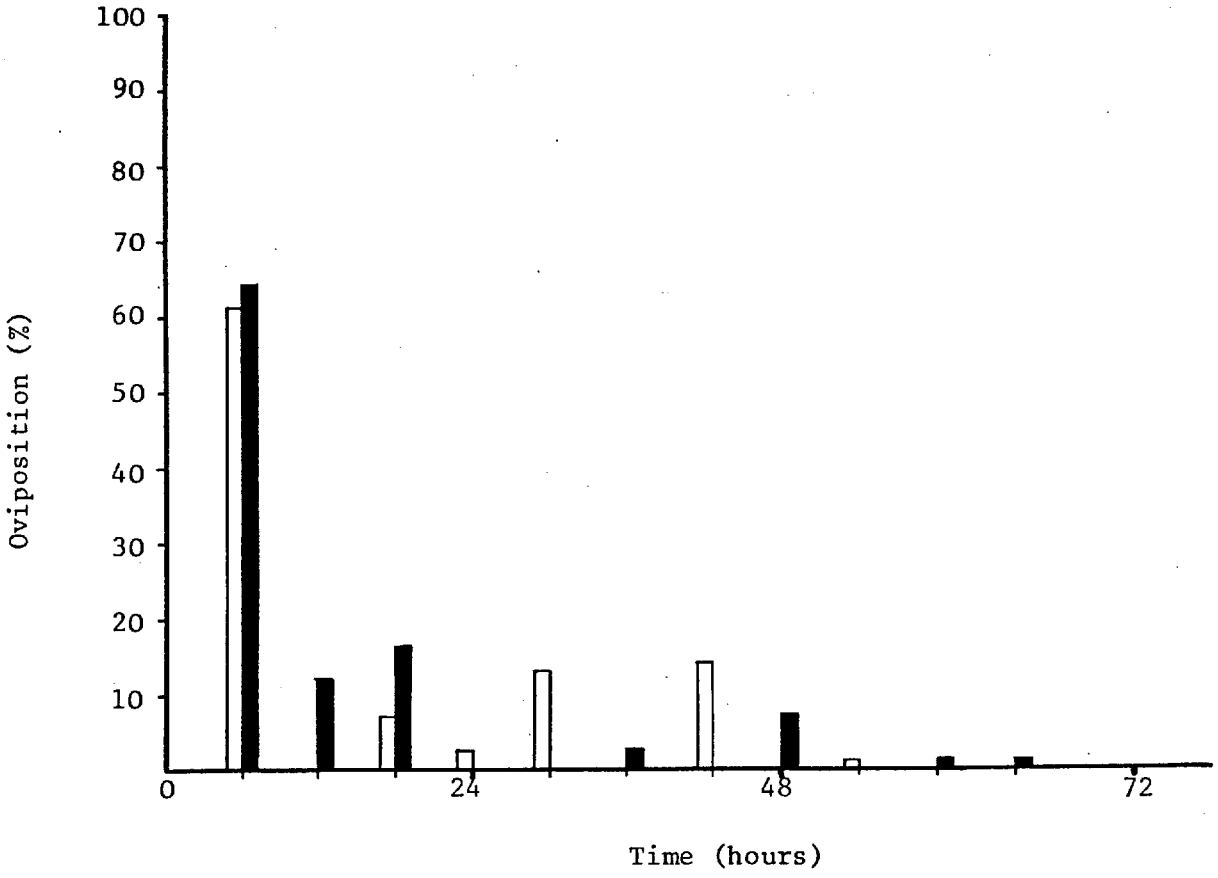



Figure 17. Oviposition of virgin (□) and mated (■) *Anagrus* sp. C females.

Figures 18 and 19 shows the ovarian egg of *Anagrus* sp. B and Fig. 20 that of *Anagrus* sp. C.

Several *Anagrus* sp. B and sp. C ovarian eggs were measured and the results are shown in Tables 5 and 6.

It was noticed that the average length is the same for both species but *Anagrus* sp. B eggs are significantly wider than *Anagrus* sp. C ($p<0.001$) (Fig. 19 and 20).

Unfortunately, the width of the ovarian egg is not reliable as a criteria to differentiate both species. A few hours after the death of the female, the ovarian eggs were seen to change in volume and consequently, changes in width were frequently detected.

Inside the ovarioles the eggs are always oriented with the pedicel end upwards.

Laying has been shown to alter the shape of the egg. Satterthwait (1931) reported a reduction in size in *Anaphoidea calendra* and, with *Anaphes flavipes*, eggs become narrow and longer (Anderson and Paschke, 1969). Jackson (1969) confirmed this with *Caraphractus cinctus*, the distortion being noted for up to 10 hours after oviposition.

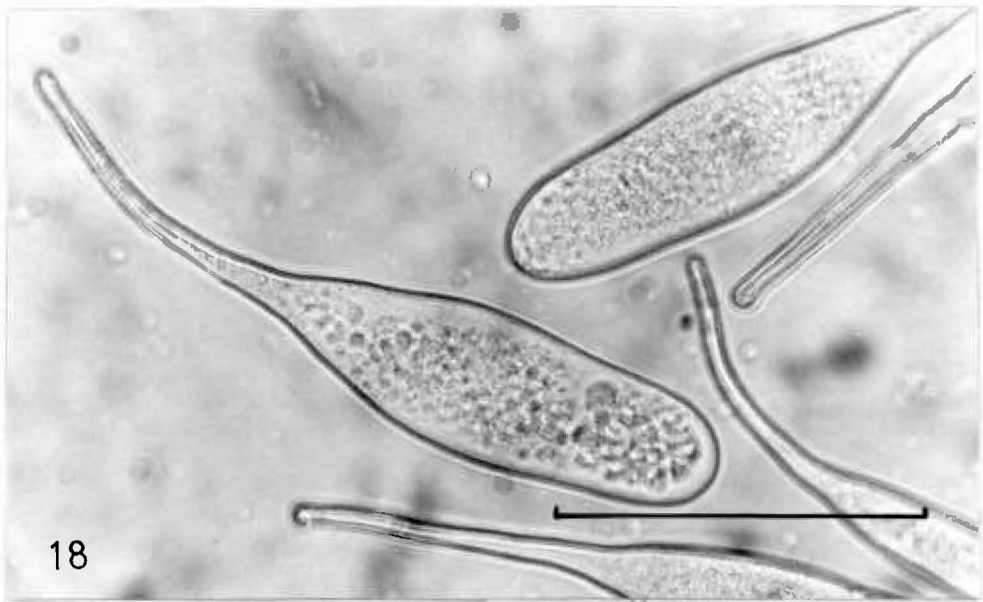
The elastic chorion of the egg facilitates the passage through the ovipositor and once inside the host egg, the egg quickly increases in size as the embryo develops.

Several *Anagrus* sp. C females were allowed to parasitize *C. viridis* eggs for a period of four hours. The host eggs were kept at 20°C and a number of them were dissected one, two, three or four days after oviposition.

Figure 18 and 19. The ovarian egg of *Anagrus* sp. B.

Figure 20. The ovarian egg of *Anagrus* sp. C.

Scale 100 μ


18


19


20

Table 4 shows that hatching starts three days after the eggs were laid and is almost completed by the fourth day.

During the second day, the eggs were considerably swollen but no increase in length was observed (Fig. 21).

At hatching, the chorion of the swollen egg splits longitudinally, starting from the anterior pole and it remains attached to the posterior end of the first instar larvae (Figs. 22-24).

The head of the larvae was located at the base of the pedicel.

b) The larval stage

A synopsis of the larval morphology of the Mymaridae was given by Bakkendorf (1933-1934). He recognised only two larval instars. The larvae were classified into two groups. The group I was characterized by the presence of a cylindrical second instar larva with two cephalic outgrowths (first pair of legs) below the mouth. The first instar larvae (at that time only known for *Anagrus*) was described as bag shaped with clumsy cephalic and caudal parts. In this first group he placed the genera *Anagrus*, *Erythmelus* and *Caraphractus*. According to Jackson (1961) the first instar larvae of *Caraphractus* does not conform to these types.

In the second group, he included the genus *Polynema*, *Alaptus*, *Lymaenon*, *Ooctonus* and *Anaphoidea* whose first instar larvae showed a frontal process above the mouth and a slender tapering caudal appendage.

Clausen (1940) recognized two types of first instar Mymaridae larvae. The "sacciform", represented by *Anagrus* (Group I of Bakkendorf) and the "mymariform" as present in *Polynema*, *Anaphes*, *Ooctonus* and *Anaphoidea* (Group II of Bakkendorf, in part).

Table 4. Hatching of *Anagrus* sp. C eggs at 20°C.

| Days after oviposition | Number of *Anagrus* eggs recovered | Number of early first instar larvae | Number of *C. viridis* eggs dissected |
|---|---|---|---|
| 1 | 161 | 0 | 48 |
| 2 | 240 | 0 | 105 |
| 3 | 19 | 51 | 23 |
| 4 | 1 | 20 | 9 |

The development of the immature stages of

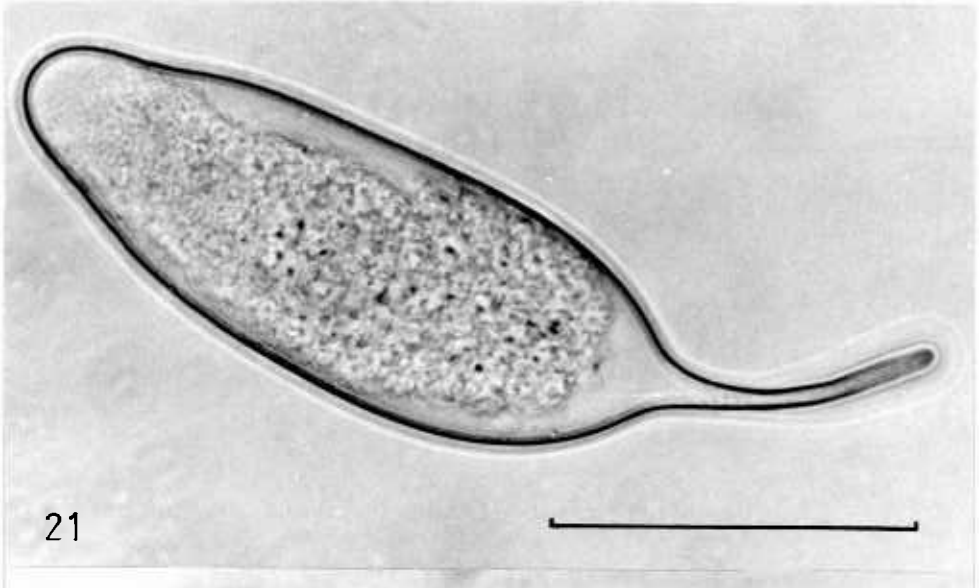
*Anagrus* sp. C parasitizing *C. viridis* eggs

Figure 21. Egg dissected 48 h after laying.

Figure 22. Newly hatched first instar larvae.

Figure 23. First instar larvae, approximately 24 h before the end of the stadium.

Scale 100 µ



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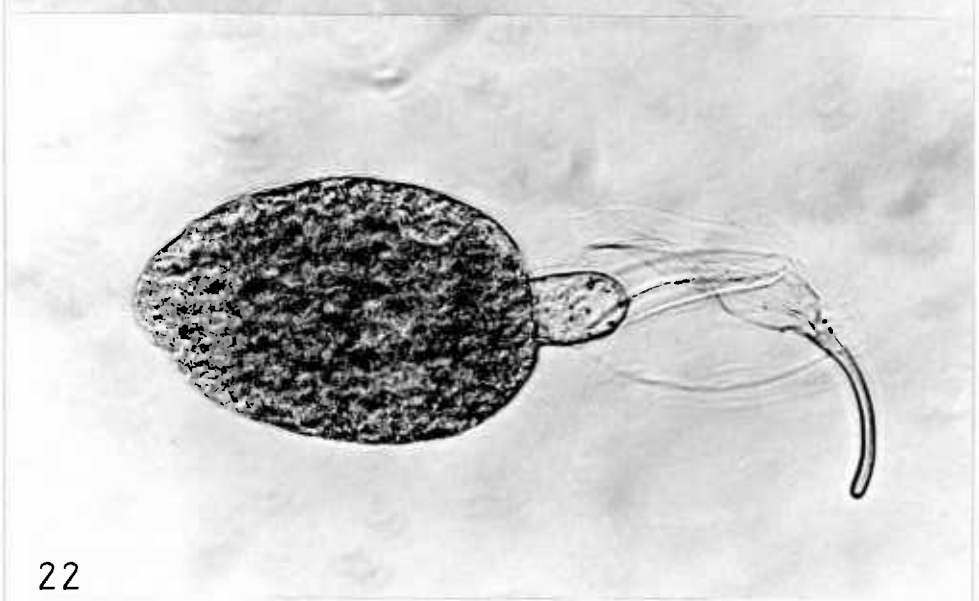

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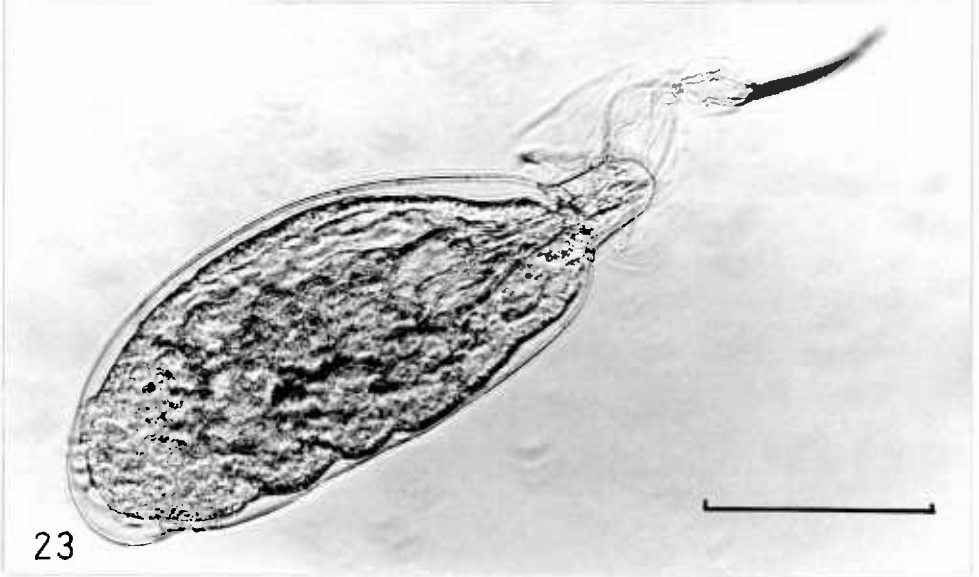

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The mymariform first instar larva was reported by several authors (Bakkendorf, 1933-1934; Anderson and Paschke, 1969; Balduf, 1928; Broadhead and Wapshere, 1966; Kuwayama, 1935; New, 1969; Satterthwait, 1931) and Tooke (1955) showed that the sex can be differentiated in the mymariform larvae of *Anaphoidea nitens*. He found the cast skins of "form A" first instar larvae always associated to female pupae, in hosts where only one parasitoid had developed.

The first instar larvae

Ganin (1869) described the larval stages of a *Polynema*, which according to Henriksen (1922) must belong to the genus *Anagrus* and possibly to the species *subfuscus* Foerster. He published some figures showing the development of the first instar larvae.

The newly hatched first instar larvae (Fig. 22) *Anagrus* sp. C is oblong, with a constriction on its basal portion. Frequently the eggshell remains attached to the basal part of the larva (Fig. 22, 23).

As development proceeds, the cephalic end shows a constriction which becomes more evident toward the end of the stadium (Fig. 23).

The second instar larva can be seen through the tegument of the late first instar larva (Fig. 23). The segmentation shows clearly, but the cephalic portion still remains undifferentiated.

At the end of the first instar, the cephalic portion of the future second instar larva is completely developed, showing the mandibles and the cephalic outgrowths. A few hours later, the second instar larva hatches, leaving behind the remains of the first instar larva with the eggshell still attached to it (Fig. 24).

At 20°C, the first instar larvae of *Anagrus* sp. C were found in dissected hosts three to six days after oviposition (see Table 4).

Clausen (1940) reported that the first instar larvae are entirely incapable of movement, they lie in the host fluids. Respiration, and possibly a certain intake of food material is by diffusion through the skin.

Several *Anagrus* sp. B and sp. C first instar larvae were observed but no movement was detected. The food material was taken by diffusion and at the end of the instar, the estomodeum was differentiated and filled with liquid contents but with no trace of yolk spheres.

*Anagrus* sp. C five days old first instar larvae were measured, and the results are shown in Table 5.

Henriksen (1922) observed the first instar larva of *Anagrus brocheri* Schulz and described it as having the head end separated from the body through a constriction. Dumbleton (1934) showed a newly hatched first instar larva of *Anagrus armatus* Ashmead and reported that he found two larvae apparently on the verge of moulting, as each was found to contain a larva with the characteristic cephalic appendages of the last instar larva.

Witsack (1973, Fig. 18b) reported the late form of the first instar larvae of *Anagrus* and his Fig. 18c showed a second instar larva hatching.

Mac Gill (1934) dissected an *Erythroneura* egg, known to have been parasitised by *A. atomus*, and found a structure that she believed to be an egg of *Anagrus*. According to her description, the stalk of the egg seemed to have completely disappeared. The structure was described as an oval translucent body. Although she did not publish an illustration,

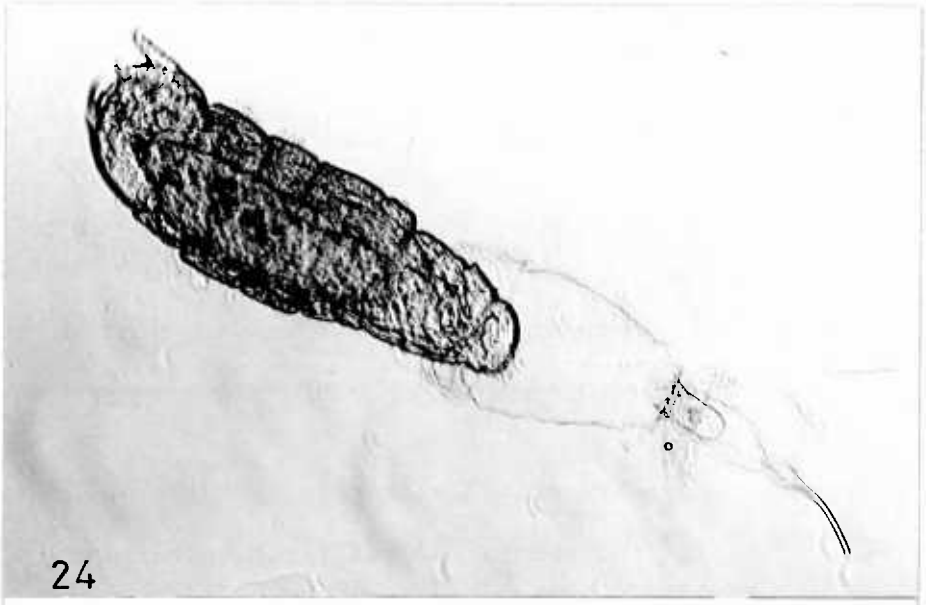
The development of the immature stages of

*Anagrus* sp. C parasitizing *C. viridis* eggs

Figure 24. Second instar larvae in the process of hatching. The larvae leaves behind the remains of the first instar larvae with the eggshell still attached to it.

Figure 25. Second instar larvae. The same larvae as in Fig. 24, the picture was taken 3 h. later.

Scale 100 µ



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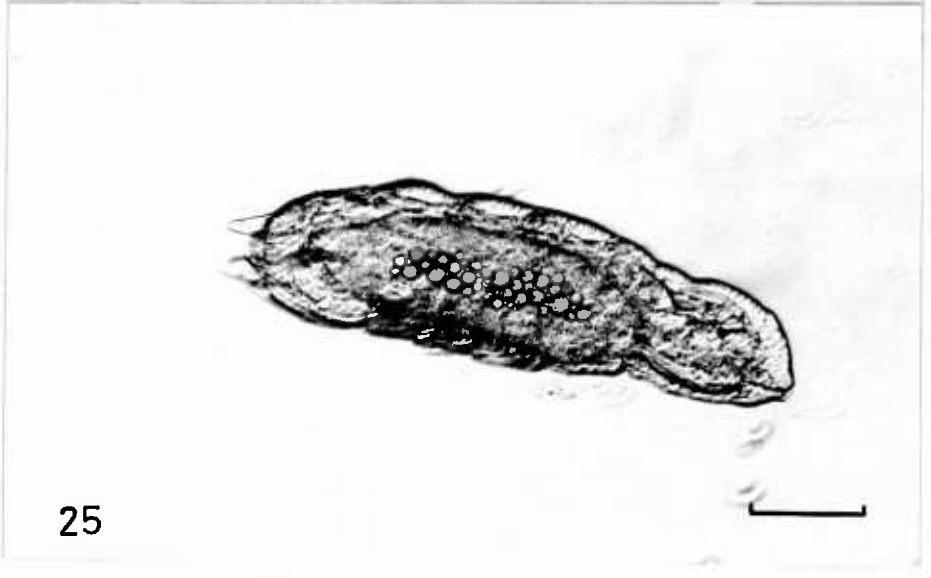


25

her description fits better that of the first instar larva.

Other authors who misinterpreted the first instar larva of *Anagrus* were May (1971), Tay (1972) and Whalley (1969). Their descriptions of first stage larvae (Whalley, 1969; May, 1972) and newly hatched larvae (Tay, 1972) all fall within the category of early second instar larvae. The presence of mandibles and cuticular outgrowths in the illustrations are characteristic to the second instar larvae.

Whalley's illustration of an *Anagrus* egg at hatching (1969, Fig. 1a) undoubtedly belongs to a first instar larva, with the eggshell attached to the basal portion.

The second instar larvae

In the Mymaridae the number of larval instar following the first is very uncertain. Several authors agree that there are only the first and the mature forms, though in most species there are said to be three (Clausen, 1940).

Balduf (1928) reported as many as four instars in *Polynema striaticorne*.

The second instar larva of *Anagrus* was first reported by Ganin (1869). He coined the term "histriobdella-like" to describe larvae which were cylindrical in form, divided into six segments, by constrictions. The head bears a pair of large, conical or cylindrical fleshy processes and the mandibles. The last segment bears a pair of large ear-like organs, of unknown function.

The histriobdellid larvae have been associated only with the sacciform first-instar larvae and are not known in any species as having mymariform larvae (Clausen, 1940). It has been reported for various

species of *Anagrus* by several authors, including Armstrong (1935); Bakkendorf (1925, 1933-1934); Dumbleton (1934); Enock (1914); Henriksen (1922); Ison (1959); Mac Gill (1934); Maillet (1960); May (1971); Mulla (1956); Otake (1968); Rothschild (1962, 1966); Whalley (1969) and Witsack (1973).

In the laboratory, the larval development of *Anagrus* sp. C was followed until the emergence of the adult. Eggs known to be parasitized due to the presence of a characteristic black mark on the chorion (Fig. 33) were kept at 20°C and checked every day.

The egg and the motionless first instar larvae cannot be seen unless the host is dissected, but the very active second instar larvae is noticed as early as 5 days after oviposition.

The second instar larva (Fig. 24) is colourless and has well developed mandibles and two cephalic outgrowths ("antennae" of Ganin (1869) and Henriksen (1922); "first pair of legs" of Bakkendorf, (1933-1934); "labial processes" of Whalley, (1969)). Soon after the egg has hatched the larva starts feeding. The yolk spheres of the host egg are sucked in by contraction and dilation of its oesophagous.

At the 6th day, the gut of the larvae is already distended by the food ingested.

Several six day old larvae were dissected, their measurements are given in Table 5.

White spherical bodies can be seen scattered over the whole of the stomodeum. These aggregations were first reported by Ganin (1869), and Bakkendorf (1933-1934) believed them to be "symbiotic cells" which were found to be placed on the wall of the stomach.

The aggregations, which can be first noticed in seven day old larvae, are very small but their size increases as the larva grows.

Jackson (1958a) concluded that the conspicuous opaque spots occur in the wall of the mid gut and they consist of single cells, each containing minute spheres believed to be products of excretion.

These spots can be seen to move in all directions with the churning movements of the gut contents. These movements are enhanced by the whirling movements of the larvae.

The colourless larvae shows a shade of orange at the 8th day. The coloration increases in intensity as the larva develops, becoming orange reddish by the 11th day and red when the larva reaches the prepupa stage on the 12th day.

The larva remains very active, churning up the contents of the host eggs. It was suggested by Whalley (1969) that this makes more food available to the larvae by keeping the host egg contents in a continuous circulation.

The mature larvae (10-11 days old) become less active, rolling their bodies over very slowly. Finally all movements cease at the 12th day when the larvae are developed into prepupae

The second larval instar lasts approximately 7 days.

c) The prepupal stage

The prepupal stage lasts one day. The prepupa shows constrictions revealing head, thorax and abdomen of the future pupae. The aggregations now become free in the gut and they coalesce, forming an opaque mass which occupies a part of the thorax and abdomen.

This stage ends with the pupa shedding the larval exuvia. It can be noticed after dissecting the host, the larval mandibles and exuvia remain attached to the caudal end of the newly formed pupae.

d) The pupal stage

The pupal stage lasts 6-7 days and several changes, can be noticed, mainly in coloration. These changes in coloration permit the estimation of the age of the pupae. Jackson (1961) already showed that the age of the pupae of *Caraphractus cinctus* can be roughly assessed from its coloration.

At the 13th day, the newly formed pupae show all the aggregations contained in the abdomen and they will be discharged as meconium after emergence. The compound eyes of the pharate imago and all the ocelli are noticeable. They are pale brown and orange red, respectively.

During the 14th and 15th day the colour of the compound eyes and ocelli darkens , becoming brown and by the end of the 15th day, the mandibles are dark brown.

The body of the pupae is red becoming dark red to brown at the time of emergence.

The appendages are fully formed by the 14th day but they are only noticed by dissecting the pupa out of the host. The darkening is gradual and they can be seen at the 16th day when the brown tip of the ovipositor, is first detected.

The mandibles and the tip of the ovipositor are brown by the 17th day and all the appendages are evident. The body is dark red to brown with the head showing dark brown compound eyes and ocelli.

One day before emergence (i.e. the 20th day), the pupa is dark brown showing the black patches on the dorsum, thorax and abdomen. Movement is observed at this stage with all the pupal appendages freed. The antennae and legs change position frequently but the body does not change place.

Emergence occurs as early as the 21st day, but the majority of the adults emerged between the 23rd-24th day after oviposition.

Three *C. viridis* eggs containing three *Anagrus* sp. C pupae each, were dissected and the pupae were measured. The average length for the male and female pupae is given in Table 5.

The female pupa is slightly longer than the male one due to the projection of the ovipositor.

e) The number of larval instars

The minute size of the early stages combined with the lack of sclerotized structures of fixed form, make the identification of the larval instars a very difficult task.

The presence of a first and second instar in *Anagrus* sp. C larvae is shown in Fig. 24, but it was not known how many instars followed the first.

The mandibles and cuticular outgrowths are characteristic of the second instar larvae and are still present when the larvae mature. The size of the outgrowths are reduced as the larvae grow.

The increase in size of the second instar larvae is considerable. Measurement of six day old second instars and ten day old mature *Anagrus* sp. C larvae, dissected out *C. viridis* eggs containing three individuals each, were made and the results are given in Table 5. The results showed

Table 5. Measurements of the developmental stages of *Anagrus* sp. B and sp. C, bred in *C. viridis* hosts.

| Species | Stage/instar | Length (mm) | | | Width (mm) | | | Number of observation |
|---|---|---|---|---|---|---|---|---|
| | | Mean | S | Range | Mean | S | Range | |
| *Anagrus* sp. C | ovarian egg | 0.185 | 0.014 | 0.17 - 0.21 | 0.019 | 0.0051 | 0.013 - 0.025 | 20 |
| | first instar | 0.33 | 0.02 | 0.28 - 0.35 | 0.12 | 0.01 | 0.11 - 0.13 | 11 |
| | early second | 0.51 | 0.03 | 0.48 - 0.54 | 0.13 | 0.01 | 0.12 - 0.14 | 6 |
| | late second | 0.97 | 0.05 | 0.86 - 1.04 | 0.24 | 0.01 | 0.22 - 0.26 | 11 |
| | male pupa | 0.96 | 0.05 | 0.90 - 1.01 | - | - | - | 4 |
| | female pupa | 1.03 | 0.06 | 0.98 - 1.11 | - | - | - | 4 |
| *Anagrus* sp. B | ovarian egg | 0.185 | 0.017 | 0.16 - 0.20 | 0.027 | 0.0047 | 0.02 - 0.035 | 25 |

that the larvae doubled their size in this instar.

During the present study, several host eggs were dissected and many mature second instar larvae and pupae were recorded, but no definite evidence was found that a moult took place. The pupae showed the cast larval skin, with the mandibles, attached to the tip of the abdomen.

The length of the mandibles of early second and mature larvae of *Anagrus* sp. B and sp. C was measured and the results are shown in Table 6.

A t-test showed no difference in either species between the measurement of the mandibles of early second instar and mature larvae.

It is considered that mandible size is a good indicator of instar, remaining the same when body size doubled, and therefore it is concluded that the mature larvae is merely the late second instar larva. Thus, the average length of the mandibles of the second instar larvae was obtained by pooling all the data for each species. The results are shown in Table 6. The mandibles of sp. B are twice the size of those of sp. C, a difference that is highly significant ("t" = 21.48, D.F. = 24).

The size of the mandibles, together with the presence of abdominal outgrowths in *Anagrus* sp. B larvae, are useful criteria to separate larvae of both species. Both *Anagrus* sp. B and sp. C have well defined cephalic outgrowths.

8. Length of the developmental period

a) Introduction

The importance of temperature on the duration of growth and development of insects has long been realized. Mathematical descriptions of the effect of temperature on developmental rates have been discussed by

Table 6. Average size of the mandibles (in mm) in *Anagrus* sp. B and sp. C larvae.

| Stage | *Anagrus* sp. B | | | *Anagrus* sp. C | | | Number of observations |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | S | Range | $\bar{X}$ | S | Range | |
| early second instar | 0.056 | 0.004 | 0.050 - 0.061 | 0.027 | 0.003 | 0.023 - 0.032 | 6 |
| mature larvae | 0.054 | 0.003 | 0.050 - 0.057 | 0.027 | 0.002 | 0.025 - 0.030 | 7 |
| second instar (pooled data) | 0.055 | 0.0037 | 0.050 - 0.061 | 0.027 | 0.0026 | 0.023 - 0.032 | 13 |

Andrewartha and Birch (1954), Howe (1967), Watt (1968) and Wigglesworth (1972). These authors share a common viewpoint, namely that a mathematical model that would describe accurately the relationship between temperature and development is not yet available.

Experiments are generally carried out at a number of constant temperatures and the results are presented as temperature-time and temperature-velocity curves.

The reciprocal of the developmental period at a constant temperature is often regarded as the speed of development (Davidson, 1944).

The term "threshold of development" is usually considered as the point on the temperature scale at or below which development ceases. When the reciprocal of developmental time in days is plotted against temperature a linear relationship results, which on extrapolation gives the value of the "developmental zero". Experiments have shown that a non linear relationship between temperature and the rate of development is usual. However, Eguagie (1972) showed that within the range of $15^{o}$ to $30^{o}$C the rate of development data of various Heteroptera and other insects, has been adequately described by a linear regression equation.

The time required for the complete development of several mymarids has been recorded by several authors (Anderson and Paschke, 1968; Armstrong, 1935; Clancy and Pierce, 1966; Kuwayama, 1935; New, 1969; Mac Gill, 1934; May, 1971; Otake, 1970b; Pickles, 1932; Raatikainen, 1967; Rothschild, 1962, 1967; Tay, 1972; Whalley, 1956, 1959).

The relationship between developmental time and temperature was studied in *Anagrus* nr. *flaveolus* by Otake (1970b) and in *Anagrus incarnatus* by Witsack (1973).

Anderson and Paschke (1969, 1970a) showed differences in developmental rates when comparing biological data on five European cultures of *Anaphes flavipes*.

No work seems to have been reported on Mymaridae on the changes of size and fecundity of females due to changes in rearing temperatures.

b) Material and methods

The duration of development from egg to adult were determined in *Anagrus* sp. C developing in *D. hamata* eggs. Newly emerged *Anagrus* sp. C females were allowed to parasitize *D. hamata* eggs during 24 hrs at 20°C. After 24 hours all the females were removed and the parasitized host eggs were transferred to C.T. rooms at 15°, 20°, 25° and 30°C. The breeding cages were checked daily until complete emergence of the adult parasitoids had occurred.

The observed times for development were plotted against temperature to obtain the temperature-time curve. The reciprocals for time were plotted against temperature. Each of the reciprocals was multiplied by 100, so that the values in the ordinate represented the average percentage of development in one day at a given temperature. The "developmental zero" point was estimated graphically, by extending the regression line until it intercepted the temperature axis (y = 0).

In order to investigate the effect of rearing temperature on adult fecundity, five newly emerged females bred from *D. hamata* at each of the four temperatures tested were dissected. The number of eggs present in the ovaries, the length of the forewing and the length of the hind tibia was also recorded.

Table 7. The effect of temperature on the developmental period of *Anagrus* sp. C

| Temperature in °C | Sex of adults | Mean development in days (y)* | Range (days) | 't' value | Average development in one day (100 y) | Host |
|---|---|---|---|---|---|---|
| 15 | males | 34.91 ± 1.130 (43) | 33 - 37 | 4.1253 | 2.86 | *D. hamata* (Boh.) |
| | females | 35.72 ± 0.839 (57) | 33 - 38 | | 2.80 | |
| 20 | males | 23.40 ± 1.465 (20) | 21 - 26 | 2.5123 | 4.27 | *D. hamata* (Boh.) |
| | females | 24.45 ± 1.693 (66) | 21 - 28 | | 4.09 | |
| 25 | males | 13.46 ± 0.706 (26) | 13 - 15 | 3.0545 | 7.43 | *D. hamata* (Boh.) |
| | females | 14.10 ± 0.900 (40) | 13 - 16 | | 7.09 | |
| 30 | males | 10.75 ± 0.689 (114) | 10 - 13 | 0.9462 | 9.30 | *D. hamata* (Boh.) |
| | females | 10.66 ± 0.739 (163) | 10 - 14 | | 9.38 | |

* mean ± SD (number of observations)

c) Results

The effect of temperature on the developmental period

Results of duration of development from egg to adult in *Anagrus* sp. C are given in Table 7. The mean developmental time in days (y) and the average percentage of development in one day ($100 \cdot y^{-1}$) are shown for both sexes. Figures 26 and 27 show the relationship between temperature and the time and rate of development for males and females developing in *D. hamata* eggs. A rise in temperature within the range $15^{o}$ - $30^{o}$C reduced the period of development by days.

Males developed faster than females when reared at $15^{o}$, $20^{o}$ and $25^{o}$C ($p<0.01$) but at $30^{o}$C the difference was non significant. A regression line was fitted to the temperature - rate of development data in males and females. The coefficient of determination "$r^2$" of the relationship ($r^2 = 0.980$ and $r^2 = 0.979$; $p<0.01$) showed that the data was adequately described by a linear regression. A t-test showed no difference in the slope of the regression line for males and females.

The temperature threshold of development, i.e. "developmental zero" point, was obtained by extrapolation from the regression lines of speed of development on temperature (Table 8; Figures 26 and 27). The "developmental zero" point was estimated as $9.2^{o}$C for males and $9.6^{o}$C for females.

The effect of temperature on fecundity

The results of the effect of rearing temperatures on the fecundity of the adult are given in Appendix Table 4. Figure 28 shows the average number of eggs in the ovaries of dissected, newly emerged females.

Females reared at $15^{o}$C showed the highest fecundity ($\bar{x} = 65.4$ eggs; SD = 2.07; n = 5). The lowest fecundity was recorded at $30^{o}$C ($\bar{x} = 38.0$

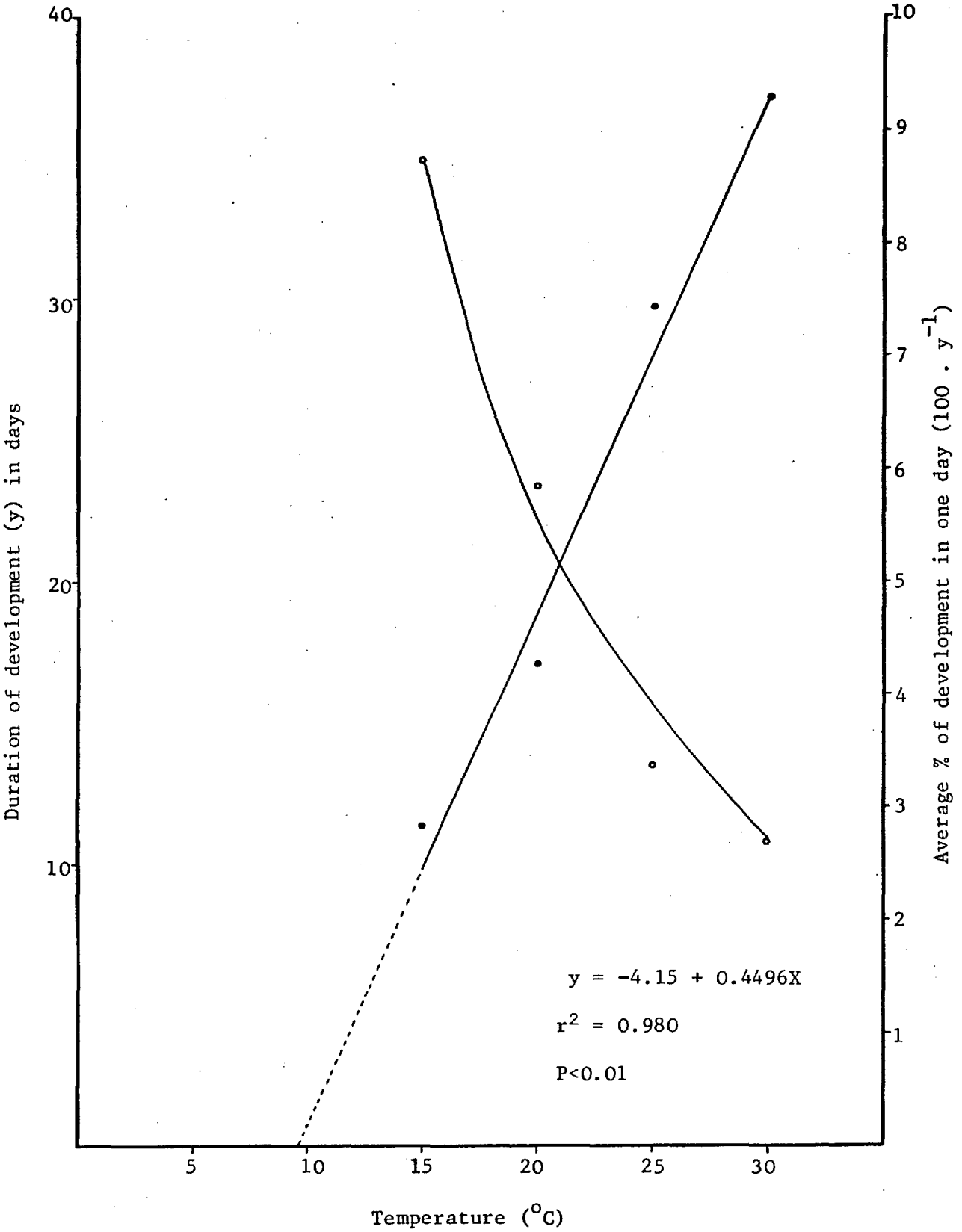



Figure 26. Temperature-time curve (o-o) and graphical determination of temperature threshold (•-•) for development in *Anagrus* sp. C males parasitising *D. hamata*.

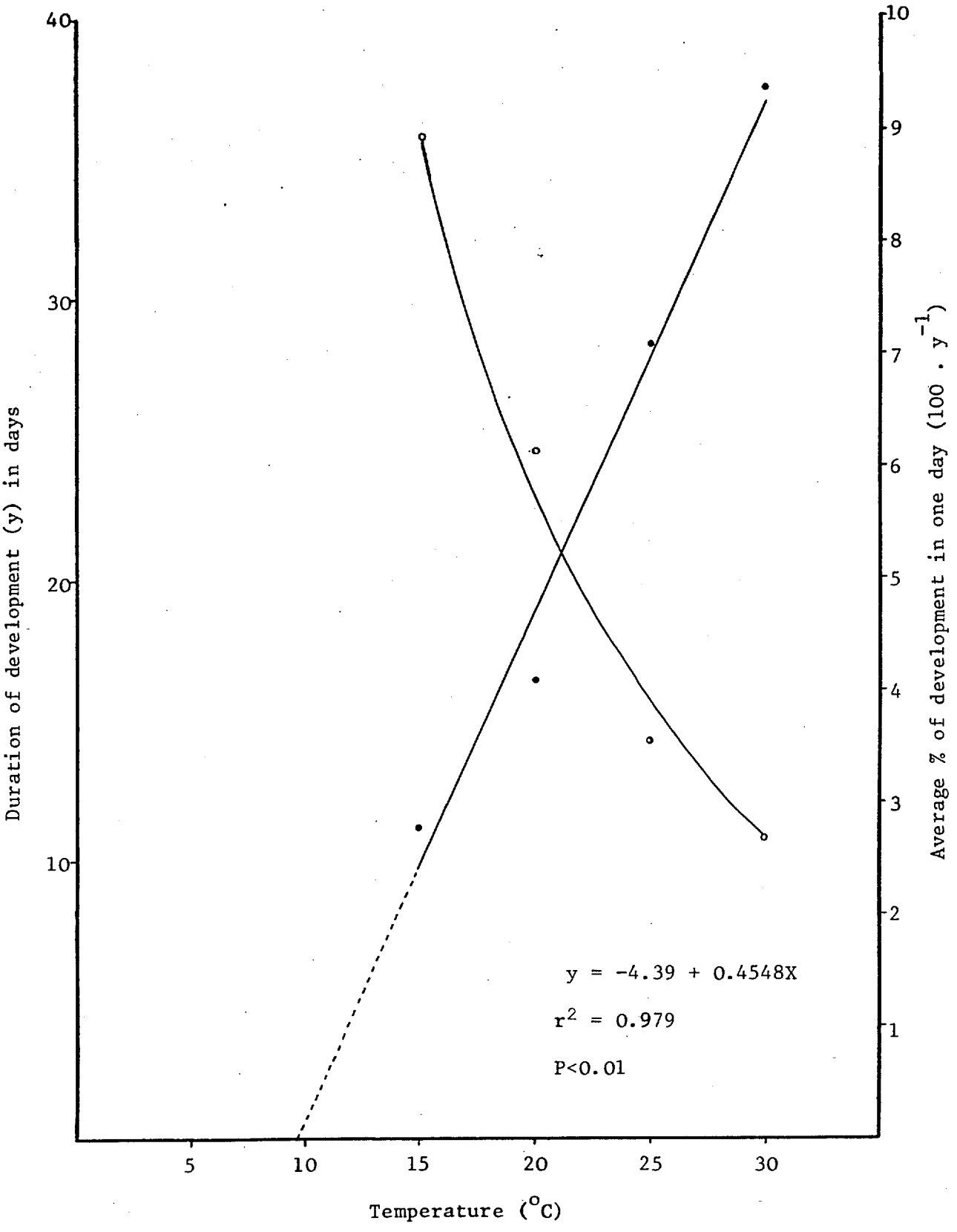



Figure 27. Temperature-time curve (o-o) and graphical determination of temperature threshold (●-●) for development in *Anagrus* sp. C females parasitising *D. hamata*.

eggs; SD = 3.54; n = 5).

When the average fecundity is plotted against temperature a significant ($p<0.01$) linear relationship results.

The effect of temperature on body size

The size of *Anagrus* sp. C females reared at different temperatures was estimated by measuring the length of the forewing and that of the hind tibia. Results are shown in Appendix Table 5. When the average length of the forewing and the average length of the hind tibia were plotted against temperature, a linear relationship resulted. The correlation coefficients obtained were 0.969 and 0.891 and the t-test rejected the null hypothesis ($p<0.05$; $p<0.01$) in both cases (Fig. 29).

d) Discussion

The rate of growth and development of insects is obviously affected by temperature and since temperature appears to be fairly easily measured and controlled, it has become a routine procedure to examine its influence upon species of economic importance (Howe, 1967).

The development of *Anagrus* sp. C from egg to adult was affected by temperature. A minimum of 14 days (at 30°C) and a maximum of 35 days (at 15°C) was ascertained for the complete development of *Anagrus* sp. C in *D. hamata* eggs. No significant difference was found in the average of daily development in males and females. Although, males tended to develop faster than females in *D. hamata* at 15°, 20° and 25°C ($p<0.05$). Witsack (1973) and Anderson and Paschke (1968, 1969, 1970b) observed slight proterandry in adult emergence.

The temperature threshold for development (i.e. "developmental zero") was approximately 9.5°C for males and females. Witsack (1973) showed

Table 8. The relationship between developmental time (days) and temperature in *Anagrus* sp. C parasitizing *D. hamata*.

| Sex | Regression equation | Probability | Coefficient of determination | "Developmental zero" point in °C (y = 0) |
|---|---|---|---|---|
| Males | y = -4.15 + 0.4496 X | <0.01 | 0.980 | 9.23 |
| Females | y = -4.39 + 0.4548 X | <0.01 | 0.979 | 9.65 |

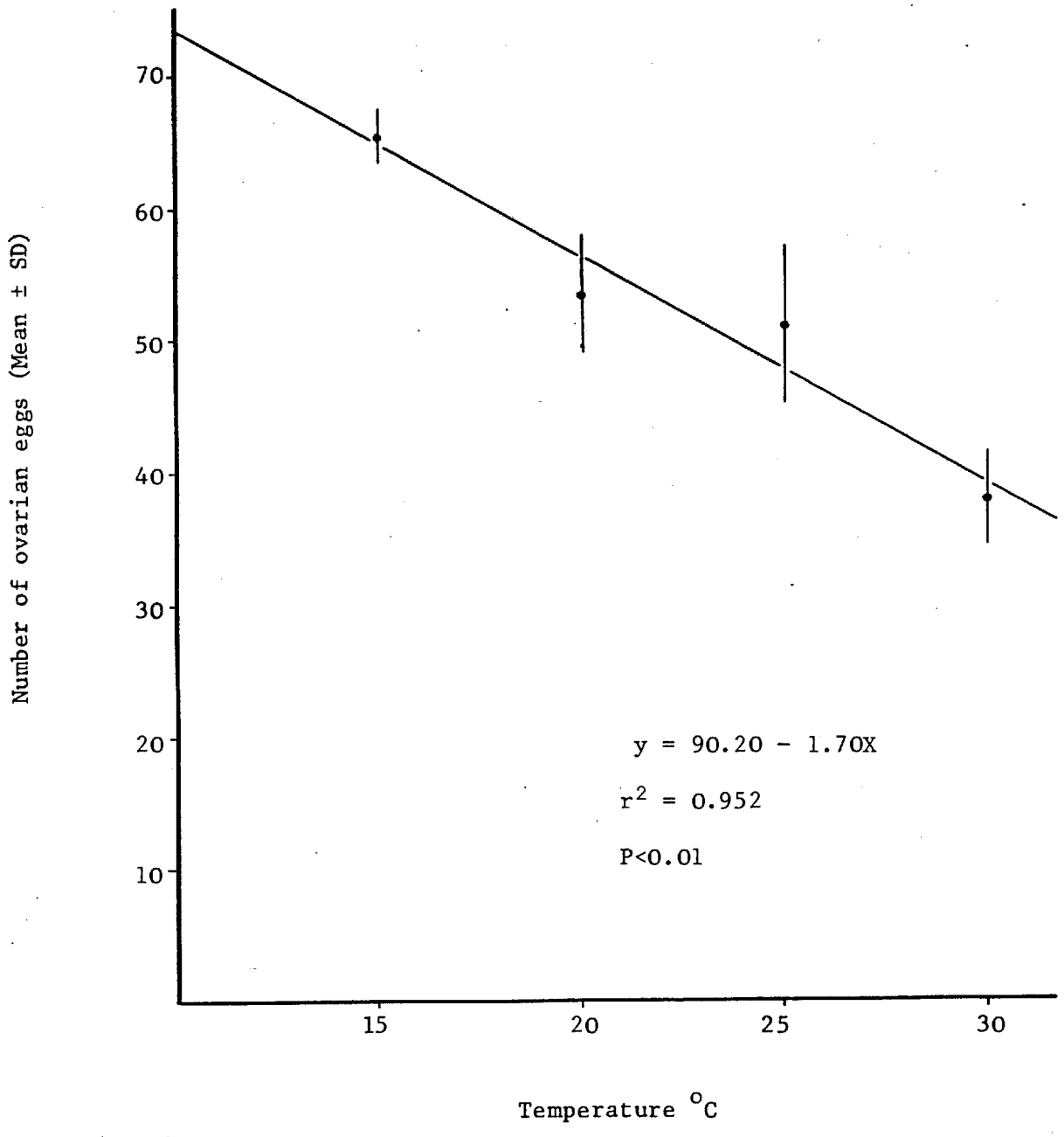



Figure 28. Effect of temperature on the fecundity of *Anagrus* sp. C females bred from *D. hamata*.

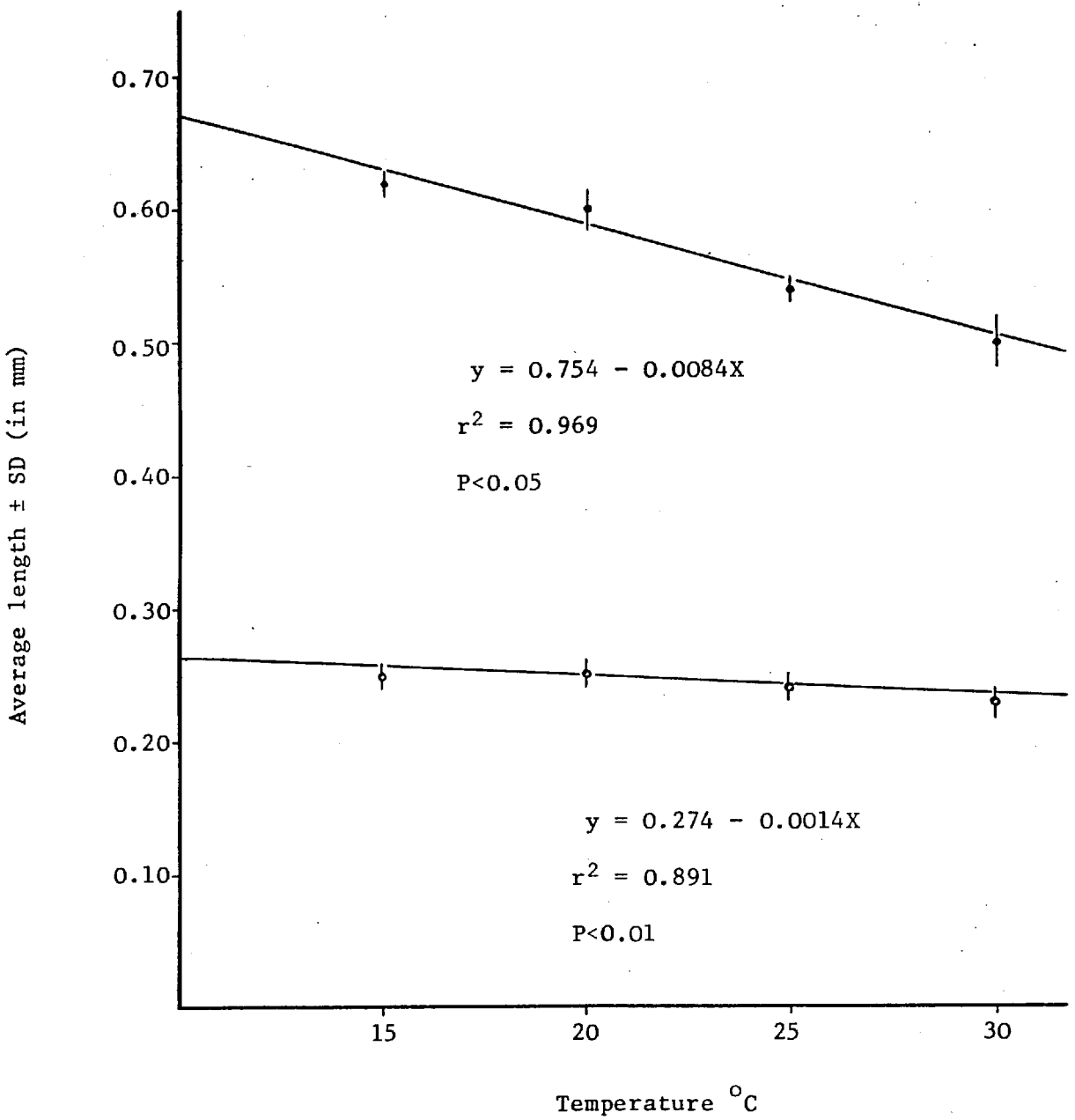



Figure 29. Effect of temperature on the length of the hind tibia (o-o) and the forewing (•-•) in *Anagrus* sp. C females bred from *D. hamata*.

that coolness (below 8°C) caused larval dormancy (thermic quiescence) in *Anagrus incarnatus* and Anderson and Paschke (1969) reported that, although early development can proceed at 10°C, complete development and emergence of *Anaphes flavipes* adults do not occur at this temperature. Temperatures below 10 - 12.2°C arrested development in *Anaphes* without significant mortality for at least 3 weeks (Anderson and Paschke, 1969) and Walker (in press) showed that host eggs, parasitized under laboratory conditions, can be kept refrigerated for several weeks (2 - 4) and the development of *Anagrus* is retarded accordingly.

The rearing temperature had a marked effect on the fecundity and size of the resultant female adult. A rise in temperature reduced the average number of ovarian eggs as well as the length of the forewing and the metathoracic tibia.

The effect of the host on the length of the developmental period of *Anagrus* spp will be discussed later (Chapter III).

v. Field observations

1. Introduction

Several authors reported parasitism by *Anagrus* in overwintering *C. viridis* eggs in Silwood Park (Rothschild, 1962, 1966; Tay , 1972; Walker, in press).

Tay (1972) considered that *A. atomus* (identified as sp. C by Walker, in press) overwinters as larva reassuming development in the following Spring. Whalley (1969) showed that *Anagrus atomus* and *A. incarnatus* females (considered as sp. C and sp. B by Walker, in press) were able to parasitize *C. viridis* eggs containing advanced embryos. Thus, at least two and possibly three generations of parasitoids could develop in one generation of *C. viridis* eggs (Whalley, 1969; Tay, 1972). Similar results

were reported for *Anagrus incarnatus* (identified as sp. E by Walker, in press) parasitising overwintering *C. anceps* eggs (Rothschild, 1962, 1966).

Overwintering *C. viridis* eggs were collected, in Silwood Park, in order to obtain information on field parasitism by *Anagrus* sp. B and sp. C. During the Autumn-Winter 1975, a sampling program was also carried out.

2. The area of study

The work was done in an area known as the Rush Meadow by the northern shore of Silwood Lake. Fig. 30 shows the location of the area where *Juncus effusus* L., the host plant of *C. viridis*, was sampled and the places where *Anagrus* sp. B and sp. C were collected.

3. Studies of parasitism by *Anagrus* sp. B and sp. C in the field

In an attempt to obtain information about the host-parasitoid relationship in the field, a sampling programme was carried out during the Autumn-Winter 1975 and periodic collections were made during the Winter 1976-1977.

a) The sampling programme

Samples of 20 stems were taken from each of 10 clumps of *Juncus effusus* L. along a transect marked by a 250 m string. The clumps to be sampled were those nearest to ten points, 5 m apart, marked on the string. Resampling the same clump was avoided by commencing the series of marked sites on the string at a position between two previous samples.

The results of the sampling are presented in Table 9. No *C. viridis* ovipositions were recorded on the 13th and 21st August. Ten *C. viridis* collected on each of these occasions were dissected and only one and six mature females were recorded on these dates.

Table 9. Parasitism by *Anagrus* sp. C in the field.

| Sampling occasion | Number of stems with *Cicadella* eggs | Total number of *Cicadella* eggs | | % of *Cicadella* eggs parasitized |
|---|---|---|---|---|
| | | Unparasitized | Parasitized* | |
| 13 - VIII - 75 | 0 | 0 | 0 | 0 |
| 21 - VIII | 0 | 0 | 0 | 0 |
| 27 - VIII | 18 | 287 | 0 | 0 |
| 2 - IX | 40 | 537 | 0 | 0 |
| 16 - IX | 66 | 1082 | 0 | 0 |
| 27 - IX | 56 | 1312 | 8 (24) | 0.6 |
| 17 - X | 95 | 2736 | 5 (16) | 0.2 |
| 4 - XI | 63 | 1895 | 0 | 0 |
| 13 - XII | 70 | 1938 | 6 (18) | 0.3 |

* Number of parasitoids in brackets

Tay (1972) showed that *C. viridis* adults started laying eggs as from last week of August and continued till the end of November; by then most individuals had died.

In 1975, *C. viridis* started egg laying after the 21st August and the first parasitoids appeared on the 27th September. Parasitoids were recorded in two other samples on the 17th October and the 13th December. One *C. viridis* egg batch was parasitized each time and only *Anagrus* sp. C adults were obtained from them.

Tay (1972) assessed *C. viridis* egg mortality. Over the period 1969-1971, he collected samples of *Cicadella* eggs in the area shown in Fig. 30. He recorded 9.13% parasitism by *Anagrus atomus* (Walker's sp. C) in May 1969; 9.65 and 6.09% in March and May 1970, and 4.14, 3.44, 4.70% in February, March and May 1971. Tay's results were considerably higher than the values of eggs parasitized for September, October and December 1975.

The sample size in the present study was less than half of Tay's sample size and only the first 15 m of the line transect was laying within the boundaries of Tay's study area. Two out of three *C. viridis* ovipositions parasitized by *C. viridis* were found within the first 9 m of the line transect, the third was found 194 m from its beginning. Furthermore, collections made during the winter 1976-1977 within Tay's study area yielded a considerable number of egg batches of *C. viridis* parasitized by *Anagrus*. One cannot be certain that the differences are due to yearly variations in parasitoid level, the changes in the size of the sample and the sampling could be responsible.

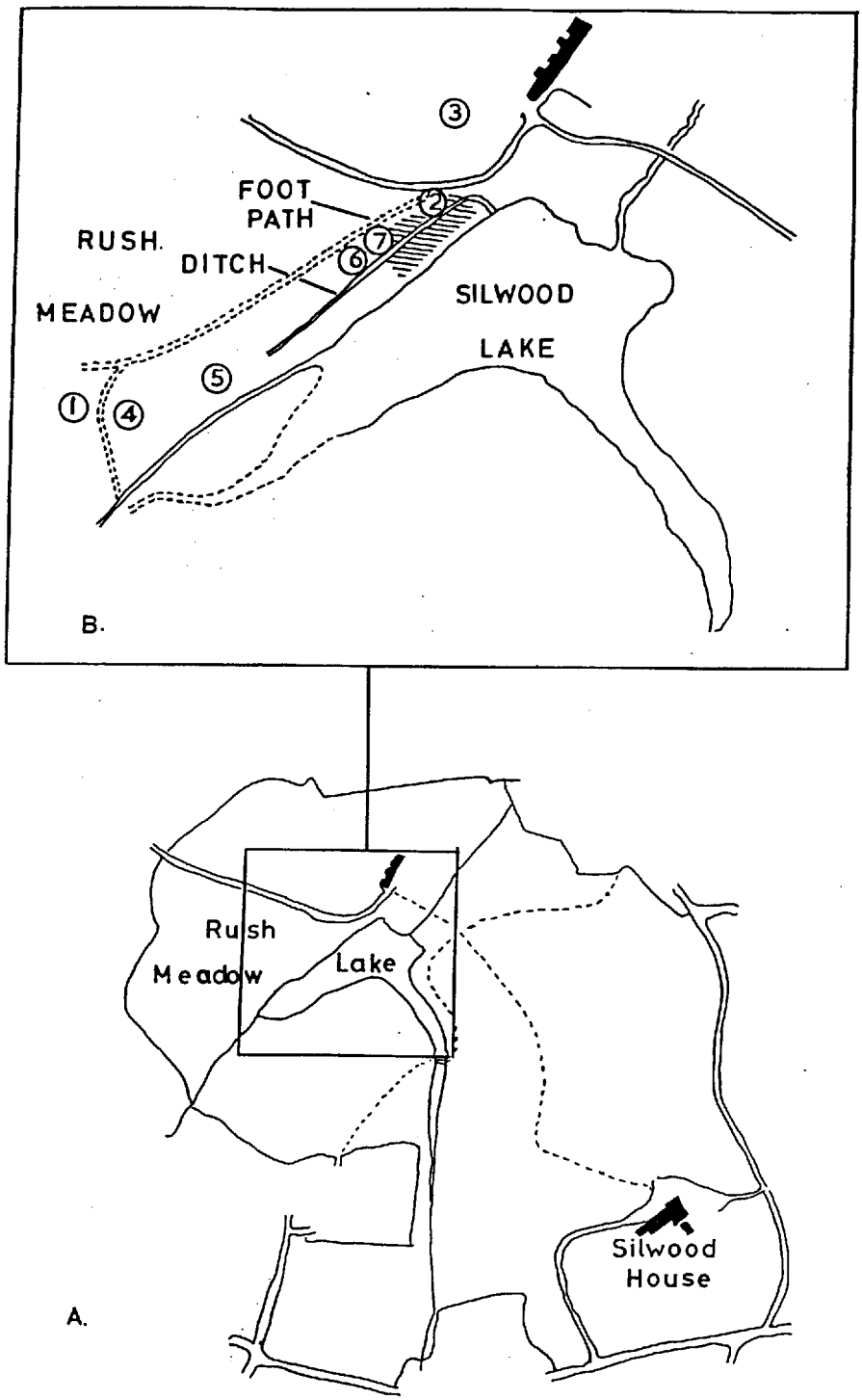



Figure 30. Sketch of Silwood Park (a) with an enlargement of the area surrounding the study site (b).

①-③ Places where *Anagrus* sp. B and sp. C were collected.

④-⑦ Places where *Anagrus* sp. C was collected or sampled.

Tay's study area.

b) Periodic collections

Several hundreds of *Juncus* stems bearing *C. viridis* eggs were collected during the winter months to provide hosts for *Anagrus* sp. B and sp. C in the laboratory. During the winter 1976-1977, the site where the stem came from and the number and sex of the parasitoids reared were recorded. Fig. 30 shows that *Anagrus* sp. C was present in sites 1-7 and only sites 1-3 yielded some *Anagrus* sp. B as well.

The size of *C. viridis* egg batches parasitized in the field by *Anagrus* sp. B and sp. C is given in Table 10. About 80% of the parasitized batches fell within the range 7-12, with an average of 9.5 eggs per batch (SD = 2.80; n = 10; range = 5-14) when parasitized by *Anagrus* sp. B and 10.3 eggs per batch (SD = 2.57; n = 61; range 6-16) recorded for *Anagrus* sp. C parasitism.

Tay (1972) showed that the average number of *C. viridis* eggs per batch was 10.48 (n = 428; SE = 0.14; range 1-19) and that 70% of the frequency distribution of number of eggs per batch was included within the range 8-13.

It is interesting to note that both species of *Anagrus* did not parasitize batches smaller than 5 (sp. B) or 6 (sp. C) and that the frequency distribution of number of *C. viridis* eggs per batch in parasitized egg batches is very similar.

The average number of *C. viridis* eggs parasitized per egg batch in the field is shown in Table 11. The average number of eggs parasitized by *Anagrus* sp. B was significantly different from that of *Anagrus* sp. C ($0.05>P>0.01$).

Table 10. Size of *C. viridis* ovipositions parasitized by *Anagrus* sp. B and sp. C in the field*.

| | Mean | SD | Range | Number of observations |
|---|---|---|---|---|
| *Anagrus* sp. B | 9.5 | 2.80 | 5-14 | 10 |
| *Anagrus* sp. C | 10.3 | 2.57 | 6-16 | 61 |

* Number of *C. viridis* eggs per egg-batch.

Table 11. Average number of *C. viridis* eggs parasitized by *Anagrus* sp. B and sp. C per egg batch in the field.

| | Mean | SD | Range | Number of observations | t-value | Probability |
|---|---|---|---|---|---|---|
| *Anagrus* sp. B | 3.5 | 1.90 | 2-7 | 10 | 2.37 | 0.05>p>0.01 |
| *Anagrus* sp. C | 6.1 | 3.31 | 1-16 | 61 | | |

4. Number of parasitoids per *C. viridis* egg in the field

The number of parasitoids per *C. viridis* egg in field collected egg batches was recorded and is given in Table 12. Results showed that the number of *Anagrus* sp. B per host egg varied from 2-4, with 75% of unparasitized eggs. The parasitoid laid 3 eggs per host more frequently than 2 or 4. Almost the same high proportion of unparasitized eggs were found in *Anagrus* sp. C (72%) but in this case, 3 or 4 parasitoids per host were the most frequent categories.

The average number of parasitoid per parasitized field collected *C. viridis* egg was significantly different for both species ($p<0.001$) (Table 13).

The result for *Anagrus* sp. C is remarkably similar to Tay's (1972) results. He found that the number of *Anagrus atomus* (Walker's, sp. C) per host varied from one to five with an average of 3.56 (SE = 0.13; n = 45). Some *C. viridis* eggs collected by Morcos (1953) in Silwood Park on May 1948, were found parasitized by *Anagrus incarnatus*, each egg containing from three to eleven parasitoids. Whalley (1969) reported that the number of *Anagrus atomus* (Walker's sp. B and sp. C) in the field seemed to be limited to four, while Maillet (1960) came across ten parasites per host from a field population of *Anagrus atomus* in France.

5. Overwintering in *Anagrus* sp. B and sp. C

So far as known, *Anagrus* overwinters as mature (late second instar) larvae inside the overwintering host egg (Bakkendorf, 1925; Mulla, 1956; Rothschild, 1962, 1967; Tay, 1972; Walker, in press). Witsack (1973) showed that the larvae were in termic quiescence and they developed to emergence after a raise in temperature had occurred.

Tay (1972) stated that *Anagrus atomus* (Walker's sp. C) overwintered as larvae and resumed development in the following spring. For winter the

Table 12. Frequency of *Anagrus* sp. B and sp. C adults per *C. viridis* eggs bred from field collected egg-batches.

| Number of *C. viridis* eggs containing | *Anagrus* sp. B | | *Anagrus* sp. C | |
|---|---|---|---|---|
| | number | % | number | % |
| 0 parasitoid | 112 | 75.2 | 665 | 72.0 |
| 1 " | - | - | 4 | 0.4 |
| 2 parasitoids | 11 | 7.4 | 14 | 1.5 |
| 3 " | 21 | 14.1 | 114 | 12.3 |
| 4 " | 5 | 3.3 | 114 | 12.3 |
| 5 " | - | | 13 | 1.5 |
| TOTAL | 149 | 100.0 | 924 | 100 |

Table 13. Average number of parasitoids per parasitized, field collected *C. viridis* egg.

| | Mean | SD | Range | Number of observations | t-value | Probability |
|---|---|---|---|---|---|---|
| *Anagrus* sp. B | 2.8 | 0.65 | 2-4 | 37 | | |
| | | | | | 4.81 | <0.001 |
| *Anagrus* sp. C | 3.5 | 0.74 | 1-5 | 259 | | |

larva goes into a quiescent stage rather than diapause, since they resume development when they are brought into high temperature.

Characteristic post-diapause developmental periods were noted in *Anagrus* overwintering within *Juncus* (Walker, in press). She kept *Juncus* collected during the winter inside the refrigerator and regarded the number of days between removal from the refrigerator and emergence of the host parasitoid as a good indication for species difference. Using this method, Walker (in press) differentiated between *Anagrus* sp. C (bred from *C. viridis*), sp. B and sp. D (bred from *M. fairmairei*) and sp. E (bred from *C. anceps*).

The effect of temperature on the rate of development and the temperature threshold for development in *Anagrus* sp. C has already been discussed (see II-iv-8). In the present study, overwintering *Anagrus* sp. C individuals were kept in a refrigerator at 5-7$^{o}$C for several weeks as a standard procedure (see II-ii-2-b). The development of the parasitoids was retarded accordingly without apparent increase in mortality. In one occasion, overwintering parasitoids were kept for over four months, but mortality was considerably high and the emerging adults were rather weak. Only a few females laid eggs which developed successfully.

Periodic field collections from December to February of overwintering *C. viridis* eggs containing overwintering *Anagrus* sp. B and sp. C showed that both parasitoid species overwinters as mature larvae, prepupae or early pupae (compound eggs of the pharate imago pale brown in colour). As early as in November, several *Anagrus* sp. C collected in front of Silwood Farm (Fig. 30, site 3) were at the prepupal or early pupal stage.

In Mymaridae, the host eggs containing developing parasitoid larvae are recognizable by a distinctive coloration (Clausen, 1940; Jackson,

1961; Balduf, 1928; New, 1969). This is true in several species of *Anagrus*, where the host eggs containing advanced larvae and pupae are bright red or yellow in colour. The shape and colour of the larvae are clearly visible through the delicate chorion (Bakkendorf, 1925; Clausen, 1940; Enock, 1914; Ison, 1959; Mac Gill, 1934; May, 1971; Morcos, 1953; Mulla, 1953; Olmi, 1970; Otake, 1968; Rothschild, 1966, 1967; Tay, 1972; Whalley, 1969). This characteristic change in coloration made the overwintering *Anagrus* sp. B and sp. C conspicuous inside the *C. viridis* overwintering eggs. The developmental stage of the collected material was assessed through the chorion of the host as well as the number and sex of the parasitoids.

6. Sex ratio in field collected parasitoids

Information regarding the sex ratio of the Mymaridae is available for only a small number of species (Clausen, 1940).

The proportion of sexes is biased toward the males in *Polynema striaticornis* (Balduf, 1928) but generally females outnumber the males (Armstrong, 1935; Anderson and Paschke, 1968, 1969; Jackson, 1966; Kuwayama, 1935; Maillet, 1960; May, 1971; Mossop, 1929; Otake, 1969; Pickles, 1932; Raatikainen, 1967; Satterthwait, 1931; Tay, 1972; Walker, in press; Whalley, 1969). The sex ratio of samples of *Caecilius flavidus* (Stephens) did not differ consistently from unity (New, 1969).

Male and female *Anagrus atomus* (Walker's sp. C) were frequently recorded by Tay (1972) together within a single *C. viridis* host egg, though he found several hosts with individuals of the same sex. Whalley (1966, 1969) recorded a sex ratio of three females to one male in *Anagrus atomus* and *A. incarnatus* (Walker's sp. B and sp. C) which were found parasitizing *C. viridis* overwintering eggs.

Walker (in press) gave the sex ratio of field material, which, according to her, should reflect the "natural" value. She found 71% of females in *Anagrus* sp. C bred from *C. viridis* and 65% of *Anagrus* sp. B females bred from *M. fairmairei*.

Egg batches of *C. viridis* were collected periodically (see Section II-v-3-b) and the sex of the *Anagrus* sp. B and sp. C adults, obtained from parasitized batches, was recorded whenever possible. Results are shown in Table 14.

The sex ratio of *Anagrus* sp. B was calculated as 72.38% females and as 71.84% females in *Anagrus* sp. C. These results agree with Whalley's (1968 and 1969) and Walker's (in press) results. Tay (1972) recorded 58.75% of females in *Anagrus atomus*, (Walker's sp. C) which were considerably lower than the other results.

The sex ratio of the progeny of *Anagrus* sp. B and C bred from field collected *C. viridis* eggs in relation to the number of parasitoids present in the host egg is shown in Fig. 31 and Appendix Table 6.

Evidence supporting the occurrence of parasitism by a virgin female, was recorded in only 3 of the 37 observations (8.1%) in *Anagrus* sp. B and 15 of the 259 observations (5.8%) in *Anagrus* sp. C. Both species showed a high proportion of parasitized hosts with a majority of female parasitoids, 81% in sp. B and 87% in sp. C. The presence of male and female parasitoids in the same host egg would also facilitate mating.

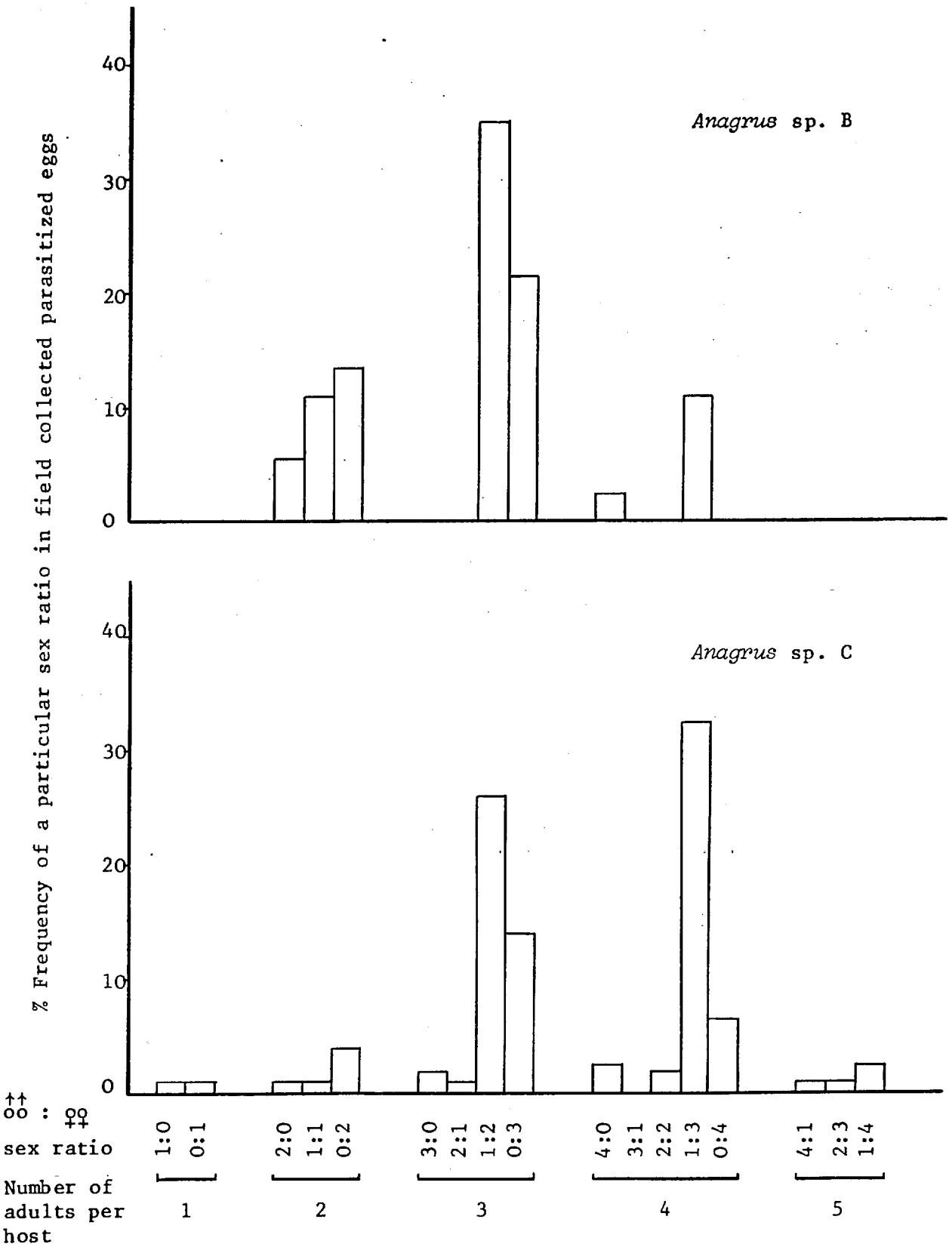



Figure 31. Sex ratio of *Anagrus* sp. B and sp. C, parasitizing field-collected *C. viridis* eggs in relation to the number of parasitoids present in the host egg.

Table 14. Sex ratio of *Anagrus* sp. B and sp. C, parasitising *C. viridis* in the field.

| | Number of hosts collected | Number of parasites | | | Sex ratio % ♀♀ |
|---|---|---|---|---|---|
| | | ♂♂ | ♀♀ | ♂♂ + ♀♀ | |
| *Anagrus* sp. B | 37 | 29 | 76 | 105 | 72.38 |
| *Anagrus* sp. C | 259 | 252 | 643 | 895 | 71.84 |

# CHAPTER II

## THE OVIPOSITION BEHAVIOUR OF *ANAGRUS* SPP

### i. Introduction

The manner by which hosts are actually found, and the many factors that determine the existence and maintenance of a particular host-parasitoid relationship are among the most challenging and fascinating research problems in the biology of parasitoids (Doutt, 1964).

After emergence, the adult female parasitoid is often in an alien habitat. She must find a suitable host in order to propagate. With a parasitoid as minute as *Anagrus* with presumably corresponding difficulties of directionally controlled long range movement, the problem is even more intriguing.

Combining the information of Salt (1935) and Flanders (1953), Doutt (1959) divided the process that results in successful parasitism into four steps: host-habitat location, host-finding, host-acceptance and host-suitability. Vinson (1975), proposed a fifth step, that of host-regulation, in order to adequately describe the factors necessary for successful parasitism. After the host has been accepted for oviposition, the female appears to inject materials, along with the eggs. Vinson (1975) concluded that the evolutionary significance of host regulation can only be speculated. 'Host regulation' was an unfortunate choice of terms because it is extensively used by ecologists in another context. Perhaps 'host modification' would have been a better choice.

In this section, the host finding and oviposition behaviour of *Anagrus* sp. B and sp. C will be described and compared. Evidence on avoidance of superparasitism will be given.

ii. Material and methods

Laboratory reared *Anagrus* sp. B and sp. C females were used. Both species of parasitoids were bred from laboratory cultured *D. hamata* eggs and overwintering *C. viridis* eggs. Parasitized *C. viridis* eggs containing three individuals were selected and the females emerging from them were used. The newly emerged females were allowed to mate and then confined in an observation chamber made from a corked glass tube (9 x 3 cm). An entomological pin was deeply inserted in the center of the cork which held a length of *Juncus* bearing the *C. viridis* eggs or an oat seedling containing *D. hamata* eggs. The *Juncus* stem was split open to expose the egg batch. A holder was glued to the outside of the cork and attached to a stand to allow the apparatus to rotate. Observations were made with the aid of a stereoscopic dissecting microscope and the activity of the wasp was recorded for 60 min on a four track event recorder or registered by a video tape recorder. The host eggs were dissected 48 hours after the experiment and the number of marks observed on the chorion of the host egg and the number of parasitoid eggs present in each host were recorded. The experiments were carried out at 20°C.

iii. Size of the host egg

The length and the greatest width of *C. viridis* overwintering eggs were measured and the results are given in Table 15.

Thompson (1977) measured the eggs of *D. hamata*, his results are also shown in Table 15.

The difference in size of the three host species considered in this study is shown in Fig. 32. The eggs of *M. fairmairei* and *D. hamata* are similar in size whilst both species have eggs considerably smaller than those of *C. viridis*.

Table 15. Size of *C. viridis* and *D. hamata* eggs.

(measurements in mm)

| | Length | | | Width | | | Number of observations |
|---|---|---|---|---|---|---|---|
| | Mean | SD | Range | Mean | SD | Range | |
| *C. viridis* | 1.76 | 0.060 | 1.60 - 1.90 | 0.45 | 0.035 | 0.37 - 0.54 | 50 |
| *D. hamata* (Thompson, 1977) | 0.92 | - | 0.84 - 1.00 | 0.21 | - | 0.18 - 0.24 | 20 |

Several *C. viridis* overwintering eggs were weighed. An average of 0.178 mg (n = 23; SD = 0.075, range 0.169 - 0.195) was calculated. Hill (1976) estimated the dry weight of *D. hamata* eggs, killed in the deep freeze, as 0.013 mg (n = 250; 95% fiducial limits = 0.0002). Assuming that the fresh weight of *D. hamata* eggs is approximately five times greater than its dry one, it can be estimated that the fresh weight of *C. viridis* eggs is two or three times greater than that of *D. hamata*.

iv. Host finding and oviposition behaviour of *Anagrus* sp. B and sp. C

The series of events which lead to oviposition in an unparasitized host or to the rejection of an already parasitized host by *Anagrus* sp. B and sp. C were studied in the laboratory.

The aims of this section are twofold: firstly, to describe and compare the host finding behaviour and the handling of unparasitized and already parasitized hosts by *Anagrus* sp. B and sp. C, and secondly, to investigate the effect the host species may have on the female's ability to handle these hosts.

1. Material and methods

The activity of several *Anagrus* sp. B and sp. C females, bred from *C. viridis* eggs, parasitizing eggs of *D. hamata* and *C. viridis*, was recorded with the aid of a video tape recorder attached to a stereoscopic dissecting microscope. A four track event recorder was used for timing the activity of the females.

A newly emerged, mated *Anagrus* sp. B or sp. C female, bred from *C. viridis* eggs, was introduced into an observation chamber which contained a stem of an oat seedling with batches of *D. hamata* eggs or a piece of *Juncus* stem containing *C. viridis* eggs.

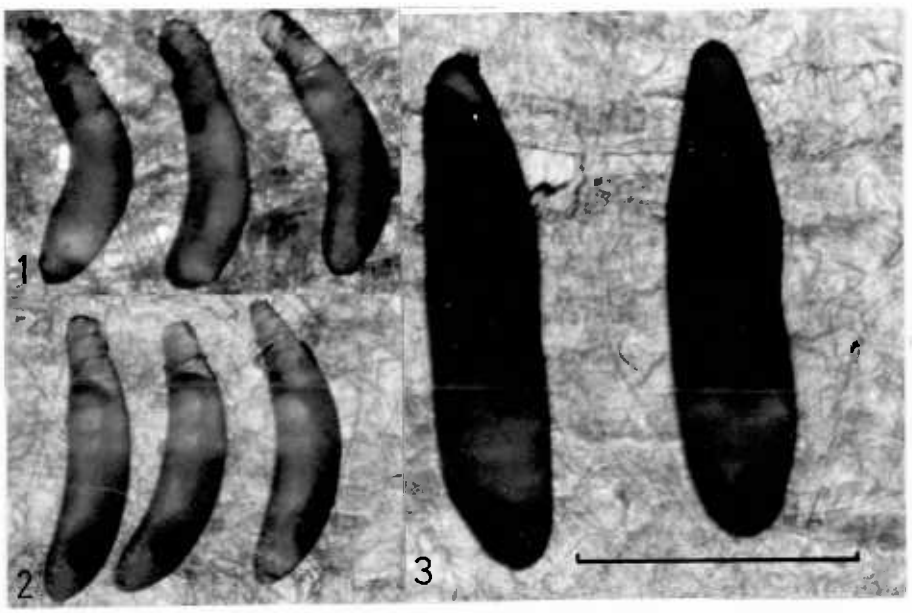



Figure 32. Size of the host egg.

1. *Müellerianella fairmairei* (Perris)
2. *Dicranotopis hamata* (Boh.)
3. *Cicadella viridis* (L.)

Scale 100 µ

The position of the egg batches in the stem was known. For convenience, the parasitoid females used in this experiment were labelled B(vv) and C(vv) when bred from *C. viridis* and offered *C. viridis* eggs to parasitize; B(vh) and C(vh) when bred from *C. viridis*, parasitizing *D. hamata* eggs and B(hh) and C(hh) when bred and offered *D. hamata* eggs.

After the experiment the eggs were dissected out of the stem and the number of marks on the chorion and the number of parasitoid eggs in the host egg were recorded.

2. Results

The activity of females B(vh); B(vv); C(vh) and C(vv) was studied with the aid of a video tape recorder.

Experiments with females B(vh)

The *Anagrus* sp. B female moved relatively quickly over the stem of the oat seedling while searching for the batch of eggs, constantly tapping the substratum with the last subsegment of the antennae. The antennal flagelum was held at right angles to the scapus. When the female was on the walls of the observation chamber, she walked faster than on the stem and the search was less careful or persistent.

Upon finding a batch of eggs, the female slowed down her pace. The frequency of tapping with the antennae increased considerably, with the tips remaining very close to the stem.

The presence of host eggs was marked by a scar made when they were laid. When the eggs were laid parallel to the surface of the stem, an elevation or bump could be seen. If the eggs were laid perpendicular or at an angle to the surface, no bump was apparent.

Usually the female first examined the scar, then the bump, but sometimes only the bump. Frequently in her search, she probed into bumps which did not contain a scar or eggs.

When the female encountered a bump, she walked over it, until her antennae touched the other edge of the bump. Then she turned through $180^{o}$ and retraced her steps. Sometimes she repeated this procedure up to four times, tapping continuously with her antennae. After her last turn, she stopped almost immediately and in so doing placed herself on top of the bump. The tapping ceased completely and the antennae were raised over the head. They were held almost motionless throughout the rest of the process, except when they moved with the rest of the body.

The female arched her body and this helped to unsheath the ovipositor, which was then lowered, perpendicular to the stem. The female's body formed an angle of approximately $30^{o}$ to the stem and was parallel to its main axis.

The stem appeared to offer little resistance to the penetration of the ovipositor whose tip reached the chorion in about ten seconds. Drilling proceeded immediately. If the female missed the host egg or no egg was present in the bump, the ovipositor was inserted to almost its full length before being withdrawn.

The action of drilling was produced by quick, sideway movements of the whole body. It was completed when there was a sudden lack of resistance to the downward drive of the ovipositor, which indicated that the chorion was pierced. At the same time, all apparent motion stopped and the female remained motionless for a few seconds. Contractions in the area where the ovipositor is attached to the base of the abdomen, were then observed. The female resumed movement with a see-saw-like,

pumping motion, over the ovipositor. The ovipositor, which was inserted $^2/_3$ of its length into the stem, remained stationary, whilst the whole body, including the antennae, moved. The pumping went on with different intensities but continuously until the action was completed and the ovipositor withdrawn.

In the cases where the female came across an oviposition scar with no apparent bump, she inspected the scar with her antennae and made one or two turns over the scar, similar to those she did over a bump. Once in position, she inserted her ovipositor somewhere in the vicinity of the scar; but never directly over the scar.

It was observed that the female was more successful in attacking hosts in a bump, lying close and parallel to the surface, than when she attacked eggs laying perpendicular or at an angle to the surface of the stem.

The whole process was observed several times and the parasitized hosts were removed from the stems and dissected. The position of the eggs on the stem and those which were parasitized were recorded. The number of times a particular host was attacked, was found by direct observation and verified by counting the number of marks left on the chorion where the ovipositor came in contact with it. Fig. 33, shows the typical marks left by the ovipositor on the chorion of *C. viridis* eggs.

Irrespective of the number of times each host was attacked, only one parasitoid egg was found on dissection. In the times when a second attack was witnessed only one parasitoid egg but two marks on the chorion of the host egg were recorded. During the first attack, the female always performed the whole sequence of events as described above, i.e.

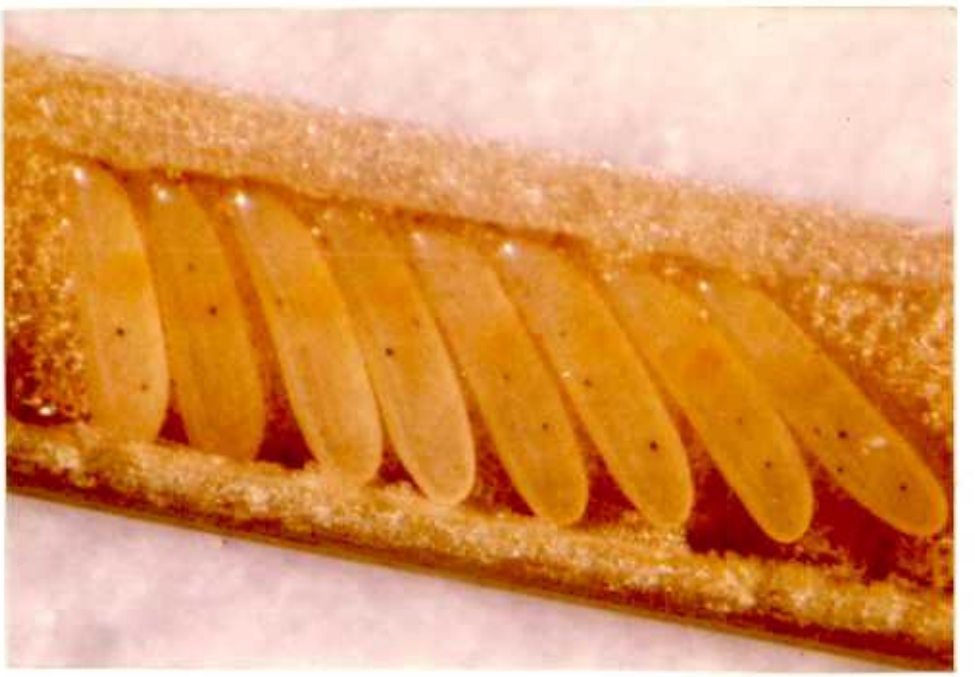


Figure 33. Parasitized overwintering *C. viridis* eggs showing the oviposition marks left by the ovipositor of *Anagrus*.

drilling; pumping; withdrawal (from here on this whole process will be named "stinging"). When a second attack was made on the same host, no pumping was observed, and the ovipositor was withdrawn immediately after the drilling stopped, i.e. an already parasitized host was rejected (from here on this will be known as "rejecting").

The absence of the pumping movement during rejection and the fact that only one parasitoid egg was ever found in a *D. hamata* host, justifies the conclusion that pumping was correlated directly with egg laying.

After an attack was completed, the female resumed her search. Sometimes, she inspected the same bump and made further attempts to attack eggs. She might or might not encounter the same egg, when this happened, the host was rejected. Most often the female moved away and continued her search elsewhere; or she might groom different parts of her body. The antennae were groomed by the strigil of the prothoracic tibia; the prothoracic legs were groomed by using the mouthparts and the metathoracic legs groomed the wings, abdomen and ovipositor sheath. On other occasions the female remained motionless for a while.

Experiments with females C(vh)

The series of events which lead to attacks on *D. hamata* eggs by *Anagrus* sp. C females was studied in order to compare it with the attacks of B(vh) females. Both species had similar behaviour but they differed in a few respects. The C(vh) female had to arch her body more than B(vh) because her longer ovipositor was more difficult to unsheath and place over the stem. This also caused the body of C(vh) females to make less of an angle with the stem than B(vh) females whilst attacking the host.

Experiments with females B(vv)

*Anagrus* sp. B females, bred from *C. viridis* were offered *C. viridis*

hosts in order to obtain information on the effect the offered host may have on the performance of the female parasitoid.

The pattern of behaviour of females B(vv) was seen to be very similar to that of females B(vh) (see above).

A row of several *C. viridis* eggs on a piece of *Juncus* stem was offered to the female. Normally she searched along the stem when she came across the eggs, but did not necessarily inspect the first egg in the row. She began her inspection by walking slowly over the length of the egg, tapping with her antennae. On reaching one end, she turned through 180°, then retraced her steps until she reached the other end and turned again. This procedure might or might not be repeated. Normally, after a turn, she stopped and attempted to sting the egg. However, sometimes the ovipositor skidded on the surface of the chorion which prevented her from stinging the egg; further attempts were made on the same spot. After one or several failures she resumed her search. This search took her to the other end of the same egg or onto the *Juncus* stem, whereupon turning she mounted the same or another host.

Normally, all attempted attacks by the female were made with her body in line with the length of the host. When the female successfully placed her ovipositor, drilling followed immediately. Noticeable stops during a long pumping period were observed. On several occasions, the number of times pumping stopped during a single attack were recorded. On dissection, the number of parasitoid eggs found in the host corresponded to the number of times pumping was stopped. Up to four parasitoid eggs were found in hosts attacked only once.

On encountering an already parasitized host, the female might or might not reject it. Usually she did so but sometimes more eggs were

laid. Such cases where eggs were laid in an already parasitized host, are examples of superparasitism.

Experiments with females C(vv)

Basically, the pattern of behaviour of C(vv) females followed that of C(vh) previously described. When attacking the big *C. viridis* eggs, she handled them in a similar way to B(vv), but on encountering already parasitized hosts, she rejected them more often than superparasitizing them.

3. Discussion

Witsack (1973) studied the oviposition process of *Anagrus incarnatus* attacking *Anakelisia fasciata* and concluded that his results can be widely applied to other species of *Anagrus*. He only described the handling of unparasitized hosts.

The basic pattern of behaviour of *Anagrus* sp. B and sp. C was found to be very similar to that of *A. incarnatus* described by Witsack (1973).

The role of the antennae in host finding by mymarid parasitoids has been described by several authors (Anderson and Paschke, 1968; Bakkendorf, 1925; Balduf, 1928; Dumbleton, 1934; Enock, 1914; Ison, 1959; Mac Gill, 1933; May, 1971; Mossop, 1929; Rothschild, 1962, 1967; Tooke, 1955 and Witsack, 1973). In the present study, *Anagrus* sp. B and sp. C appeared to use their antennae to locate the batches of host eggs in the plant stem.

In handling unparasitized *D. hamata* hosts, *Anagrus* sp. B and sp. C females were observed to drill on the host and only one parasitoid egg was laid. After the attack was completed, the female resumed her search. Grooming and resting were also observed.

After encountering an already parasitized host, rejection always occurred. Drilling but never pumping was seen in these instances.

Morphological differences between both species, i.e. length of the ovipositor, were seen to affect the handling of the host.

On handling unparasitized *C. viridis* hosts, *Anagrus* sp. B and sp. C females were observed to drill and up to four parasitoid eggs were laid in a single attack. One to three eggs per host were laid by *Anagrus* sp. B and two to four eggs per host were laid by *Anagrus* sp. C.

The number of times both parasitoid females stopped during pumping gave a clear indication of the number of eggs laid in the host.

After the attack was completed, the female resumed her search. Grooming and resting were also observed.

On encountering an already parasitized host, rejection did not always occur. In some cases superparasitism was observed. Drilling but never pumping was observed during rejection.

*Anagrus* sp. C did not superparasitize as often as *Anagrus* sp. B. This will be discussed later.

On observation it appeared that there were varying differences in time during the handling of unparasitized and already parasitized *D. hamata* and *C. viridis* hosts by either parasitoid species. Experiments were set up to confirm this and are explained in the next section. In the present study, handling time was considered as the lapse of time between the insertion and withdrawal of the ovipositor.

v. The time spent handling unparasitized and parasitized hosts by *Anagrus* sp. B and sp. C females

In the last section, the handling of unparasitized and parasitized *D. hamata* and *C. viridis* hosts by *Anagrus* sp. B and sp. C females was observed to differ. In this section, the handling times for *D. hamata* and *C. viridis* hosts were studied and compared.

1. Material and methods

The activity of females B(vv), B(vh), B(hh), C(vv), C(vh) and C(hh) was studied in the laboratory. A four track event recorder was used to measure the time spent handling the hosts.

Three of the four tracks of the event recorder were used. The "stinging" and "rejecting" events were recorded on track 1, starting from the moment when the ovipositor made contact with the chorion, until the ovipositor was withdrawn. The exact position of the host attacked was also recorded. This gave the information whether a particular host, attacked for the second time, was superparasitized or rejected. Track 2 was used to record when the "drilling" event was finished, i.e. the ovipositor succeeded to pierce the chorion. Therefore, "pumping", the egg-laying event, was estimated by subtracting the time spent "drilling" from the time spent "stinging". On several occasions, the number of eggs laid in a single attack was recorded. On track 3, which was used for this purpose, the number of stops during "pumping" was recorded.

After the experiment, the eggs were dissected out of the stem and the number of marks on the chorion and the number of parasitoid eggs in the host egg were counted.

2. Results

Results of the time spent "drilling" and "stinging" in hosts or "rejecting" already parasitized host eggs by *Anagrus* sp. B and sp. C females are given in Appendix Table 7.

The time spent egg-laying was estimated. Results of "egg-laying", "drilling" and "rejecting" are summarized in Table 15.

The duration of the "drilling", "egg-laying" and "rejecting" events was compared within and between both parasitoid species which attacked *D. hamata* and *C. viridis* hosts. Results are given in Table 17.

3. Discussion

Comparisons within both parasitoid species showed that when the large females bred from *C. viridis* were allowed to parasitize the small, *D. hamata* hosts or the large, *C. viridis* hosts, the "drilling" and "rejecting" events took longer on *D. hamata* than on *C. viridis* hosts. *Anagrus* sp. B and sp. C females, bred from *D. hamata* hosts, were smaller than females bred from *C. viridis*. No difference in the laying of an egg or in "rejecting" were observed when these females were allowed to parasitize *D. hamata* eggs.

The bigger B(vh) females drilled faster than the smaller B(hh) females. A similar result was observed for *Anagrus* sp. C, but the difference was non significant ($0.10 > p > 0.05$).

Comparisons between *Anagrus* sp. B and sp. C, showed that when large females bred from *C. viridis* were allowed to parasitize the small, *D. hamata* hosts, the "drilling", "laying one egg" and "rejecting" events took considerably longer in sp. B.

Table 15. Time spent drilling and laying eggs in unparasitized host eggs or in rejecting already parasitized host eggs by *Anagrus* sp. B and sp. C females*.

| *Anagrus* sp. | Bred from | Parasitizing | TIME SPENT (sec) Drilling | Laying one egg | Laying two eggs | Laying three eggs | Laying four eggs | Rejecting | Average number of hosts attacked |
|---|---|---|---|---|---|---|---|---|---|
| B(vv) | *C. viridis* | *C. viridis* | 32.6 ± 8.9 (23) | 74.0 ± 11.0 (6) | 129.3 ± 42.7 (7) | 204.0 ± 26.9 (10) | - | 42.2 ± 7.9 (5) | 6.5 ± 0.6 (4) |
| B(vh) | *C. viridis* | *D. hamata* | 64.3 ± 9.3 (13) | 81.8 18.8 (13) | | | | 57.2 ± 11.2 (19) | 11.0 ± 2.0 (2) |
| B(hh) | *D. hamata* | *D. hamata* | 53.2 ± 10.6 (18) | 70.4 16.2 (17) | | | | 59.8 ± 14.4 (12) | 12.0 ± 2.8 (2) |
| C(vv) | *C. viridis* | *C. viridis* | 34.5 ± 11.8 (49) | - | 120.6 ± 42.8 (13) | 188.2 26.5 (30) | 260.4 ± 49.2 (2) | 33.9 ± 11.5 (42) | 7.6 ± 0.5 (7) |
| C(vh) | *C. viridis* | *D. hamata* | 56.1 ± 10.8 (19) | 63.8 ± 6.3 (17) | | | | 47.3 ± 4.7 (10) | 22.0 ± 9.6 (3) |
| C(hh) | *D. hamata* | *D. hamata* | 50.7 ± 8.1 (27) | 62.0 ± 7.9 (27) | | | | 48.1 ± 6.9 (11) | 16.5 ± 2.1 (2) |

* Mean ± SD, (number of observations)

Table 17. Comparison between the time spent by *Anagrus* sp. B and sp. C females drilling and laying eggs in unparasitized host eggs and in rejecting already parasitized hosts.

| Comparison between | Event | t-value | Probability | Degree of freedom |
|---|---|---|---|---|
| B(vv) : B(vh) | drilling | 10.04 | p<0.001 | 34 |
| | laying one egg | 1.04 | N.S. | 17 |
| | rejecting | 2.79 | 0.05>p>0.01 | 22 |
| B(vv) : B(hh) | drilling | 6.76 | p<0.001 | 39 |
| | laying one egg | 0.17 | N.S. | 21 |
| | rejecting | 2.54 | p<0.05 | 15 |
| B(vh) : B(hh) | drilling | 3.02 | 0.01>p>0.001 | 29 |
| | laying one egg | 1.72 | N.S. | 28 |
| | rejecting | 0.56 | N.S. | 29 |
| C(vv) : C(vh) | drilling | 6.94 | p<0.001 | 66 |
| | rejecting | 2.79 | 0.01>p>0.001 | 50 |
| C(vh) : C(hh) | drilling | 1.94 | N.S. | 44 |
| | laying one egg | 0.51 | N.S. | 42 |
| | rejecting | 0.53 | N.S. | 19 |
| C(vv) : C(hh) | drilling | 6.34 | p<0.001 | 74 |
| | rejecting | 4.04 | p<0.001 | 19 |
| B(vv) : C(vv) | drilling | 0.12 | N.S. | 60 |
| | laying two eggs | 1.40 | N.S. | 18 |
| | laying three eggs | 1.63 | N.S. | 40 |
| | rejecting | 1.56 | N.S. | 38 |
| B(vh) : C(vh) | drilling | 2.22 | 0.05>p>0.01 | 30 |
| | laying one egg | 3.71 | p<0.001 | 28 |
| | rejecting | 2.67 | 0.05>p>0.01 | 27 |

Table 17. Continued

| Comparison between | Event | t-value | Probability | Degree of freedom |
|---|---|---|---|---|
| | drilling | 0.90 | N.S. | 43 |
| B(hh) : C(hh) | laying one egg | 2.32 | 0.05>p>0.01 | 42 |
| | rejecting | 2.33 | 0.05>p>0.01 | 21 |

When the small *Anagrus* sp. B and sp. C females, bred from *D. hamata*, were allowed to parasitize *D. hamata*, the "laying one egg" and "rejecting" events also took longer in sp. B than in sp. C. However, the difference in "drilling" times were surprisingly not significant between the species although if there had been more data perhaps they would.

When the larger *Anagrus* sp. B and sp. C females were allowed to parasitize *C. viridis*, none of the comparisons were significant. However, the results shows that *Anagrus* sp. B were slightly slower.

Further experiments may succeed in showing this difference.

vi. Avoidance of superparasitism

Superparasitism is avoided when the female rejects an already parasitized host instead of laying more eggs on it.

During the experiments discussed above, varying degrees of avoidance of superparasitism were observed in both parasitoid species.

1. Results and discussion

*Anagrus* sp. B and sp. C females were seen to avoid superparasitism in *D. hamata* hosts to a great extent. All the attacks on already superparasitized hosts resulted in the rejection of these hosts. Amongst hundreds of *D. hamata* host, checked during the mass-culturing of the parasitoids, in only one occasion, a host with two *Anagrus* sp. B larvae was found.

A number of *D. hamata* hosts dissected yielded only one parasitoid egg per host. Canibalism was never witnessed nor any evidence of it was ever found.

*Anagrus* sp. B and sp. C females were also seen to avoid super-

parasitism in *C. viridis* hosts but not to the same degree. Table 18 shows that the number of attacks made by both parasitoid species recorded during the experiment, were very similar to the number of punctures left on the chorion of the host. The number of times rejection, or failure to reject i.e. super-parasitism, occurred is also shown.

The number of attacks recorded for *Anagrus* sp. C females was greater than for *Anagrus* sp. B but the difference was non significant ($0.1>p>0.05$).

Not only *Anagrus* sp. B females accepted already parasitized *C. viridis* hosts more often than *Anagrus* sp. C but several females were seen to superparasitize on more than one occasion. All four *Anagrus* sp. B females laid eggs in already parasitized hosts but only two out of seven *Anagrus* sp. C did the same, superparasitizing only once.

The lapse of time between two consecutive attacks on the same *C. viridis* hosts by *Anagrus* sp. C females varied between 30 and 130 sec. Rejection after the first attack occurred any time between 30 and 90 sec. On six occasions, rejection took place before 60 sec and on three occasions it happened later. On one occasion superparasitism took place 53 sec after the first attack and on another occasion, it occurred after 130 sec. It is interesting to note that an already parasitized *C. viridis* host was rejected as early as 30 sec after the first attack.

*Anagrus* sp. B females were seen to superparasitize *C. viridis* hosts from 24 to 60 sec ($n = 4$) after the first attack. Superparasitism was also observed after 9 and 16 minutes after the first attack.

vii. General discussion

The host finding and oviposition behaviour of *Anagrus* sp. B and sp. C is similar.

Table 18. The handling of *C. viridis* hosts by *Anagrus* sp. B and sp. C females bred from *C. viridis* hosts.

| Female No. | eggs attacked | attacks recorded | punctures on chorion | rejections | Times superparasitism occur | parasitoid eggs found |
|---|---|---|---|---|---|---|
| C sp. | | | | | | |
| 028 | 8 | 18 | 17 | 10 | 0 | 24 |
| 030 | 7 | 14 | 14 | 6 | 0 | 18 |
| 031 | 8 | 25 | 26 | 17 | 0 | 18 |
| 035 | 7 | 13 | 13 | 4 | 0 | 12* |
| 036 | 8 | 13 | 13 | 5 | 0 | 25 |
| 037 | 7 | 12 | 12 | 4 | 1 | 24 |
| 038 | 8 | 11 | 11 | 2 | 1 | 26 |
| B sp. | | | | | | |
| 003 | 7 | 12 | 12 | 3 | 2 | 18 |
| 044a | 7 | 10 | 10 | 1 | 2 | 27 |
| 044b | 6 | 9 | 9 | 2 | 1 | 17 |
| 045 | 6 | 8 | 8 | 0 | 2 | 12 |

* One host was attacked and went bad before dissection was carried out.

The antennae appear to play an important role, not only finding the batch of eggs, but also helping the female in positioning herself on top of the host egg. When the ovipositor encounters the chorion of the host, "drilling" starts immediately. "Pumping", i.e., "egg laying", follows after the chorion is pierced. The parasitoid female would lay one or several eggs depending on the host. If the parasitoid female is observed while attacking a *C. viridis* host, the number of eggs she lays can be assessed.

Witsack (1973) reported that only one *A. incarnatus* adult emerged from superparasitized *Anakelisia fasciata* eggs due to canibalism. There is no evidence of canibalism in *Anagrus* sp. B and sp. C.

*Anagrus* sp. B tend to be slower handling hosts than sp. C. When both parasitoid species, bred from *C. viridis* hosts, are offered both species, *D. hamata* hosts tend to be handled more slowly than *C. viridis*. If females bred from different host species are offered the same host, the small females bred from *D. hamata* tend to handle their hosts more quickly than the ones bred from *C. viridis*.

Both *Anagrus* species are able to reject an already parasitized host. Rejection always takes place after drilling.

The rejection of hosts after ovipositor insertion has also been observed for a number of parasitoid species (Doutt, 1964; Fisher, 1961; Jackson, 1969; King and Rafai, 1970; Van Lenteren, 1976; Wylie, 1965).

Wylie (1965) and Jackson (1966) suggested that secretions from the poison reservoir deposited during egg laying might render the host unacceptable to another female. Van Lenteren (1976) showed that the factor which causes avoidance of superparasitism needed a period for

building up.

The results from the present study show that when the smaller *D. hamata* hosts are attacked, both *Anagrus* spp. completely avoid superparasitism but when they attack the larger *C. viridis* hosts, the degree of avoidance varies. *Anagrus* sp. C is more efficient at avoiding superparasitism. Rejection can occur as early as 30 sec after the first attack. Whereas *Anagrus* sp. B, less efficient avoiding superparasitism, can superparasitize up to 15 min after the first attack.

# CHAPTER III

## THE EFFECT OF THE HOST SPECIES UPON THE PARASITOID

### i. Introduction

The effect of the host species upon their parasitoids was discussed by Salt (1940, 1941). He was concerned with the changes the host species were able to produce in the morphology, physiology and behaviour of their parasitoids.

New (1969) showed that the size and developmental time of the mymarid *Alaptus pallidicornis* was affected when bred from three different species of psocid. The longevity of the females was also affected, but the total progeny reared from females of different sizes did not differ greatly.

The observed changes in the behaviour of *Anagrus* sp. B and sp. C, as a result of attacking different host species have already been discussed. In this section, the morphological and physiological changes that the different host species could have on both parasitoid species will be studied and discussed.

### ii. Material and methods

*Anagrus* sp. B and sp. C females bred from *D. hamata* and *C. viridis* hosts were labelled B(h), B(v), C(h), and C(v). Standard B(v) and C(v) females selected from host eggs which contained three parasitoids were used.

A newly emerged, mated female bred from a known host was introduced into a breeding chamber and provided with plenty of hosts. *C. viridis* and *D. hamata* hosts, or a mixture of both hosts were provided. The female was allowed to parasitize the hosts for 24 hrs and then dissected.

The number of eggs in the ovaries and the size of the female was recorded. The host eggs were dissected out of the stem and the number of hosts attacked and the number of parasitoids per host was recorded as soon as the parasitoid larvae were seen inside the host egg. The sex and number of adult parasitoids which emerged in each breeding cage was recorded daily. The experiments were carried out in a $20^{o}$ C.T. room.

iii. Effect on size

Several *Anagrus* sp. B and sp. C females bred from *D. hamata* and standard females bred from *C. viridis* were measured and compared. The lengths of the ovipositor; the hind tibia and forewing were used to estimate the size of the females. The results are shown in Tables 19-21.

Standard *Anagrus* sp. B and sp. C females bred from *C. viridis* had the ovipositor and the hind tibia considerably larger ($p<0.001$) than females bred from *D. hamata* hosts. The length of the forewing was also larger in females bred from *C. viridis*; the difference was significant (*Anagrus* sp. B, $p<0.001$; *Anagrus* sp. C, $0.05>p>0.01$).

iv. Effect of fecundity

The females considered in the previous section were dissected, immediately after emergence, and the number of eggs in their ovaries were counted. The results are shown in Table 22.

The standard *Anagrus* sp. B and sp. C females bred from *C. viridis* had more eggs in the ovaries than those bred from *D. hamata*.

v. Effect on developmental time

A newly emerged, mated, standard female bred from *C. viridis*, was introduced into a breeding chamber and provided with a mixture of *C. viridis* and *D. hamata* hosts. The female was allowed to parasitize the

Table 19. The effect of the host on the length of the ovipositor of *Anagrus* sp. B and sp. C females*.

| | Length of the ovipositor in mm | t-value | DF | Probability |
|---|---|---|---|---|
| B(v) | 0.474 ± 0.011 (14) | 34.50 | 29 | p<0.001 |
| B(h) | 0.325 ± 0.013 (17) | | | |
| C(v) | 0.555 ± 0.023 (11) | 6.55 | 15 | p<0.001 |
| C(h) | 0.488 ± 0.009 (6) | | | |

* Mean ± SD (number of observations)

Table 20. The effect of the host on the length of the hind tibia of *Anagrus* sp. B and sp. C females*.

| | Length of the hind tibia in mm | t-value | DF | Probability |
|---|---|---|---|---|
| B(v) | 0.281 ± 0.019 (14) | 10.16 | 29 | p<0.001 |
| B(h) | 0.228 ± 0.007 (17) | | | |
| C(v) | 0.285 ± 0.008 (11) | 8.96 | 15 | p<0.001 |
| C(h) | 0.248 ± 0.008 (6) | | | |

* Mean ± SD (number of observations)

Table 21. The effect of the host on the length of the forewing of *Anagrus* sp. B and sp. C*.

| | Length of the forewing in mm | t-value | DF | Probability |
|---|---|---|---|---|
| B(v) | 0.639 ± 0.029 (14) | 10.15 | 29 | p<0.001 |
| B(h) | 0.552 ± 0.018 (17) | | | |
| C(v) | 0.633 ± 0.024 (11) | 2.85 | 15 | 0.05>p>0.01 |
| C(h) | 0.602 ± 0.015 (6) | | | |

* Mean ± SD (number of observations)

Table 22. The effect of the host on the fecundity of *Anagrus* sp. B and sp. C females*.

| | Number of the in the ovaries | t-value | DF | Probability |
|---|---|---|---|---|
| B(v) | 61.93 ± 7.77 (14) | 3.87 | 29 | p<0.001 |
| B(h) | 48.82 ± 10.51 (17) | | | |
| C(v) | 73.55 ± 9.78 (11) | 4.90 | 15 | p<0.001 |
| C(h) | 57.33 ± 6.95 (6) | | | |

* Mean ± SD (number of observations)

hosts for 24 hrs and then removed from the chamber. The hosts were dissected out of the stem and each host species was kept in separate chambers until the emergence of the parasitoids. The breeding chambers were checked daily until the total emergence of the parasitoid adults was recorded. Replicates of the experiments where the females parasitized both hosts offered were selected and an overall mean of the length of the developmental period was estimated and compared. The results are shown in Table 23 and Table 24 shows the results of the comparison.

*Anagrus* sp. C developed faster than *Anagrus* sp. B in both host species, the difference was highly significant ($p<0.001$).

The length of the developmental period of *Anagrus* sp. B which developed in *D. hamata* hosts was significantly shorter ($p<0.001$) than those which developed in *C. viridis*. *Anagrus* sp. C developed significantly faster in *C. viridis* ($p<0.001$) than in *D. hamata*.

vi. Effect on number of progeny

A newly emerged, mated female, bred from a known host, was introduced into a breeding chamber and provided with an abundance of *C. viridis* or *D. hamata* hosts. The female was allowed to parasitize the host for 24 hrs.

The host eggs were dissected out of the stem and the number of progeny was recorded as soon as the parasitoid larvae were seen inside the host egg. The sex of the adult parasitoids which emerged in each breeding cage was recorded.

Table 25 shows the results of the number of females which produced progeny and the total number of females studied. The sex ratio of the resultant progeny is also shown.

Table 23. The effect of the host on the length of the developmental period in *Anagrus* sp. B and sp. C*.

| Progeny | Length of the developmental period in days |
|---|---|
| B(h) | 26.5 ± 2.26 (152) |
| B(v) | 27.8 ± 1.44 (122) |
| C(h) | 24.1 ± 1.17 (39) |
| C(v) | 22.6 ± 1.14 (47) |

* Mean ± SD (number of observations)

Table 24. Comparison between the length of the developmental period of *Anagrus* sp. B and sp. C bred from different hosts.

| Comparison between | t-value | Probability | Degrees of freedom |
|---|---|---|---|
| B(h) : B(v) | 5.78 | $p<0.001$ | 272 |
| C(h) : C(v) | 5.99 | $p<0.001$ | 84 |
| B(h) : C(h) | 9.16 | $p<0.001$ | 189 |
| B(v) : C(v) | 24.61 | $p<0.001$ | 167 |

The results showed that irrespective of the host they were bred from, all the *Anagrus* sp. B females produced progeny in *D. hamata* hosts. However, when the females were offered *C. viridis* hosts, only 50% of the females bred from *C. viridis* produced progeny; but all the females bred from *D. hamata*, failed to produce any.

The percentage of *Anagrus* sp. C females which produced progeny was higher when parasitizing *C. viridis* hosts rather than when parasitizing *D. hamata*.

There was no apparent difference in the sex ratio of the progenies reared from different hosts.

The average number of progeny produced by *Anagrus* sp. B and sp. C females in both host species was estimated and compared. Tables 25 and 26 show the results and Table 27 shows the result of the comparisons.

The host offered did not affect the average number of progeny produced by *Anagrus* sp. B females, bred from *C. viridis* hosts (B(vh) : B(vv); $p>0.05$). However, when females bred from *D. hamata* were offered *C. viridis* hosts, they failed to produce progeny. The average number of progeny produced in *D. hamata* by females bred from the same host, did not differ from the progeny produced by females bred from *C. viridis* hosts (B(hh) : B(vh); $p<0.05$).

The average number of progeny produced by *Anagrus* sp. C females bred from *D. hamata* and *C. viridis* was affected by the host offered (C(hh) : C(hv), $p<0.01$; C(vh) : C(vv), $p<0.001$).

The progenies produced from *C. viridis* hosts were larger than those from *D. hamata*.

Table 25. Number of *Anagrus* sp. B and sp. C females which produced progeny and sex ratio of their progeny in *D. hamata* and *C. viridis* hosts.

| Female | Host offered | Number of females Studied | Number of females Producing progeny | % | Overall sex ratio male : female (% of females) |
|---|---|---|---|---|---|
| B(h) | h | 18 | 18 | 100.0 | 101 : 282 (73.6) |
| | v | 14 | 0 | 0 | 0 |
| B(v) | h | 17 | 17 | 100.0 | 37 : 209 (87.1) |
| | v | 22 | 11 | 50.0 | 101 : 282 (73.6) |
| C(h) | h | 8 | 5 | 62.5 | 6 : 10 (62.5) |
| | v | 9 | 8 | 88.9 | 44 : 153 (77.7) |
| C(v) | h | 11 | 5 | 45.5 | 12 : 41 (77.3) |
| | v | 17 | 12 | 70.6 | 66 : 286 (81.3) |

Table 26. Number of progeny produced by *Anagrus* sp. B and sp. C females which parasitized *C. viridis* and *D. hamata* hosts.

| Female | Host offered | Average number of progeny (± SD) | Number of females which produced progeny |
|---|---|---|---|
| B(h) | h | 25.3 ± 11.7 | 18 |
| | v | 0 | 14 |
| B(v) | h | 22.4 ± 8.7 | 17 |
| | v | 27.0 ± 8.9 | 11 |
| C(h) | h | 3.6 ± 2.7 | 5 |
| | v | 25.6 ± 14.0 | 8 |
| C(v) | h | 11.0 ± 9.4 | 5 |
| | v | 39.8 ± 12.3 | 12 |

Table 27. Comparison between the number of progeny produced by *Anagrus* sp. B and sp. C females which parasitized *C. viridis* and *D. hamata* hosts.

| Comparison between | t-value | Probability | Degrees of freedom |
|---|---|---|---|
| B(vh) : B(vv) | 1.37 | p>0.05 | 26 |
| B(hh) : B(vh) | 0.84 | p>0.05 | 33 |
| C(hh) : C(hv) | 3.42 | p<0.01 | 11 |
| C(vh) : C(vv) | 4.64 | p<0.001 | 15 |
| C(hh) : C(vh) | 1.77 | p>0.05 | 8 |
| C(hv) : C(vv) | 2.38 | p<0.05 | 18 |

The number of progeny produced in *C. viridis* hosts was affected by the size of the female (C(hv) : C(vv); $p<0.05$) females bred from *C. viridis* produced larger progeny than those bred from *D. hamata*. However, the size of the progeny produced in *D. hamata* hosts was affected by the size of the female but the difference was not significant (C(hh) : C(vh); $p>0.05$). If more females were tested, then a significant difference would be expected.

vii. Discussion

The size of *Anagrus* sp. B and sp. C is affected by the size of their hosts. Both species have larger individuals when bred in *C. viridis* hosts.

The host, through its effect on size, affects certain physiological characteristics, such as fecundity. *Anagrus* sp. B and sp. C females bred from *C. viridis* have more eggs in the ovaries than those bred from *D. hamata*. New (1969), showed that the fecundity and developmental time of the mymaridae *Alaptus pallidicornis* was affected by its psocid hosts. However, the total progeny reared from females of different sizes was similar. The present study showed that the number of progeny produced in the first 24 hours of the female's life is affected by the host the female was bred from and the hosts she was offered. Small *Anagrus* sp. B females, failed to produce progeny in *C. viridis* hosts. Large *Anagrus* sp. C females produced more progeny than small ones and, irrespective of size, their progeny were larger when *C. viridis* hosts were offered.

That the host may have some effect on the length of the developmental period of their parasitoids has already been demonstrated (Salt, 1940; Narayanan and Subba Rao, 1955; Whalley, 1956, 1958; New, 1969). The results in the present study confirm these views. *Anagrus* sp. B

develops faster in *D. hamata* hosts and *Anagrus* sp. C develops faster in *C. viridis* hosts.

Salt (1940) suggested that the size of the host may influence the developmental period of its parasitoids. One would expect, then, both parasitoid species to develop faster in *D. hamata* hosts than in *C. viridis* or vice versa. The present study, however, showed that this is not the case. Intrinsic characteristics of the host species, i.e. its nutritional value, hardness of the egg chorion, may have differently affected the developmental rate of both parasitoid species.

# CHAPTER IV

## ECOLOGICAL ASPECTS OF HOST-PARASITOID INTERACTION

### i. General introduction

In this chapter, several aspects of the interaction between *Anagrus* sp. B and sp. C and their host, *C. viridis* eggs, were studied. Some of these aspects are the effect of increasing host density, the effect of increasing adult parasitoid density and the effect of larval competition in the host egg.

Studies along these lines concerning two closely related species are of general interest, and it was hoped that they would provide insight into how these species utilize common resources. It was also hoped that these experiments would shed light on possible mechanisms which allow the two species to coexist in the field.

### ii. The effect of larval density

#### 1. Introduction

The number of *Anagrus* sp. B and sp. C individuals which developed in a field parasitized *C. viridis* host has already been shown. Up to four *Anagrus* sp. B and five *Anagrus* sp. C adults were obtained from these hosts. During the mass culturing of both parasitoid species, it was observed that, although both species were capable of avoiding to superparasitize *C. viridis* hosts, an increase in the number of laying females produced a noticeable increase in the rate of superparasitism. Therefore, it was possible to select hosts where different numbers of parasitoid larvae were developing. The resultant female progenies were measured and the female fecundity was estimated.

In this section, the effect a change in larval density might have in the size of the resulting females is investigated.

2. Material and methods

Several *C. viridis* eggs which contained different numbers of *Anagrus* sp. B and sp. C pupae were selected and transferred singly into breeding chambers. Those hosts which showed a majority of females were chosen whenever possible. After the females emerged, the length of the ovipositor, forewing and fourth antennal subsegment (antenna IV) were measured and the number of eggs in the ovaries was recorded. Up to ten individuals per host in *Anagrus* sp. B and up to thirteen in *Anagrus* sp. C were found.

3. Results

a) Larval competition as a cause for variation in size

The size of the *C. viridis* eggs had little variation (Fig. 34). It was expected that an increase in the number of parasitoid larvae in the egg would increase the competition for the available food.

The results on the effect the larval competition had on the size of the resultant adult *Anagrus* sp. B and sp. C females is shown in Appendix Tables 8 and 9. The length of the ovipositor, forewing and antenna IV were used to quantify the size of the female. Figures 35 and 36 show these values plotted against the number of individuals per host.

The extent of competition for food is clearly shown in both parasitoid species. An increase in the number of *Anagrus* sp. B and sp. C individuals in the host egg decreased the size of the resultant female.

b) Changes in fecundity caused by larval competition

The females used in the previous experiment were dissected. The

Figure 34. *C. viridis* eggs showing pupae of *Anagrus* sp. B (on the right) and *Anagrus* sp. C (on the left). From top to bottom, 2, 3 or 4 pupae per host egg can be seen.

Figure 35. Effect of larval competition on the size of the resultant *Anagrus* sp. B females (n = 94).

1) Length of forewing (●); $Y = 0.68 - 0.025X$; $r^2 = 0.81$; $p>0.001$

2) Length of ovipositor (o); $Y = 0.51 - 0.016X$; $r^2 = 0.80$; $p>0.001$

3) Length of antenna IV (⊙); $Y = 0.10 - 0.005X$; $r^2 = 0.81$; $p>0.001$

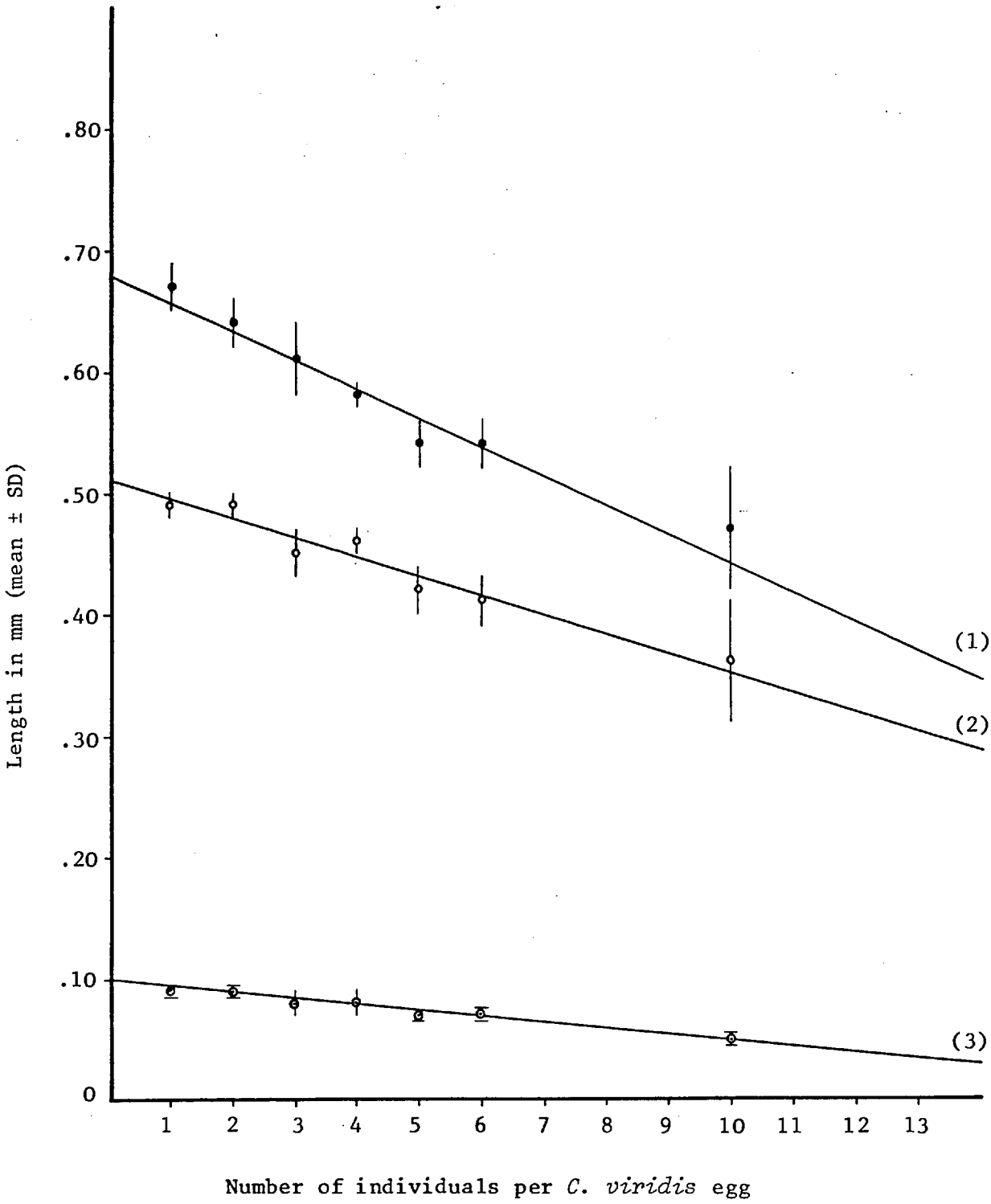
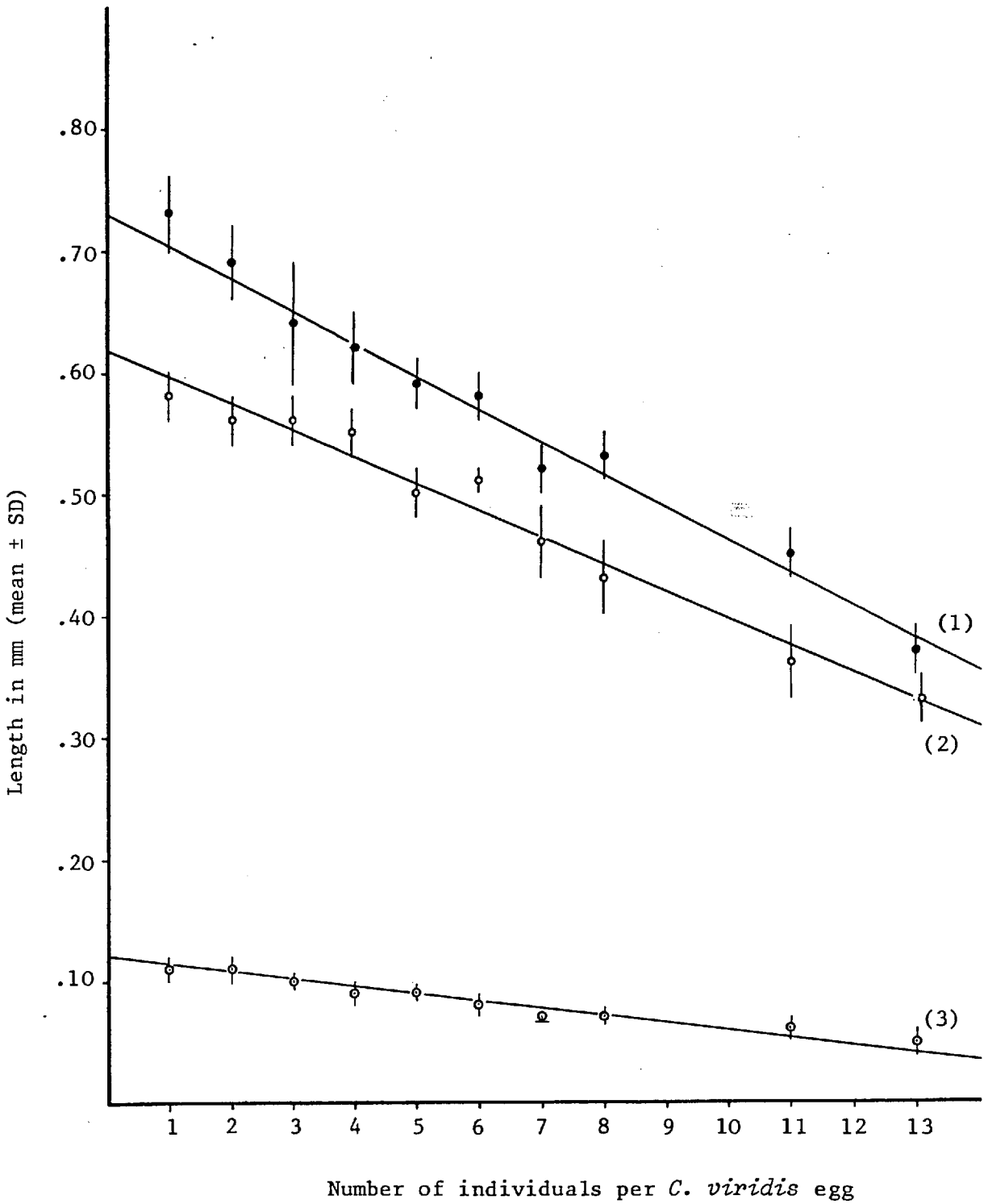

.80
.70
.60
.50
.40
.30
.20
.10
0
Length in mm (mean ± SD)
1
2
3
4
5
6
7
8
9
10
11
12
13
(1)
(2)
(3)
Number of individuals per C. viridis egg

Figure 36. Effect of larval competition on the size of the resultant *Anagrus* sp. C females (n = 139).

1) Length of forewing (●); $Y = 0.73 - 0.027X$; $r^2 = 0.85$; $p>0.001$

2) Length of ovipositor (o); $Y = 0.62 - 0.022X$; $r^2 = 0.89$; $p>0.001$

3) Length of antenna IV (⊙); $Y = 0.12 - 0.006X$; $r^2 = 0.91$; $p>0.001$


.80
.70
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Length in mm (mean ± SD)
(1)
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4
5
6
7
8
9
10
11
12
13
Number of individuals per C. viridis egg

fecundity of these females, i.e. the number of eggs in the ovaries, was measured (Appendix Tables 8 and 9). Figures 37 and 38 show these values plotted against the number of individuals per host. An increase in the number of *Anagrus* sp. B and sp. C individuals in the *C. viridis* egg decreased the fecundity of the resultant female.

c) Measure of the variation in the size and fecundity of the female caused by larval competition

The coefficient of variation in the size and fecundity of the *Anagrus* sp. B and sp. C females caused by larval competition was estimated. The coefficient of variation ($CV = 100 \cdot SD \cdot \bar{X}^{-1}$) of the length of the ovipositor, forewing and antennal subsegment IV and that of the fecundity of the females, was then calculated. These results are shown in Table 28.

4. Discussion

The effect an increase in the number of individuals reared from the same host on the resultant parasitoids has already been demonstrated (Chacko, 1969; Flanders, 1935; Salt, 1940). They concluded that when superparasitism occurs in *Trichogramma* there is a reduction in fecundity and size. The results in the present study confirm these views. An increase in the number of *Anagrus* sp. B and sp. C individuals developing in *C. viridis* eggs decrease the size and fecundity of the resultant female. The size of the smaller *Anagrus* sp. B females was 30 to 40% the size of the larger females, whilst in *Anagrus* sp. C, the size of the females was reduced up to 40 to 50%. This reduction in size was accompanied by a drastic reduction in fecundity. The number of eggs in the ovaries was reduced by 70 or 80% in the smaller individuals.

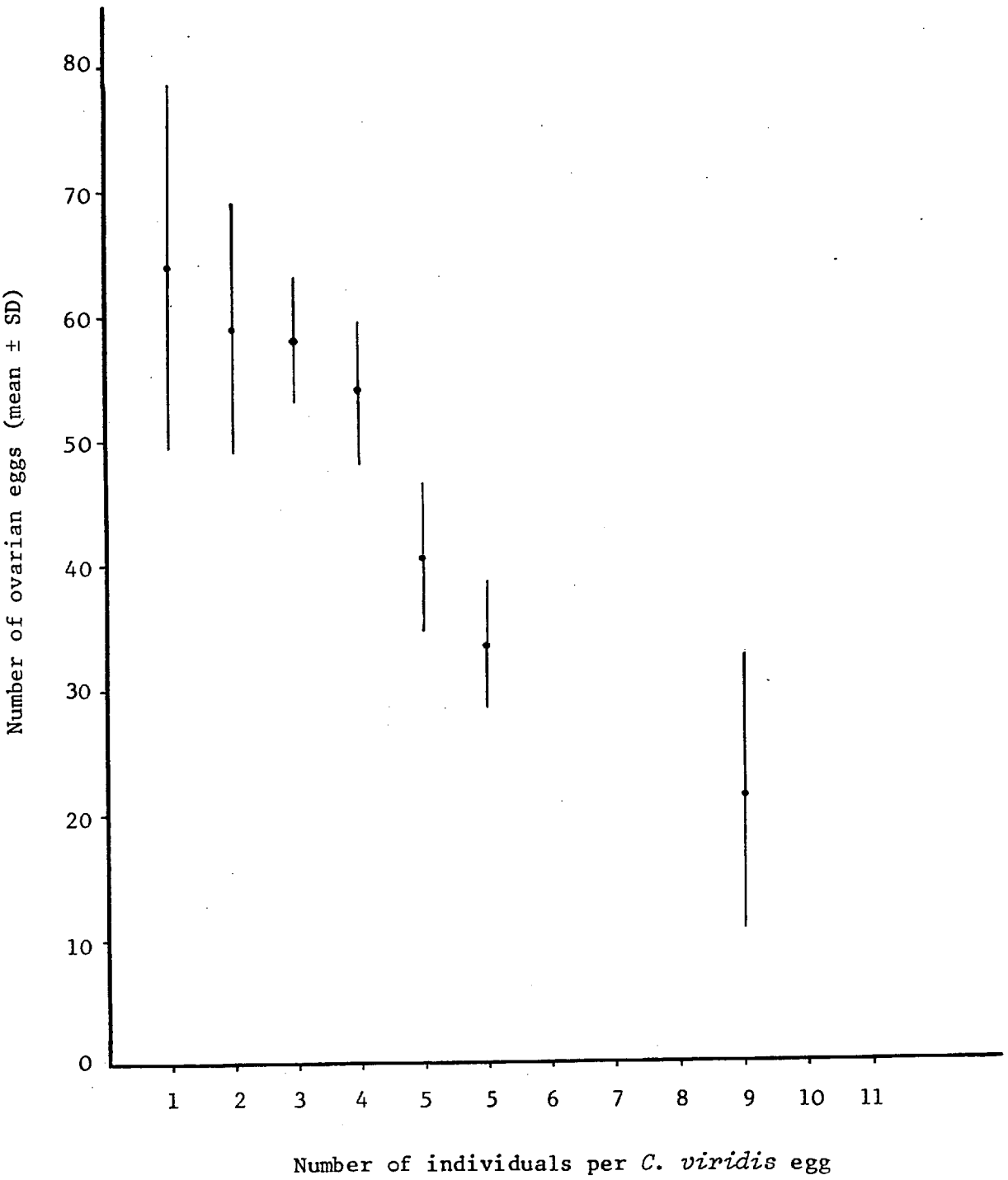



Figure 37. Effect of larval competition on the fecundity of the resultant *Anagrus* sp. B females.

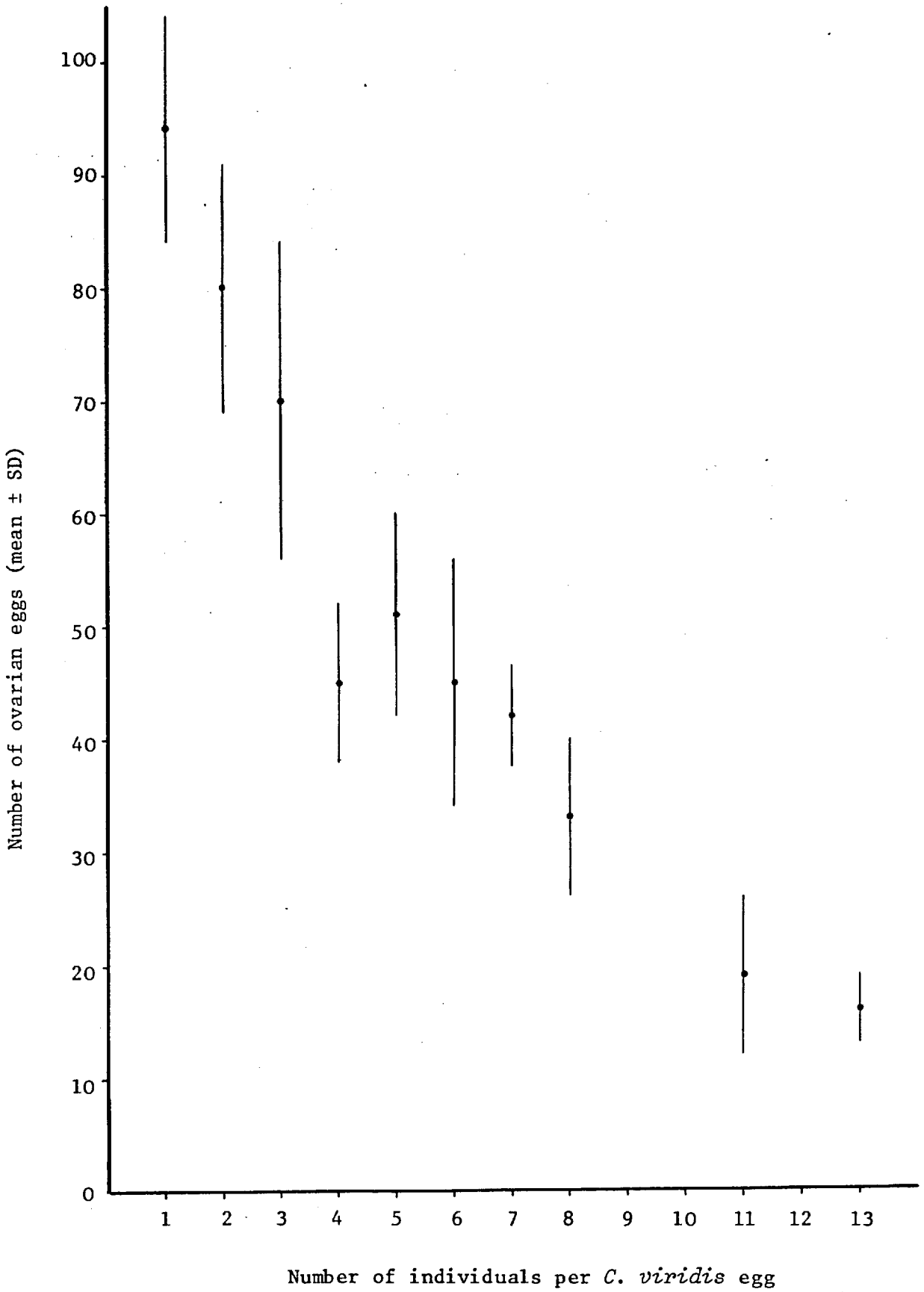



Figure 38. Effect of larval competition on the fecundity of the resultant *Anagrus* sp. C females.

Table 28. Measure of variation in the size and fecundity of *Anagrus* sp. B and sp. C females caused by larval competition.

| Measurement | Overall $\bar{X}$* | Overall SD | CV |
|---|---|---|---|
| *Anagrus* sp. B | | | |
| antenna IV | 0.08 | 0.011 | 13.8 |
| ovipositor | 0.45 | 0.037 | 8.4 |
| forewing | 0.58 | 0.058 | 9.9 |
| fecundity | 49.4 | 14.24 | 28.8 |
| *Anagrus* sp. C | | | |
| antenna | 0.09 | 0.018 | 19.4 |
| ovipositor | 0.61 | 0.088 | 14.4 |
| forewing | 0.52 | 0.070 | 13.4 |
| fecundity | 58.5 | 23.6 | 40.4 |

* Measurements in mm.

It is interesting to note that *Anagrus* sp. C achieves greater fecundity than *Anagrus* sp. B in *C. viridis* eggs, which is most evident in the lower density (c.f. Figure 37 and 38).

The amount of variation (as measured by the coefficient of variation) in female fecundity is much greater than the variation in female size (c.f. Table 28) in either species.

This tends to suggest that at times of a shortage of nutrients for investment, evolutionary pressures on these species have lead to investment in individuals of the 'normal' size, capable of finding and handling their hosts, having priority over investment in preproduction. It has already been demonstrated that the size of the female has drastic effect on her ability to handle hosts.

iii. The effect of host density

1. Introduction

The relationship between the number of hosts per parasitoid at different host densities (functional response) has been recently reviewed by Hassell et al. (1976). The response of *Anagrus* sp. B and sp. C to different densities of *C. viridis* eggs was studied in the laboratory.

It was hoped that a comparison between the functional responses would reveal differences in the rate at which hosts were attacked by these parasitoid species.

2. Material and methods

Newly emerged, mated, standard *Anagrus* sp. B or sp. C females, were allowed to parasitize different densities of *C. viridis* eggs for 12 hours. Each female was introduced into a breeding cage (a glass vial of 9 cm high and 3 cm in diameter) containing one or several stems of *Juncus*

bearing 2, 4, 8, 16, 32 or 64 *C. viridis* eggs. The number of hosts parasitized and the number of parasitoid larvae per host were recorded as soon as the parasitoid larvae were seen through the chorion of the host egg.

The data was analysed fitting the random parasite model of Rogers (1972). The model was fitted by non-linear least squares method (Draper and Smith, 1966). The procedure of Powell (1964) was used to minimise the residual sum of squares. The computer programme used was the Harwell subroutine VA04A (Hopper, 1973).

3. The functional response of *Anagrus* spp

The number of *C. viridis* parasitized and the number of progeny produced by *Anagrus* sp. B or sp. C females varied in relation to host density. The results are given in Appendix Table 10 and are shown in Figure 39. The parameters 'attack rate', a', and 'handling time' Th were estimated for each species by fitting the random parasite model to the data on the observed number of parasitized hosts.

The 'attack rate' of *Anagrus* sp. B (a' = 0.012) is greater than that of *Anagrus* sp. C (a' = 0.010), whilst the 'handling time' of *Anagrus* sp. B (Th = 31.8 min) is greater than that of *Anagrus* sp. C (Th = 21.5 min).

The average number of progeny produced by *Anagrus* sp. B and sp. C females in relation to host density also varied.

Results are shown in Figures 40 and 41. The number of progeny produced by *Anagrus* sp. B was slightly higher than that of sp. C at lower densities. However, at higher densities, *Anagrus* sp. C parasitized more hosts.

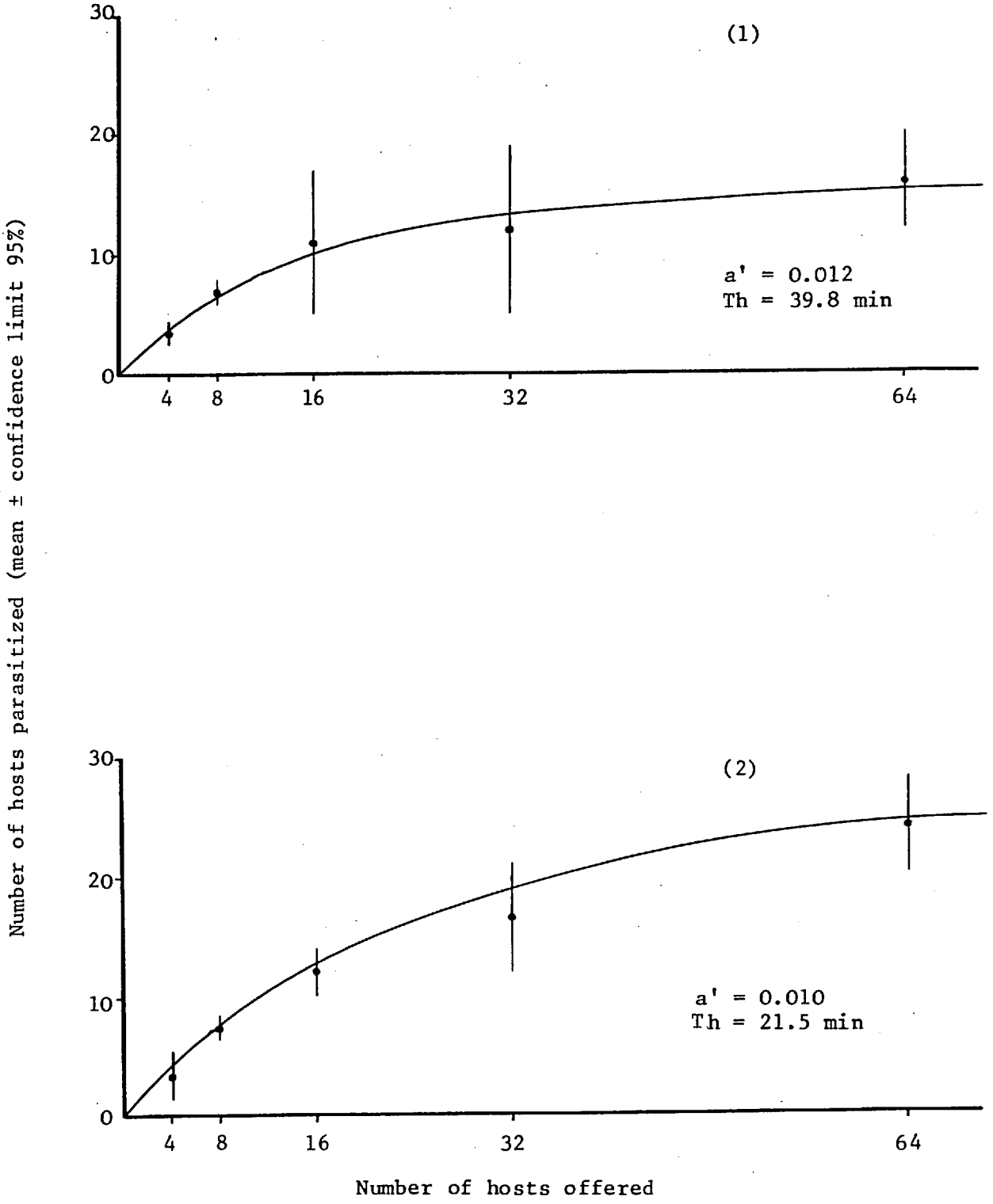



Figure 39. The functional response of *Anagrus* spp. The attack rate, a', and handling time, Th, are shown in each case.

(1) *Anagrus* sp. B; (2) *Anagrus* sp. C

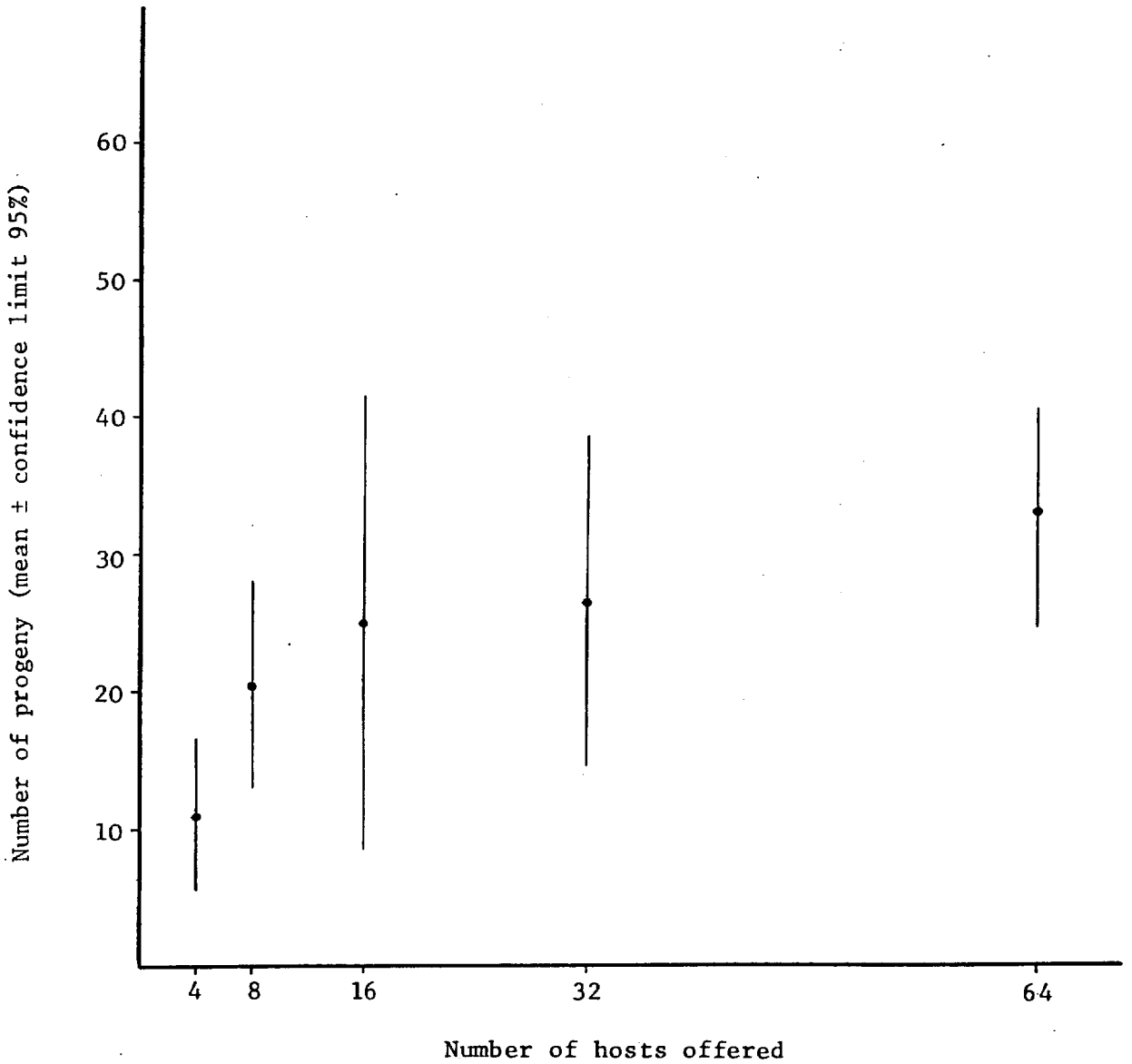



Figure 40. Number of progeny produced by *Anagrus* sp. B females in relation to *C. viridis* density.

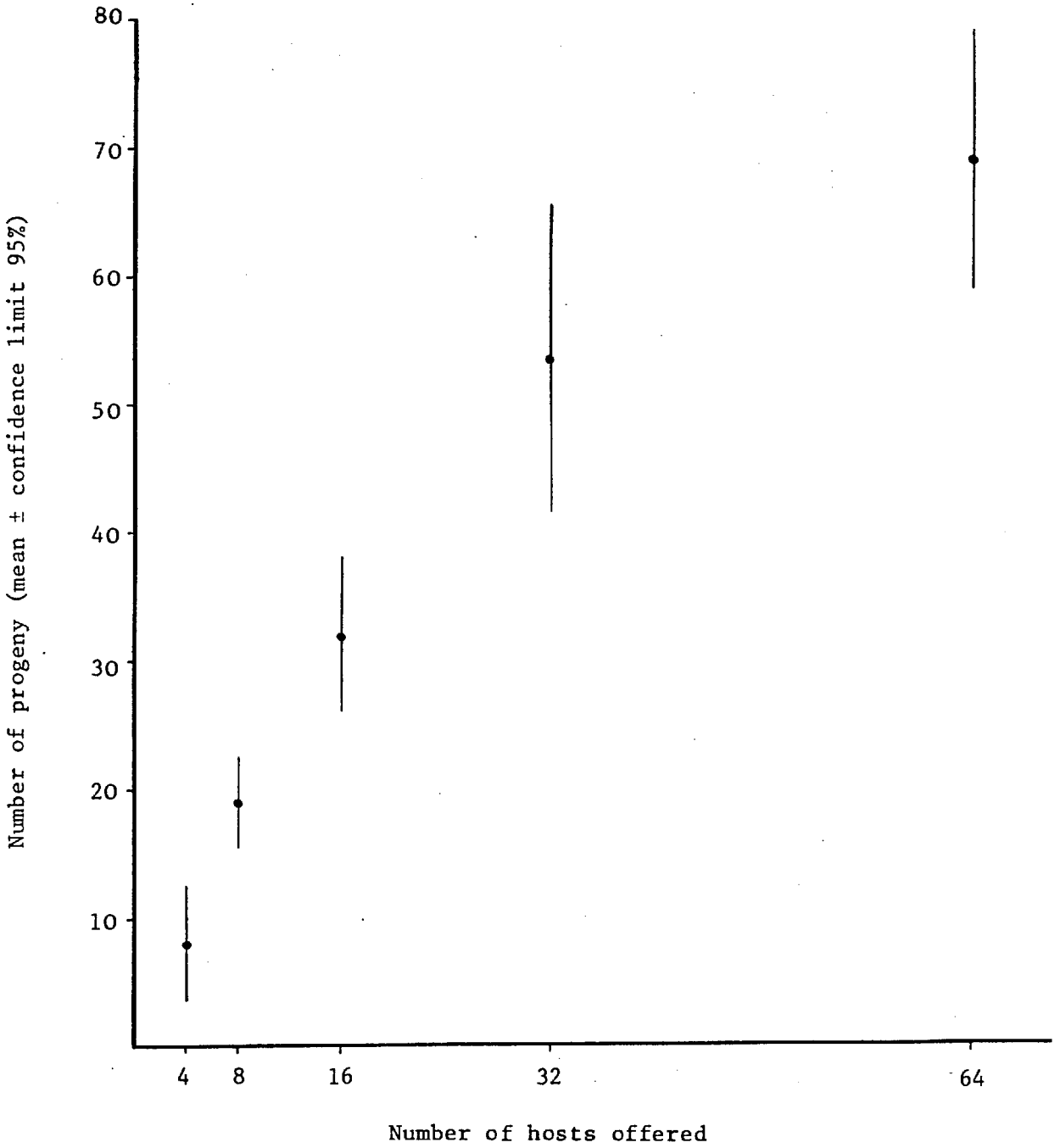



Figure 41. Number of progeny produced by *Anagrus* sp. C females in relation to *C. viridis* density.

4. Discussion

The relationship between the number of *C. viridis* eggs parasitized by *Anagrus* sp. B and sp. C and the host density was curvilinear for both species (Holling's, 1959a; Type II functional response curve).

At lower densities, both species parasitized similar number of hosts. However, at higher densities the number of hosts parasitized by *Anagrus* sp. C was greater than that of sp. B.

The attack rate, a', estimated in the model was similar for both species, whilst the estimated 'handling time' for *Anagrus* sp. B was larger than that of sp. C.

Clearly, the 'handling time' estimated by the model is far greater than the actual handling time as it was measured in Chapter II, i.e., from starting to drill to resumption of search. This is due to the fact that the model's estimate of 'handling time' also incorporates the resting period between spells of oviposition.

The degree of superparasitism can be measured only by direct observation. Therefore, it is difficult to quantify the relative effect superparasitism might have on the number of hosts parasitized. At low host densities (4 to 16 hosts offered), both species parasitized similar number of hosts, however, *Anagrus* sp. B produced slightly higher number of progeny than sp. C. It was already demonstrated that *Anagrus* sp. B avoided superparasitism to a lesser extent that *Anagrus* sp. C. A higher densities, the amount of superparasitism is expected to decrease. Therefore, the observed differences in number of hosts parasitized at higher densities appeared to be due to differences in the 'handling time' of both species. Unfortunately the model's estimate of 'handling time' is not a sufficiently detailed description of the female's use of the

time available to allow a meaningful conclusion to be drawn. More information on the way the female parasitoid invests the time she has available for attacking hosts is needed in order to compare these closely related species. The effect superparasitism (or avoidance of it) may have on the female's time budget is also an important factor to be considered.

These results suggest a slight competitive advantage of sp. B at low densities, whilst at high density, the greater searching efficiency of sp. C gives it the advantage. It is however possible that if superparasitism occurs, B with its large mandibles always wins.

iv. Effect of parasitoid density

1. Introduction

Hassell and Varley (1969) suggested that mutual interference between insect parasitoids would have an important effect on the host-parasitoid interaction.

In several occasions, two or three *Anagrus* sp. B or sp. C females were observed in the laboratory laying eggs on the same batch of host eggs. These females did not seem to be affected by the presence of neighbour females.

The effect an increase in the female parasitoid density may have on their searching efficiency was investigated.

2. Material and methods

Different numbers of newly emerged, mated, standard *Anagrus* sp. B and sp. C females, were allowed to parasitize 16 *C. viridis* eggs for 24 hours. One, two, four, six or eight females were introduced into a breeding cage containing two stems of *Juncus* bearing one batch of eight

*C. viridis* eggs in each stem.

The number of hosts parasitized and the total number of attacks (measured as number of punctures left on the host egg chorions) were recorded.

The data were analysed by the method proposed by Hassell and Varley (1969), where a linear regression is fitted to data relating searching efficiency (a) to parasitoid density (P), i.e.

$$\log_{10} a = Q + m \log_{10} P$$

In this analysis, the slope of the regression (m) gives a measure of mutual interference, and the intercept is the value of $\log_{10} a$ when the log density of parasitoids is zero (i.e. when P = 1).

The searching efficiency was calculated in two ways, when considering the number of parasitized hosts, searching efficiency was calculated (Hassell and Varley, 1969) as

$$a = \frac{1}{PT} \ln \frac{N}{S}$$

where P is the parasitoid density, T is time (24 hours), N is the number of hosts offered (16), and S is the number of unparasitized hosts. For analysing the data on the effect of parasitoid density on the number of attacks, the searching efficiency was calculated as Holling's (1959b) attack rate, so that

$$a = \frac{N\ p}{N\ P\ T}$$

where N, P and T are defined as above, and Np is the number of attacks (punctures)

3. Results

The number of hosts attacked and the total number of attacks increased

with an increase in parasitoid density. Results are given in Appendix Table 11. These results were used to estimate the searching efficiency (a) (Appendix Table 12). Figure 42 (1-2) shows the relationship between log searching efficiency and log parasitoid density for both species. The regression equation for each relationship is also given in Figure 42 (1-2).

An F-test for the significance of the slope was carried out and in each case the null hypothesis was not rejected ($P>0.05$).

4. Discussion

Hassell and Varley (1969) suggested that the analysis of the slope (m) of the regression between log a and log P, is a measure of mutual interference between searching parasitoids.

The analysis of the data for *Anagrus* sp. B and sp. C failed to reveal any significant reduction in their searching efficiency due to female parasitoid density, measured either as number of hosts parasitized or total number of attacks.

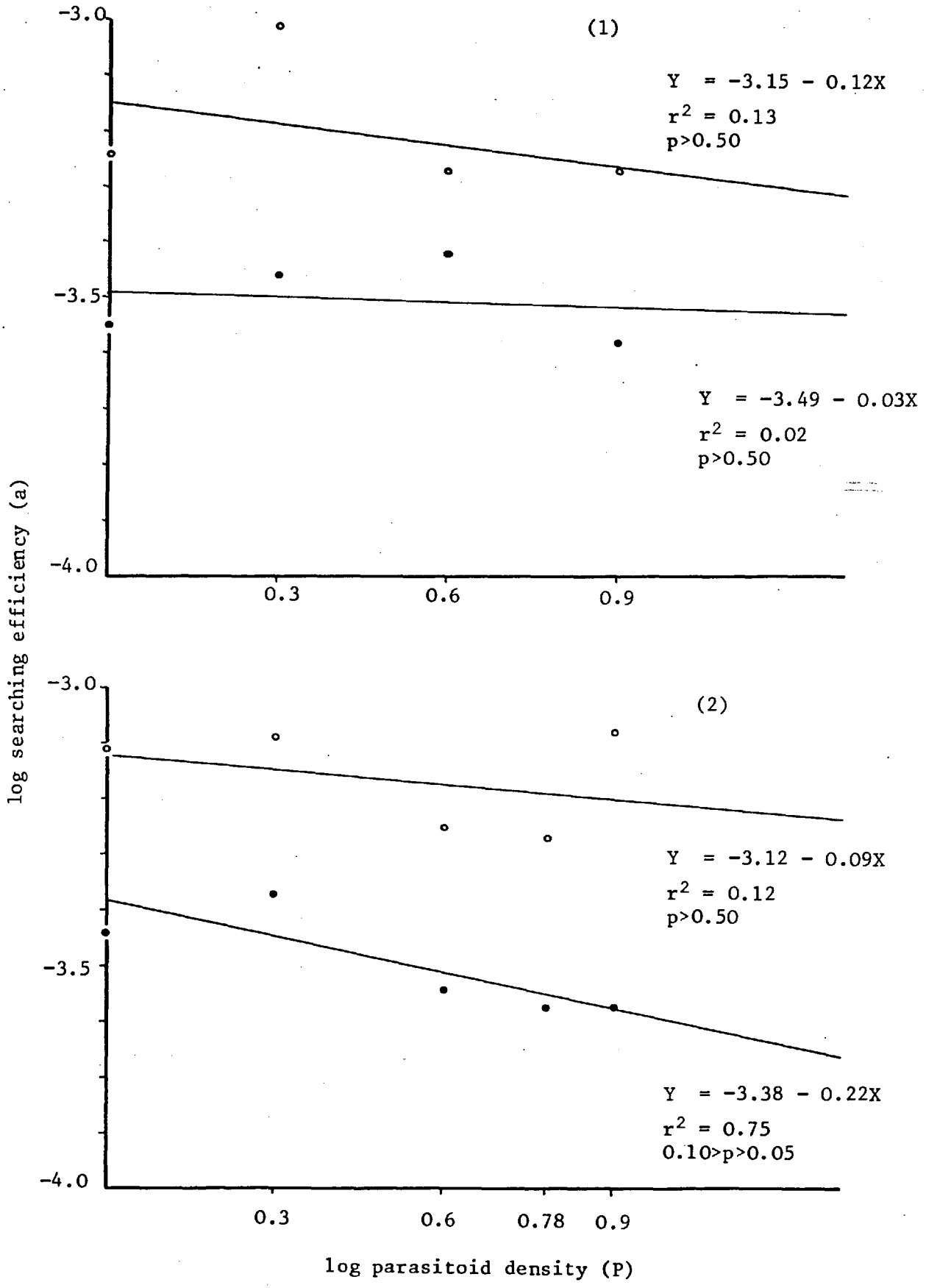
Direct observation of searching females support these findings; searching females do not appear to be disturbed by the activity of other parasitoids.

v. General discussion

The fecundity of the resultant *Anagrus* sp. B and sp. C females, which developed in *C. viridis* eggs, was drastically reduced with an increase in the number of parasitoid larvae within the host. The reduction in size was also important. It has already been shown that the size of the females could affect not only the number of their progeny but also the ability of the female to handle hosts. The oviposition pattern

Figure 42. Interference relationships between searching efficiency (a) and parasitoid density (P) on logarithmic scales. Searching efficiency was calculated using data on number of hosts attacked (o) and total number of attacks (●).

(1) *Anagrus* sp. B; (2) *Anagrus* sp. C


(1)
Y = -3.15 - 0.12X
r2 = 0.13
p>0.50
Y = -3.49 - 0.03X
r2 = 0.02
p>0.50
(2)
Y = -3.12 - 0.09X
r2 = 0.12
p>0.50
Y = -3.38 - 0.22X
r2 = 0.75
0.10>p>0.05
-3.0
-3.5
-4.0
0.3
0.6
0.78
0.9
log searching efficiency (a)
log parasitoid density (P)

of both species (i.e. one egg per *D. hamata* host and two to four eggs per *C. viridis* hosts) appeared to maximise the fecundity of the females in the progeny within a reasonable adult size range. Superparasitism, therefore, has disadvantageous effects and is avoided to different extents by both species.

Both *Anagrus* sp. responded to an increase in host density, showing an increase in the number of hosts parasitized. At high densities, the number of progeny produced by *Anagrus* sp. C almost doubled that of *Anagrus* sp. B. The attack rate of both species was similar. The time *Anagrus* sp. B spent handling hosts was considerably longer than that of sp. C. The difference between the model's estimate of 'handling time' and the actual handling time strongly suggests that in order to draw a meaningful comparison between these closely related species, more should be known about the use the female makes of her available time. A comprehensive time budget for both parasitoid species, handling small and big hosts, could provide the desired information.

An increase in parasitoid density did not affect significantly the parasitoid's searching efficiency. The degree of parasitism achieved by each *Anagrus* species in the field is invariably low (Tay, 1972). This seems to suggest that situations of high parasitoid density and potential overexploitation of the host population may have been infrequent in the evolutionary history of *Anagrus*. In consequence, behavioural interference, viewed as part of a regulatory mechanism guarding against host overexploitation, may not be highly evolved in these species.

## GENERAL DISCUSSION

The study of these two *Anagrus* species, which share common hosts, poses some intriguing questions. How does the biology of these two closely related species compare? Does this difference explain how these species coexist?

The life-histories of *Anagrus* sp. B and sp. C are very similar, but they have some differences which allowed them to be differentiated. The short lived adults are of a similar size and the presence of a bare patch on the forewing makes *Anagrus* sp. C easily distinguishable. The presence of abdominal outgrowth and long mandibles characterize the second instar larvae of *Anagrus* sp. B.

Field collected, parasitized eggs of *C. viridis*, reveals that where these two species coexist, *Anagrus* sp. C is more abundant than sp. B. The number of eggs parasitized by sp. C per egg batch of *C. viridis*, is greater than that of *Anagrus* sp. B. Also the number of parasitoids per host is also greater in sp. C than in sp. B. *Anagrus* sp. C develops faster in *C. viridis* eggs than sp. B and the number of progeny produced is greater in *Anagrus* sp. C.

The better searching capacity of sp. C, coupled with its ability of avoiding superparasitism, could explain the success of this species, attacking more hosts and producing larger progeny.

One would expect that a species with the characteristics of sp. C will increase their numbers and achieve higher values of parasitism. But, inspite of the abundance of hosts, this is not so. May be the hazards imposed by the summer and the relative abundance of the summer hosts will prove to be the constraints in the system which are responsible

for preventing the population to increase.

The large number of hosts available could be one of the factors which may explain why these two species coexists. The presence of well developed mandibles in *Anagrus* sp. B could provide the species with a pair of highly efficient weapons, making it a better competitor. This suggests that, if multiparasitism occurred, B with its large mandibles would always win.

Another interesting aspect is the difference in fecundity between these closely related species, attacking the same host. Price (1975) postulated that the major determinants of fecundity in parasitoids are the probability of finding hosts and the probability of survival once established on or in the host. One might expect that closely related species, such as *Anagrus*, attacking the same host, would tend to maximise the number of eggs produced, achieving then, similar levels of fecundity. But this is not the case in *Anagrus*. Differences in the searching capacity of these species and their ability for handling hosts, will contribute greatly to their success and will determine the number of hosts which each species would be able to parasitize in their life span. For these species, investment in the production of eggs, appear to be determined, not only the probability of finding hosts, but also determined by the number of hosts the females can handle during their short life span.

Time is a vital resource for these minute parasitoids and thus one might expect them to have evolved so as to maximise its utilisation: the rapid rate of searching and the lack of interference between females seem to be indications of this.

## SUMMARY

1. The relevant taxonomical literature was reviewed and revealed that in identifying *Anagrus* spp, use should be made of the presence of the glabrous patch on the forewing; size of the antennal subsegments and number and distribution of the sensory grooves; size and shape of the male genitalia and length of the ovipositor. It is most important that comparisons are made between individuals that have emerged from the same host species; for it was demonstrated that host species and the number of individuals developing per host, had significant effects on adult size.

2. Laboratory experiments were conducted to investigate the biology of *Anagrus* sp. B and sp. C.

3. The majority of the adults emerged during the morning (before 12:00 hr), and males tended to emerge before the females. Copulation took place soon after emergence and lasted longer in *Anagrus* sp. B than in sp. C. Females usually mated once.

4. Copulation appeared to affect the sex and size of the progeny. Virgin females produced only males in both species, and fertilized *Anagrus* sp. C females oviposited more eggs than virgin females.

5. The fecundity of proovigenic *Anagrus* sp. B and sp. C females was estimated by counting the number of eggs in the ovaries of newly emerged virgin females.

6. The fertility of *Anagrus* sp. C was studied. These females laid approximately 60% of their egg complement during their life.

7. Oviposition started soon after emergence, and up to 60% of the eggs

were laid between 6-12 hours after emergence.

8. The egg and the two larval stages of *Anagrus* sp. C were described and illustrated. The most diagnostic features for the second instar larvae of these species are the size of the mandibles and the presence of abdominal outgrowths.

9. The rate of development of *Anagrus* sp. C in *D. hamata*, from egg to adult was affected by temperature. Development took a minimum of 14 days (at 30°C) and a maximum of 35 days (at 15°C). Although no significant difference was found in the average daily development in males and females, males tended to develop faster than females.

10. The theoretical 'developmental zero' for the larval stages was found to be 9.5°C.

11. The rearing temperature had a marked effect on the fecundity and size of the resultant adults. A rise in temperature reduced the average fertility as well as the size of the adult.

12. Periodic collections of overwintering *C. viridis* eggs, revealed that in three sites, where they did coexist, *Anagrus* sp. C was more abundant than sp. B. Both species overwinter as second instar (mature larvae), prepupae or early pupae.

13. The average number of parasitoids per parasitized field collected *C. viridis* eggs, was significantly different for both species. Three and four parasitoids per host were the most frequent numbers for *Anagrus* sp. B and sp. C respectively.

14. The sex ratio of *Anagrus* sp. B and sp. C in the field, was calculated as 72% of females. Both species showed a high proportion of parasitized

hosts with a majority of female parasitoids.

15. The host finding and oviposition behaviour of *Anagrus* sp. B and sp. C were found to be similar. The antennae appeared to play an important role, not only in finding the batch of eggs, but also helping the female to position herself on top of the host egg.

16. The egg laying process was studied in both *Anagrus* spp. If the parasitoid female was observed while attacking a *C. viridis* host, the number of eggs she laid would be assessed.

17. *Anagrus* sp. B tended to be slower handling hosts than sp. C.

18. Both *Anagrus* spp were able to reject an already parasitized host. Rejection always took place after drilling. When the smaller *D. hamata* hosts were attacked, both *Anagrus* spp completely avoided superparasitism. However, when they attacked the larger *C. viridis* hosts, the degree of avoidance varied and *Anagrus* sp. C was more efficient at avoiding superparasitism.

19. Rejection of an already parasitized host by *Anagrus* sp. C occurred as early as 30 sec after the first attack, whereas *Anagrus* sp. B (less efficient in avoiding superparasitism), superparasitized 15 min after the first attack.

20. The size of *Anagrus* sp. B and sp. C was affected by the size of their hosts.

21. The host, through its effect on size, affected certain physiological characteristics, such as fecundity. *Anagrus* sp. B and sp. C females, bred from *C. viridis*, had more eggs in the ovaries than those bred from *D. hamata*.

22. The number of progeny produced in the first 24 hours of the female's life was affected by the host the female was bred from and the host she was offered.

23. The length of the developmental period of *Anagrus* sp. B and sp. C was also affected by the host in which they were developing.

24. An increase in the number of *Anagrus* sp. B and sp. C larvae developing in *C. viridis* eggs decreased the size and fecundity of the resultant female.

25. The amount of variation due to larval competition (as measured by the coefficient of variation) in female fecundity is much greater than the variation in female size in either species.

26. The relationship between the number of *C. viridis* eggs parasitized by *Anagrus* sp. B and sp. C and the host density was curvilinear for both species (Holling's Type II functional response curve).

27. The attack rate, 'a'' estimated in the model was similar for both species, whilst the estimated 'handling time' for *Anagrus* sp. B was larger than that of sp. C.

28. An increase in parasitoid density did not affect significantly the parasitoid's searching efficiency i.e. interference could not be shown.

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Appendix Table 1. *Anagrus* sp. C, pattern of emergence of adult from *C. viridis* eggs.

| Female number | Time when emergence was checked | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 03.00 | | 09.00 | | 12.00 | | 18.00 | | 21.00 | | Totals | |
| | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ |
| M191 | - | - | | 5 | 3 | 20 | - | 4 | - | - | 3 | 29 |
| M192 | - | - | 7 | 13 | 3 | 29 | - | - | - | - | 9 | 42 |
| M193 | - | - | 25 | 20 | 10 | 28 | - | - | - | - | 36 | 49 |
| M194 | - | - | 12 | 24 | 1 | 2 | - | - | - | - | 13 | 26 |
| M195 | - | - | 2 | 9 | 3 | 26 | - | - | - | - | 5 | 35 |
| M196 | - | - | 20 | 20 | 2 | 16 | - | - | - | - | 22 | 36 |
| M199 | - | - | 8 | 6 | 10 | 25 | - | - | - | - | 18 | 31 |
| Total | - | - | 74 | 97 | 31 | 146 | 1 | 5 | - | - | 106 | 248 |
| | | | 69.81 | 39.11 | 29.25 | 58.87 | 0.94 | 2.02 | | | | |
| % of females | 0.00 | | 56.73 | | 82.49 | | 83.0 | | | | 70.06 | |

Appendix Table 2. Number of progeny produced by fertilized and virgin females.

| Female number | Code* | Number of progeny | | | | | Number of eggs left in the ovaries | Life-span in days | Copulation time in seconds |
|---|---|---|---|---|---|---|---|---|---|
| | | Day 1 | Day 2 | Day 3 | Day 4 | Total | | | |
| 1 | 1 | 3 | 36 | | | 39 | 30 | 2 | 90 |
| 2 | 2 | 0 | 38 | 6 | | 44 | 27 | 3 | |
| 3 | 3 | | | | | - | 73 | - | |
| 4 | 1 | 0 | 0 | | | - | 75 | 2 | 71 |
| 5 | 2 | 19 | 10 | 1 | | 30 | 21 | 3 | |
| 6 | 3 | | | | | - | 78 | - | |
| 7 | 1 | 20 | 44 | 0 | | 64 | 0 | 3 | 52 |
| 8 | 2 | 26 | 8 | 0 | | 34 | 41 | 3 | |
| 9 | 3 | | | | | - | 75 | - | |
| 10 | 1 | 0 | 58 | 5 | | 63 | 13 | 3 | 34 |
| 11 | 2 | 5 | 0 | 20 | 2 | 27 | 40 | 4 | |
| 12 | 3 | | | | | - | 63 | - | |
| 13 | 1 | 65 | 0 | 0 | 0 | 65 | 0 | 4 | 35 |
| 14 | 2 | 47 | 16 | 0 | | 63 | 10 | 3 | |
| 15 | 3 | | | | | - | 72 | - | |
| 16 | 1 | 41 | 5 | 0 | 0 | 46 | 0 | 4 | 61 |
| 17 | 2 | 20 | 8 | 6 | | 34 | 22 | 3 | |
| 18 | 3 | | | | | - | 71 | - | |
| 19 | 1 | 25 | 0 | 38 | 8 | 71 | 0 | 4 | 62 |
| 20 | 2 | 29 | 6 | 0 | | 35 | 45 | 3 | |
| 21 | 3 | | | | | - | 79 | - | |
| 22 | 1 | 35 | 26 | 0 | | 61 | 2 | 3 | 102 |
| 23 | 2 | 26 | 0 | 26 | 1 | 53 | 24 | 4 | |
| 24 | 3 | | | | | - | 66 | - | |
| 25 | 1 | 42 | 14 | | | 56 | 0 | 2 | 99 |
| 26 | 2 | 0 | 3 | 29 | | 32 | 43 | 3 | |
| 27 | 3 | | | | | - | 68 | - | |
| 28 | 1 | 3 | 0 | 2 | | 5 | 63 | 3 | 126 |
| 29 | 2 | 2 | 0 | 24 | 0 | 26 | 42 | 4 | |
| 30 | 3 | | | | | - | 76 | - | |
| 31 | 1 | 53 | 6 | 0 | 2 | 61 | 0 | 4 | 50 |
| 32 | 2 | 14 | 27 | 0 | | 41 | 13 | 3 | |
| 33 | 3 | | | | | - | 68 | - | |
| 34 | 1 | 46 | 6 | | | 52 | 23 | 2 | 89 |
| 35 | 2 | 0 | 1 | | | 1 | 55 | 2 | |
| 36 | 3 | | | | | - | 72 | - | |
| 37 | 1 | 9 | 15 | 4 | | 28 | 46 | 3 | 93 + 40 |
| 38 | 2 | 14 | 6 | | | 22 | 44 | 2 | |
| 39 | 3 | | | | | - | 73 | - | |
| 40 | 1 | 53 | 17 | 9 | | 79 | 0 | 3 | 55 |
| 41 | 2 | 50 | 14 | 8 | | 72 | 2 | 3 | |
| 42 | 3 | | | | | - | 67 | - | |
| 43 | 1 | 54 | 0 | 0 | | 54 | 16 | 3 | 23 + 79 |
| 44 | 2 | 0 | 0 | | | - | 51 | 2 | |

Appendix Table 2. Continued

| Female number | Code* | Number of progeny | | | | | Number of eggs left in the ovaries | Life-span in days | Copulation time in seconds |
|---|---|---|---|---|---|---|---|---|---|
| | | Day 1 | Day 2 | Day 3 | Day 4 | Total | | | |
| 45 | 3 | | | | | - | 77 | - | |
| 46 | 1 | 36 | 0 | | | 36 | 21 | 2 | 75 |
| 47 | 2 | 61 | 20 | 0 | 0 | 81 | 0 | 4 | |
| 48 | 3 | | | | | - | 66 | - | |
| 49 | 1 | 53 | 0 | | | 53 | 6 | 2 | 45 |
| 50 | 2 | 35 | 25 | 0 | 0 | 60 | 0 | 4 | |
| 51 | 3 | | | | | - | 62 | - | |
| 52 | 1 | 62 | 0 | 0 | | 62 | 0 | 3 | 91 |
| 53 | 2 | 18 | 7 | | | 25 | 30 | 2 | |
| 54 | 3 | | | | | - | 71 | - | |
| 55 | 1 | 39 | 1 | 0 | | 40 | 0 | 3 | 84 |
| 56 | 2 | 0 | 5 | | | 5 | 39 | 2 | |
| 57 | 3 | | | | | - | 55 | - | |
| 58 | 1 | 29 | 2 | | | 31 | 34 | 2 | 40 |
| 59 | 2 | 0 | 0 | | | - | 76 | 2 | |
| 60 | 3 | | | | | - | 76 | - | |
| 61 | 1 | 34 | 9 | | | 43 | 29 | 2 | 75 |
| 62 | 2 | 38 | 0 | | | 38 | 33 | 2 | |
| 63 | 3 | | | | | - | 93 | - | |
| 64 | 1 | 2 | 0 | | | 2 | 70 | 2 | 55 |
| 65 | 2 | 39 | 0 | | | 39 | 17 | 2 | |
| 66 | 3 | | | | | - | 67 | - | |
| 67 | 1 | 65 | 0 | 0 | | 65 | 0 | 3 | 60 |
| 68 | 2 | 16 | 0 | | | 16 | 51 | 2 | |
| 69 | 3 | | | | | - | 70 | - | |
| 70 | 1 | 9 | 0 | | | 9 | 72 | 2 | 76 |
| 71 | 2 | 17 | 5 | | | 22 | 42 | 2 | |
| 72 | 3 | | | | | - | 74 | - | |

* Code - 1 = Fertilized; 2 = Virgin; 3 = Dissected

Appendix Table 3. Number of eggs laid 67 mated and virgin *Anagrus* sp. C.

| Female number | Number of eggs laid during the period | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0-6 hrs | 6-12 hrs | 12-18 hrs | 18-24 hrs | 24-30 hrs | 30-36 hrs | 36-42 hrs | 42-48 hrs | 48-54 hrs | 54-60 hrs | 60-66 hrs | 66-72 hrs | Total |
| Mated females | | | | | | | | | | | | | |
| 286 | 44 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 53 |
| 288 | 0 | 0 | 26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 26 |
| 291 | 38 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 38 |
| 292 | 39 | 13 | 0 | 0 | 0 | 5 | 0 | 13 | 0 | 0 | 1 | 0 | 71 |
| Σ | 121 | 13 | 31 | 0 | 0 | 5 | 0 | 13 | 0 | 2 | 3 | 0 | 188 |
| % | 64.36 | 6.91 | 16.49 | 0 | 0 | 2.66 | 0 | 6.91 | 0 | 1.06 | 1.60 | 0 | |
| Cummulative | 64.36 | 71.28 | 87.77 | 87.77 | 87.77 | 90.43 | 97.34 | 97.34 | 98.40 | 98.40 | 100.0 | 100.0 | |
| Virgin females | | | | | | | | | | | | | |
| 279 | 0 | 0 | 11 | 4 | 15 | 0 | 0 | 0 | 0 | 0 | | | 30 |
| 280 | 34 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | | | 36 |
| 281 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | | | 20 |
| 283 | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | 21 |
| 285 | 36 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | | | 41 |
| Σ | 91 | 0 | 11 | 4 | 20 | 0 | 20 | 0 | 2 | 0 | | | 148 |
| % | 61.49 | 0 | 7.43 | 2.70 | 13.51 | 0 | 13.51 | 0 | 1.35 | | | | |
| Cummulative | 61.49 | 61.49 | 68.92 | 71.62 | 85.14 | 85.14 | 98.65 | 98.65 | 100.0 | | | | |

Appendix Table 4. The effect of temperature on the fecundity of *Anagrus* sp. C bred from *D. hamata* hosts*.

| Rearing temperature in °C | Fecundity* |
|---|---|
| 15 | 65.40 ± 2.07 |
| 20 | 53.60 ± 4.67 |
| 25 | 50.80 ± 6.18 |
| 30 | 38.00 ± 3.54 |

* Number of eggs in the ovaries of dissected newly emerged females; mean ± SD; 5 observations

Appendix Table 5. The effect of temperature on the body size of *Anagrus* sp. C females bred from *D. hamata* hosts*.

| Rearing temperature in °C | Length of tibia | Length of forewing |
|---|---|---|
| 15 | 0.25 ± 0.008 | 0.62 ± 0.008 |
| 20 | 0.25 ± 0.007 | 0.60 ± 0.016 |
| 25 | 0.24 ± 0.008 | 0.54 ± 0.008 |
| 30 | 0.23 ± 0.015 | 0.50 ± 0.019 |

* Average length in mm ± SD; 5 observations

Appendix Table 6. Sex ratio of *Anagrus* sp. B and sp. C, parasitizing field collected *C. viridis* egg in relation to the number of parasitoids present in the host egg.

| | Number of parasitoids per *C. viridis* eggs | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | | 3 | | | | 4 | | | | | 5 | |
| | Number of host-eggs found in each sex-ratio category (♂ : ♀) | | | | | | | | | | | | | | | |
| | 1:0 | 0:1 | 2:0 | 1:1 | 0:2 | 3:0 | 1:2 | 2:1 | 0:3 | 4:0 | 1:3 | 2:2 | 3:1 | 0:4 | 4:1 | 2:3 | 1:4 |
| *Anagrus* sp. B n = 37 | - | - | 2 | 4 | 5 | - | 13 | - | 8 | 1 | 4 | - | - | - | - | - | - |
| *Anagrus* sp. C n = 259 | 2 | 2 | 2 | 2 | 10 | 6 | 67 | 5 | 36 | 7 | 84 | 6 | - | 17 | 3 | 3 | 7 |

Appendix Table 7. Time spent drilling and stinging unparasitized host eggs or in rejecting already parasitized host eggs by *Anagrus* sp. B and sp. C females*.

| Female number and label | Time spent drilling (sec) | Time spent stinging (sec) Number of eggs laid | | | | Time spent rejecting (sec) | Number of host eggs attacked |
|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | | |
| 003 B(vv) | - | 100.8 - (1) | 184.5 ±36.4 (7) | 297.6 - (1) | - | 46.4 7.3 (3) | 7 |
| 044a B(vv) | 33.6 ± 6.5 (9) | 100.8 - (1) | 153.6 - (1) | 245.1 ±56.1 (8) | - | - | 7 |
| 044b B(vv) | 36.8 ±12.0 (6) | 124.8 - (1) | 182.4 ± 6.8 (2) | 252.6 ±22.3 (4) | - | 36.0 ± 3.4 (2) | 6 |
| 045 B(vv) | 28.8 ± 7.7 (9) | 111.0 ±12.8 (4) | 178.3 ± 7.9 (4) | - | - | - | 6 |
| 050 B(vh) | 63.3 ± 7.7 (5) | 137.0 ±20.1 (13) | | | | 57.6 ± 8.1 (11) | 13 |
| 051 B(vh) | 62.4 ± 4.4 (4) | 134.1 ±23.2 (9) | | | | 67.2 ±16.6 (3) | 9 |
| 052 B(vh) | 67.2 ±15.2 (4) | 147.4 ±19.5 (11) | | | | 61.4 ±10.4 (5) | 11 |
| 061 B(hh) | 58.4 ± 9.9 (6) | 126.0 ±19.3 (10) | | | | 56.9 ±11.2 (7) | 10 |
| 062 B(hh) | 50.6 ±10.3 (12) | 124.8 ±19.0 (14) | | | | 63.8 ±18.7 (5) | 14 |

* Mean ±SD; number of observations in brackets

Appendix Table 7. Continued

| Female number and label | Time spent drilling (sec) | Time spent stinging (sec) Number of eggs laid | | | | Time spent rejecting (sec) | Number of host eggs attacked |
|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | | |
| 028 C(vv) | 33.9 ± 6.3 (8) | - | - | 238.2 ±21.3 (8) | - | 39.1 ± 6.8 (10) | 8 |
| 030 C(vv) | 22.4 ± 2.8 (3) | - | 144.0 ± 6.8 (2) | 172.8 - (1) | | 45.6 ±23.8 (2) | 7 |
| 031 C(vv) | 24.8 ± 4.7 (6) | - | 124.0 ± 4.7 (6) | 161.0 ±17.2 (2) | | 25.0 7.3 (15) | 8 |
| 035 C(vv) | 47.7 ±14.1 (8) | - | 203.2 ±29.3 (3) | 264.0 ±33.9 (2) | | 47.4 ±10.1 (4) | 7 |
| 036 C(vv) | 44.6 ±10.9 (7) | - | 158.4 ±54.3 (2) | 235.2 7.6 (5) | 331.2 - (1) | 36.0 ±10.2 (5) | 8† |
| 037 C(vv) | 27.3 ± 5.3 (8) | - | - | 198.0 ±16.6 (8) | | 31.2 12.1 (4) | 7 |
| 038 C(vv) | 32.3 ± 7.0 (9) | - | 199.2 ±37.3 (2) | 234.6 ±15.3 (6) | 259.2 - (1) | 37.2 ± 1.7 | 8 |
| 054 C(vh) | 55.2 ± 3.4 (5) | 122.4 ± 8.8 (6) | | | | 49.0 ± 4.0 (5) | 6 |
| 055 C(vh) | 56.4 ±12.5 (4) | 126.0 ±26.4 (14) | | | | 45.1 ± 4.6 (5) | 14 |
| 062 C(hh) | 51.2 ± 9.4 (16) | 113.9 ± 8.7 (18) | | | | 48.7 ± 7.6 (7) | 18 |
| 063 C(hh) | 49.9 6.2 (11) | 113.1 ±11.1 (15) | | | | 48.6 ± 6.6 (4) | 15 |

† Experiment stopped after 40.

Appendix Table 8. Effect of larval competition on the size and fecundity of the resultant *Anagrus* sp. B females. (mean ± SD)

| Number of individuals per *C. viridis* egg | Length (in mm) of the | | | Number of eggs in the ovaries | Number of observations |
|---|---|---|---|---|---|
| | Ovipositor | Forewing | Antenna IV | | |
| 1 | 0.49 ± 0.01 | 0.67 ± 0.02 | 0.09 ± 0.004 | 64.4 ± 14.4 | 10 |
| 2 | 0.49 ± 0.01 | 0.64 ± 0.02 | 0.09 ± 0.003 | 58.6 ± 9.9 | 14 |
| 3 | 0.45 ± 0.02 | 0.61 ± 0.03 | 0.08 ± 0.01 | 58.3 ± 4.9 | 18 |
| 4 | 0.46 ± 0.01 | 0.58 ± 0.01 | 0.08 ± 0.01 | 54.1 ± 6.1 | 14 |
| 5 | 0.42 ± 0.01 | 0.54 ± 0.02 | 0.07 ± 0.003 | 40.5 ± 5.8 | 23 |
| 6 | 0.41 ± 0.01 | 0.54 ± 0.02 | 0.07 ± 0.003 | 33.7 ± 4.8 | 10 |
| 7 | | | | | |
| 8 | | | | | |
| 9 | | | | | |
| 10 | 0.36 ± 0.03 | 0.47 ± 0.05 | 0.05 ± 0.004 | 21.4 ± 11.5 | 5 |

Appendix Table 9. Effect of larval competition on the size and fecundity of the resultant *Anagrus* sp. C females. (mean ± SD)

| Number of individuals per *C. viridis* egg | Length (in mm) of the | | | Number of eggs in the ovaries | Number of observations |
|---|---|---|---|---|---|
| | Ovipositor | Forewing | Antennae IV | | |
| 1 | 0.58 ± 0.02 | 0.73 ± 0.03 | 0.11 ± 0.01 | 94 ± 9.9 | 10 |
| 2 | 0.56 ± 0.02 | 0.69 ± 0.03 | 0.11 ± 0.01 | 80 ± 10.9 | 28 |
| 3 | 0.56 ± 0.02 | 0.64 ± 0.05 | 0.10 ± 0.003 | 70 ± 14.3 | 30 |
| 4 | 0.55 ± 0.02 | 0.62 ± 0.03 | 0.09 ± 0.01 | 45.4 ± 7.4 | 24 |
| 5 | 0.50 ± 0.02 | 0.59 ± 0.02 | 0.09 ± 0.004 | 50.7 ± 9.0 | 13 |
| 6 | 0.51 ± 0.01 | 0.58 ± 0.02 | 0.08 ± 0.01 | 45 ± 11.3 | 9 |
| 7 | 0.46 ± 0.03 | 0.52 ± 0.02 | 0.07 ± 0.00 | 42 ± 5.4 | 6 |
| 8 | 0.43 ± 0.03 | 0.53 ± 0.02 | 0.07 ± 0.003 | 33.4 ± 7.3 | 7 |
| 9 | | | | | |
| 10 | | | | | |
| 11 | 0.36 ± 0.03 | 0.45 ± 0.02 | 0.06 ± 0.01 | 18.7 ± 6.9 | 6 |
| 12 | | | | | |
| 13 | 0.33 ± 0.02 | 0.37 ± 0.02 | 0.05 ± 0.01 | 16.2 ± 3.3 | 6 |

Appendix Table 10. The functional response of *Anagrus* spp.

(T = 720 min; mean ± confidence limits 95%)

| Number of hosts offered | Number of hosts attacked | | Number of progeny | Number of observations |
|---|---|---|---|---|
| | Observed | Estimated | | |
| *Anagrus* sp. B | | | | |
| 2 | - | 1.98 | - | - |
| 4 | 3.7 ± 1.1 | 3.79 | 11.0 ± 5.5 | 3 |
| 8 | 7.0 ± 1.1 | 6.67 | 20.5 ± 7.7 | 4 |
| 16 | 11.0 ± 6.4 | 10.11 | 25.3 ± 16.5 | 3 |
| 32 | 12.0 ± 7.2 | 13.18 | 27.4 ± 13.8 | 5 |
| 64 | 15.8 ± 4.0 | 15.32 | 33.0 ± 7.7 | 6 |
| *Anagrus* sp. C | | | | |
| 2 | - | 1.99 | - | - |
| 4 | 3.5 ± 0.9 | 3.92 | 8.3 ± 4.7 | 4 |
| 8 | 7.4 ± 0.6 | 7.4 | 19.3 ± 3.5 | 8 |
| 16 | 12.3 ± 2.0 | 12.84 | 32.2 ± 5.8 | 11 |
| 32 | 16.6 ± 4.5 | 19.7 | 53.7 ± 11.8 | 9 |
| 64 | 24.2 ± 4.0 | 24.71 | 69.3 ± 9.7 | 6 |

Appendix Table 11. Interference between *Anagrus* spp females.

(mean ± confidence limits 95%)

| Number of females | Number of hosts attacked | Number of attacks | Number of observations |
|---|---|---|---|
| *Anagrus* sp. B | | | |
| 1 | 5.3 ± 4.3 | 13.3 ± 10.9 | 15 |
| 2 | 10.3 ± 8.0 | 44.8 ± 36.4 | 6 |
| 4 | 13.8 ± 5.6 | 73.5 ± 33.1 | 8 |
| 8 | 15.2 ± 1.1 | 98.7 ± 48.3 | 7 |
| *Anagrus* sp. C | | | |
| 1 | 6.8 ± 3.1 | 17.8 ± 8.7 | 11 |
| 2 | 11.3 ± 3.9 | 37.2 ± 18.5 | 8 |
| 4 | 13.0 ± 3.5 | 51.5 ± 19.2 | 11 |
| 6 | 14.4 ± 1.5 | 74.7 ± 29.1 | 7 |
| 8 | 15.3 ± 0.9 | 152.8 ± 51.0 | 9 |

Appendix Table 12. Relationship between the searching efficiency (a) and the density of female parasitoids (p).

| p | log p | Number of attacks | | Number of hosts attacked | |
|---|---|---|---|---|---|
| | | a | log a | a | log a |
| *Anagrus* sp. B | | | | | |
| 1 | 0.0 | 0.00058 | -3.24 | 0.00030 | -3.55 |
| 2 | 0.301 | 0.00097 | -3.01 | 0.00035 | -3.46 |
| 4 | 0.602 | 0.00053 | -3.27 | 0.00034 | -3.43 |
| 8 | 0.903 | 0.00054 | -3.27 | 0.00026 | -3.59 |
| *Anagrus* sp. C | | | | | |
| 1 | 0.0 | 0.00077 | -3.11 | 0.00038 | -3.42 |
| 2 | 0.301 | 0.00081 | -3.09 | 0.00043 | -3.37 |
| 4 | 0.602 | 0.00056 | -3.25 | 0.00030 | -3.54 |
| 6 | 0.778 | 0.00054 | -3.27 | 0.00027 | -3.57 |
| 8 | 0.903 | 0.00083 | -3.08 | 0.00027 | -3.57 |