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Autor(en): **Goergen, G. / Neuenschwander, P.**

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Chartocerus hyalipennis (HAYAT) (Hym.: Signiphoridae), a gregarious hyperparasitoid on mealybugs (Hom.: Pseudococcidae): biology and host range in West Africa

G. GOERGEN[1] & P. NEUENSCHWANDER[2]

[1]Institut für Phytopathologie und Angewandte Zoologie, Ludwigstr. 23, 35390 Giessen, FRG
[2]International Institute of Tropical Agriculture, B.P. 08-0932, Cotonou, Bénin

The biology and behaviour of the signiphorid *Chartocerus hyalipennis* (HAYAT) were studied in the laboratory on *Epidinocarsis lopezi* (DE SANTIS), a parasitoid of the cassava mealybug *Phenacoccus manihoti* MATILE-FERRERO. Only mummified secondary hosts, i. e. mealybugs, were accepted for oviposition. Host feeding and oviposition always occurred on the same host. The females are proovigenic and produced more eggs the more hosts they fed upon. When they had access to hosts and honey they lived significantly longer than without host feeding. On average, 2-3 relatively large eggs were laid per host and the sex ratio was strongly female biased. Larvae passed through four instars. At 28°C development from egg to adult lasted 16.0 days. In West Africa, *C. hyalipennis* is a rather unspecific ectophagous hyperparasitoid with a host range of at least seven species of primary parasitoids, all encyrtids attacking various pseudococcids.

Keywords: Pseudococcidae, Encyrtidae, hyperparasitoid, Signiphoridae, biological control

INTRODUCTION

With the exception of a few species peculiar to India and Sri Lanka, all species of the signiphorid genus *Chartocerus* MOTSCHULSKY are cosmopolitan (HAYAT & VERMA, 1980). Known host relationships from the presently 29 recorded species tend to support a hyperparasitic habit for the whole genus (WOOLLEY, 1988). Because of their small size, signiphorids have rarely been obtained from sources other than emergence samples, making them among the least studied chalcidoids (WOOLLEY, 1988). This neglect led to taxonomic inconsistencies at the generic (POLASZEK, 1993) or even the family level (WOOLLEY, 1986).

In tropical Africa, *Chartocerus* was first determined at the genus level only. It was found to be a widely distributed and common gregarious hyperparasitoid of encyrtids (mainly *Anagyrus* spp.) associated with the cassava mealybug (CM) *Phenacoccus manihoti* MATILE-FERRERO (Hom.: Pseudococcidae) (MATILE-FERRERO, 1977; FABRES & MATILE-FERRERO, 1980; BOUSSIENGUET, 1986). For the biological control of the CM, a serious pest insect of South American origin, the endoparasitoid *Epidinocarsis lopezi* (DE SANTIS)(Hym.: Encyrtidae) was successfully introduced in the early 1980s (review in HERREN & NEUENSCHWANDER, 1991). Wherever *E. lopezi* established itself, *Chartocerus* sp. became one of its most important hyperparasitoids (NEUENSCHWANDER *et al.*, 1987). Recently, this species has been identified as *C. (Xana) hyalipennis* (HAYAT) described from India (HAYAT, 1970).

The impact of the entire guild of hyperparasitoids on the biological control of the CM was shown to be only moderate (review in HERREN & NEUENSCHWANDER, 1991); but the specific contribution of *C. hyalipennis* is unknown. As a prerequisite for studies on the exact ecological role of *C. hyalipennis,* its morphology and biology, with regard to the ovipositional behaviour and immature development on *E. lopezi* in the laboratory is described and field records on indigenous hosts are given.

This study parallels the one on the other common hyperparasitoid of *E. lopezi, Prochiloneurus insolitus* ALAM (Hym.: Encyrtidae) (GOERGEN & NEUENSCHWANDER, 1990).

MATERIALS AND METHODS

Host stage selection and oviposition

Potted cassava plants were held in cages with screened sides and infested homogeneously with second and third instar CM. Female *E. lopezi* were introduced at successive time intervals to obtain all possible combinations of larval instars of the primary and secondary hosts. Cassava leaves, which contained an unknown mixture of parasitized and unparasitized CM, were removed from the potted plants and offered in a Petri dish to a freshly emerged and mated *C. hyalipennis* female, which had been deprived of hosts for 24 hours.

The foraging behaviour of the hyperparasitoid was observed and each attacked host removed after the female had completed one oviposition. The selected host, stinging time, and the number of successive ovipositor insertions were noted. In some instances, the oviposition sequence was intentionally interrupted after the female had withdrawn its ovipositor for the first time. Attacked hosts were enclosed in a gelatine capsule each and kept in a temperature chamber at 28±1°C and >65% RH for the eventual emergence of a wasp.

Immature development

To obtain data on immature development, hyperparasitized hosts were dissected 0-10 days after oviposition and the immature *C. hyalipennis* measured under a binocular microscope. In some instances, pupae of *E. lopezi* were carefully removed from the mummies directly after hyperparasitism. Eggs of *C. hyalipennis* were counted and reared together with their host pupae in small glass vials on a layer of plaster that was kept moist. Moreover some stung pupae were reared without hyperparasitoid eggs. For comparison, equal numbers of unparasitized *E. lopezi* pupae were isolated and kept under the same conditions.

Adult longevity

To determine the influence of different diets on adult longevity, the hyperparasitoids were held at 28±1°C and >65% RH and a photoperiod of 12L:12D with varying food sources with and without hosts. Newly emerged *C. hyalipennis* were offered the following food sources with and without hosts: 1) honey/no host, 2) honey/mummified CM for host-feeding, 3) no honey/mummified CM, 4) no food/no hosts. Honey was diluted with water whenever it became too viscous.

Host range

Samples of various pseudococcids were collected from different host plants in south-western Nigeria from 1983 and in the south of the Republic of Benin from 1989. Sampling was intensified during the late dry season (February-March), when mealybugs attain high population levels. Plant material infested with pseudococcids was examined under a stereomicroscope in the laboratory. Mummified mealybugs were removed and kept individually in gelatine capsules for emergence of Hymenoptera.

Evaluation

All means are given ± standard error. Comparisons among several means are made by a *t*-test according to Newman-Keuls. For regressions, the *t*-value of the slope (t_b) and the explained variance r^2 are indicated. All tests are judged at P=0.05 and significant *t*-values are marked with an asterisk.

RESULTS

Morphology and life-cycle

Usually, females attacked the same host several times. During each completed oviposition sequence, a female *C. hyalipennis* laid one to three eggs. The eggs were deposited externally within the mummy cavity and adhered to the integument of the primary host, in this case *E. lopezi.* Where several eggs had been laid, they were either scattered or stuck together.

The freshly deposited egg was cylindrical, slightly curved, with a distinct translucid peduncle, and averaged 0.27 by 0.06 mm (Fig. 1a). It was large in comparison to the size of the adult female (0.81 by 0.30 mm). At 28°C, eclosion was observed within 48 hours following oviposition.

After disrupting the chorion, the larvae were observed to crawl on the host integument in search of an appropriate place for external feeding, usually in intersegmental depressions of the host pupa. Based on the sizes and shapes of the mandibles, four larval instars were distinguished. The first instar larva was hymenopteriform, the margins of the segments already visible through the egg before eclosion. The body was composed of 13 segments of increasing length towards the abdomen and the head was minute. The average measurements for this stage, which lasted about 24 hours, were 0.19 by 0.06 mm.

Except the cephalic skeleton, the intermediate instars displayed no distinctive morphological characters. Because of steady feeding, the size of the larva doubled within 48 hours. Thus, the fully grown second instar larva averaged 0.44 by 0.21 mm. Ingestion of dark host tissue rendered the midgut visible through the translucent body of the ectoparasitoid. The tracheal system was visible and consisted of a pair of trunks ranging laterally from the prothorax to the seventh abdominal segment. These trunks were connected to four pairs of open spiracles, situated on the second thoracic and on the first three abdominal segments each. The cephalic end was marked by the tubular mouthparts, the thickened vertex with the antennal regions, and two pairs of extremities protruding posteriorily from the temporal region (Fig. 1d).

At day four, the host was nearly half consumed. The growing third instar larvae, with the same general aspect as the preceeding instars, gradually occupied the

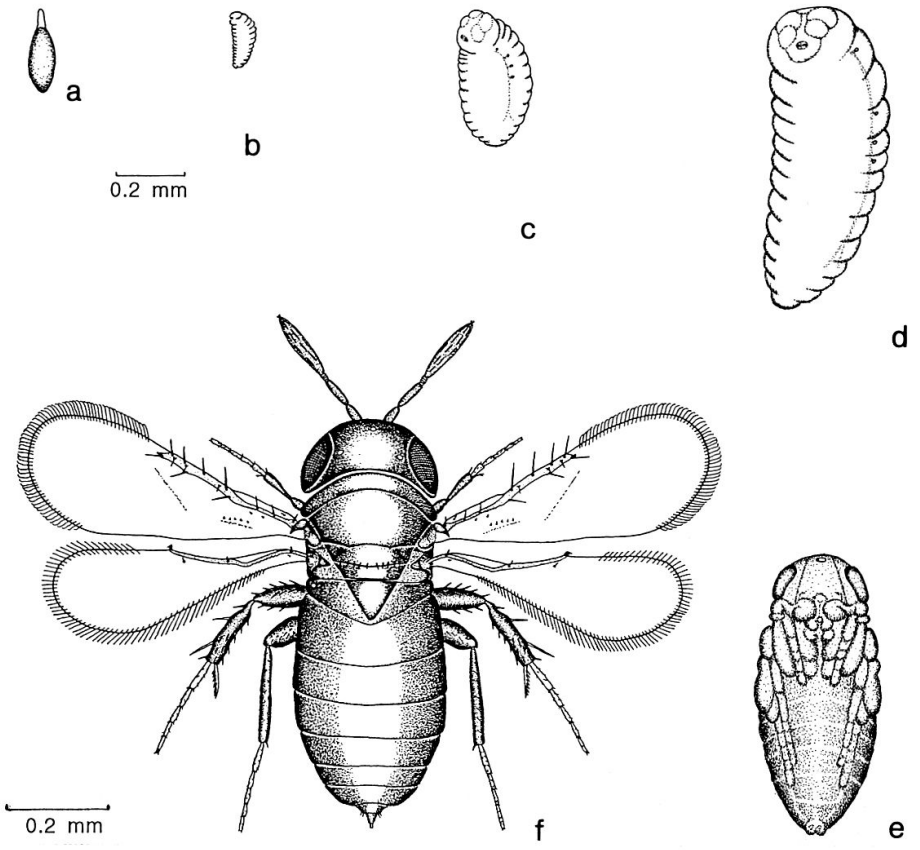

Fig. 1: Morphology of *Chartocerus hyalipennis* : a) egg, b) second-instar larva, c) third-instar larva, d) fourth-instar larva, e) pupa, f) adult female.

whole cavity of the mummy. Before molting into the final instar, the larva reached an average size of 0.71 by 0.24 mm.

The size and duration of the fourth instar larva (Fig. 1d) were strongly influenced by the availability of food. When several larvae fed simultaneously on a common host, both development time and size of individual siblings were reduced in comparison to solitary larvae. Because the host was almost totally ingested, the larvae were constrained by mutual contact. But even when food scarcity was artificially created by adding conspecific eggs from another hyperparasitized host, intraspecific larval cannibalism was never observed.

When the host was entirely consumed the larvae entered the quiescent prepupal stage. This happened between six days after oviposition for large clutches and eight days for solitary larvae. The sizes of fully grown fourth instar larvae before moulting ranged from 1.24 by 0.39 mm for solitary immatures to 0.89 by 0.29 mm for larvae of a clutch of five hyperparasitoids on the same host.

In the prepupal stage, which lasted ca. 24 hours, meconium particles were cast as a line of black pellets. In the pupal molt, a white filamentous exuvia, which remained attached to the meconium, was shed. Initially, the fresh pupa was whitish with a distinct translucid caudal end (Fig. 1e). About 36 hours later, it started to darken in a systematic manner: first, the eyes turned dark red, then, the abdominal surface

became entirely black and, finally, dark pigmentation extended simultaneously to the head and thorax.

After emergence, the adult hyperparasitoids stayed inside the host mummy for about one day. Their movements could be clearly observed through the sclerotized shell of the mealybug. In mummies containing both sexes, some mating took place.

Upon emergence, each sibling started to construct its own hole; but this activity stopped when the first opening was completed. Thus, all adult wasps left the mummy through a single irregular exit hole with ragged margins, cut open in various parts of the mummy. Occasionally, wasps that had left their mummy were observed to return into an empty, but previously hyperparasitized, mummy to mate.

On average, 2-3 *C. hyalipennis* adults emerged from an individual mummy; but 6-8 adults were counted from a single host on rare instances, i.e. 1.9% out of 2,845 reared mummies.

The duration from egg to adult emergence was 16.0 days ± 0.03 (N=944) at 28°C. Developmental times of males did not differ from those of females. The sex ratio, calculated from the pooled emergence data from all reared mummies, was strongly female biased, with 4.4 females to 1.0 male. Females kept unmated produced exclusively male progeny.

Host selection and oviposition

Dissections of adult females showed a maximum of 5-7 mature ovarian eggs at any given time. Host searching therefore started immediately after emergence. The hyperparasitoid often interrupted its search in a patch to feed on honey ejected by mealybugs. After encountering either mealybug wax, an ovisac, or a mummified CM, the female stopped and antennation was intensified. This arrestment was interpreted as a registration of chemotactile stimuli.

Among all instar combinations of primary and secondary hosts, probing with the ovipositor was only induced by mealybugs that presented a hard outer integument, i.e. mummies. Among 100 mummified mealybugs offered in batches of 10 hosts (over a period of five days), 36 mummies that had been hyperparasitized during the previous 48 hours by a conspecific female were all rejected and were not stung by another female.

Once a mummy was accepted, the female turned around and pushed the tip of the ovipositor against the sclerotized host shell. Drilling consisted in alternate rotations of the ovipositor accompanied by strong axial pressure that caused the female to tremble. Piercing the host integument required 8-26 minutes.

Once the mummy was perforated, the ovipositor was immediately thrust into the pupa or late larval instar of the primary host. The female *C. hyalipennis* stayed motionless for 10-15 minutes with the ovipositor inserted in the host's body. Withdrawal of the ovipositor was gradual and accompanied by slight forth and backward movements to form a feeding tube, which could be detected in subsequent dissections. After removal of the ovipositor, the female turned and kept its mouthparts over the drilling puncture to host feed.

After host feeding, oviposition was performed on the same host. This required 1-2 additional mummy perforations with stings of generally shorter duration. Withdrawal of the ovipositor was preceded by a series of pumping movements, which were presumed to mark the actual egg deposition. In a few instances, however, the sequence of host feeding and oviposition was reversed and resulted in a combination of both activities during a single sting. Whatever the sequence, it must

be stressed that in the 158 observed cases of host feeding and oviposition both activities were always performed on the same host.

A mated *C. hyalipennis* female spent on average 26.0 min (±1.21, N= 92) with the ovipositor inserted into its host (drilling time for mummy perforation being disregarded here). The maximum duration was 60 min. Unexpectedly, the main stinging time of unmated females was significantly shorter and lasted 22.2 min (±0.95, N=75, t= 2.40*). Each attacked mummy received on average 2.1 stings (±0.10, N=66).

Whenever *C. hyalipennis* attacked old larvae or pupae of *E. lopezi*, the development of the primary host was arrested. Wound scars were observed as small black spots. Stung hosts, which had been removed before oviposition, stayed whitish and checks made up to 33 days after the attack indicated a still turgid immature host. By contrast, unstung pupae isolated for control developed and hatched normally within 6 to 8 days after having been removed from the mummy. It is concluded that development of *C. hyalipennis* immatures is accompanied by permanent host paralysis.

Adult longevity and host feeding

Under same conditions, males lived shorter than females (Tab. 1). Longevity was maximized with a full carbohydrate and protein diet, i.e. honey together with host feeding. Life span was shortest when the females were starved. With a honey

Table 1: Effect of different diets on the longevity of adult *Chartocerus hyalipennis* at 28°C and >65% RH.

Diet	Sex	Longevity (days)*	±SE	N
honey	female	17.0[b]	0.02	363
	male	10.0[c]	0.05	115
honey + host feeding	female **	19.1[a]	0.69	27
host feeding	female **	5.3[d]	0.58	24
none	female	2.9[e]	0.13	46
	male	1.6[f]	0.09	65

* Means not followed by the same letter differ significantly at P = 0.05.
**Males do not host feed

diet, hyperparasitoid females lived significantly longer with than without access to hosts.

Host feeding alone could not compensate for honey. On average lack of honey resulted in a sharp decrease in longevity. A closer look at these data revealed, however, two tendencies: while trying to oviposit, 45% of the freshly emerged females (N=47) were unable to pierce the host integument and died within 2-4 days. These data were added to the category of hyperparasitoids that had not fed at all. The successful females (N=24), by contrast, subsisted long enough to perforate the mummified CM so they could host feed.

Because the strength to attack new mummies and to gain access to food through host feeding fluctuated widely among individual females that were not fed honey, longevity data displayed a broad range. Life span (X_0) positively affected the total number of host feeding events (Y_1): $Y_1 = -9.51+3.38X_0$ (N= 47, $r^2= 0.81$, $t_b= 13.7$*). Life span (X_0), in turn, determined to a large degree the number of offspring (Y_2): $Y_2 = -24.14 + 8.51X_0$ (N= 47, $r^2= 0.81$, $t_b= 14.0$*). Consequently, host feeding (X_1) had a large influence on reproduction (number of offspring, Y_2): $Y_2 = -0.11 + 2.50X_1$ (N= 47, $r^2= 0.99$, $t_b= 76.0$*)(Fig. 2).

Host range

In West Africa, *C. hyalipennis* was recovered from various pseudococcids on different host plants (Tab. 2). Since other mummies from the same batch yielded primary parasitoids, it is concluded that these *C. hyalipennis* had developed as hyperparasitoids, killing their primary encyrtid hosts.

In the laboratory, *C. hyalipennis* reproduced successfully also on mummies that already contained immatures of another hyperparasitoid species. Such tertiary parasitism was observed on *P. insolitus*, the other common hyperparasitoid of *E.*

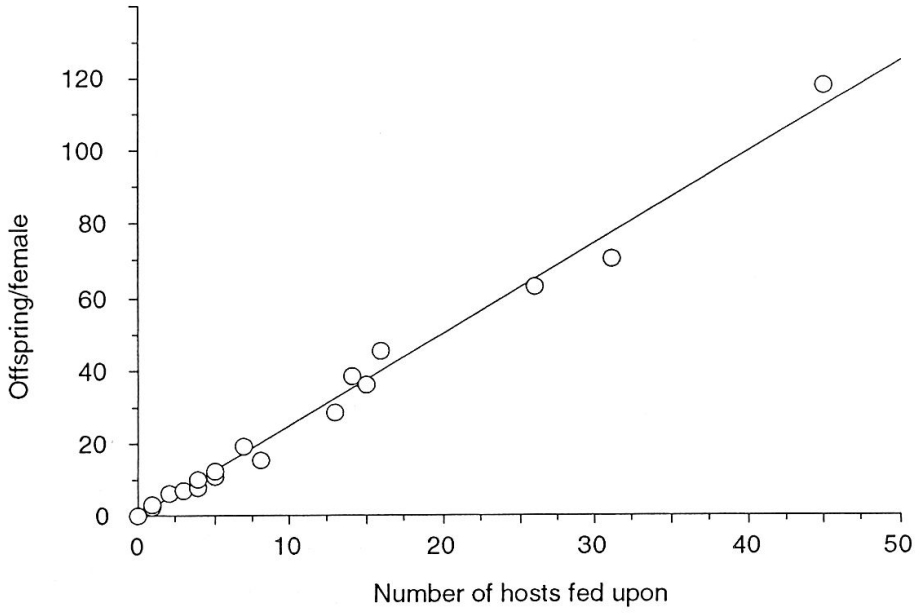

Fig. 2: Effect of host feeding on total number of offspring produced by *Chartocerus hyalipennis* females at 28°C, >65%RH (N=47). Females were offered pupae of *Epidinocarsis lopezi,* but no honey.

lopezi. Successful development took place only when *C. hyalipennis* attacked during the early larval instars of *P. insolitus*, which are endophagous or, alternatively, during the pupal stage. This timing is essential because the larva of *P. insolitus* becomes ectophagous in the fourth instar and, therefore, capable to destroy siniphorid eggs or immatures. Furthermore, *C. hyalipennis* was reared as a tertiary parasitoid on *Chartocerus subaeneus* (FÖRSTER), a solitary secondary ectoparasitoid, which had developed on a pupa of *E. lopezi* within the mummified CM.

In rare instances, the rearing of field collected CM mummies led to the simultaneous emergence of an adult *C. hyalipennis* together with a mature *Tetrastichus* sp. (Hym.: Eulophidae), which otherwise develops as a solitary secondary ectoparasitoid on pupae of *E. lopezi*. Once, simultaneous emergences of a male *P. insolitus* and *C. hyalipennis* were observed. Evidently, the primary host had provided enough food for the two hyperparasitoids to complete their development.

DISCUSSION

Literature accounts on the host range of *C. hyalipennis* are more or less anecdotal and restricted mostly to taxonomical studies carried out in India (HAYAT, 1970; HAYAT & VERMA, 1980). These records reveal only secondary hosts, namely the pseudococcids *Coccidohystrix insolita* (GREEN) (=*Centrococcus insolitus* GREEN), *Coccidohystrix* spp., *Nipaecoccus viridis* (NEWSTEAD) (=*N. vastator* (MASKELL)), and *Nipaecoccus* sp. The present study complements previous data from Africa on CM parasitoids (MATILE-FERRERO, 1977; FABRES & MATILE-FERRERO, 1980; BOUSSIENGUET, 1986; NEUENSCHWANDER *et al.*, 1987; BIASSANGAMA *et al.*, 1989). Based on the Indian studies, it is possible that the host range in Africa is still broader than recorded here.

To ensure safe development of the progeny, the female *C. hyalipennis* paralyzes its host permanently before oviposition. This feature is widespread in idio-

Table 2: Host range of *Chartocerus hyalipennis* from material sampled in south western Nigeria and in the south of the Republic of Benin, 1983-1991.

Plant	Secondary host	Primary host
Acalypha sp. *Hibiscus* sp.	*Phenacoccus madeirensis* GREEN	*Anagyrus* sp. 1
Annona muricata	*Maconellicoccus hirsutus* (GREEN)	*Anagyrus* sp. 1 *Gyranusoidea indica* SHAFEE
Manihot esculenta	*Ferrisia virgata* COCKERELL	*Anagyrus* sp. 2
M. dichotoma	*Phenacoccus manihoti* MATILE-FERRERO	*Blepyrus insularis* CAMERON *Epidinocarsis lopezi* (DE SANTIS)
Mangifera indica	*Rastrococcus invadens* WILLIAMS	*Anagyrus mangicola* NOYES *Gyranusoidea tebygi* NOYES

biont parasitic Hymenoptera (GAULD & BOLTON, 1988) and has also been described for other hyperparasitoids (BOCCHINO & SULLIVAN, 1981). Primary host paralysis does not preclude the simultaneous development of an internal *P. insolitus* immature. In the subsequent competition among the larvae of different species of hyperparasitoids, the ectophagous *C. hyalipennis* usually wins over the endophagous *P. insolitus*. Analogous observations on tertiary parasitism were made on the closely related parasitoid complex of *Pseudococcus maritimus* (EHRHORN) (Hom.: Pseudococcidae), where the gregarious hyperparasitoid *Chartocerus (=Thysanus) elongatus* GIRAULT (Hym.: Signiphoridae) attacked a pupa of *Zarhopalus corvinus* (GIRAULT) (Hym.: Encyrtidae) which had previously been hyperparasitized by the endophagous *Prochiloneurus (=Achrysopophagus) modestus* (TIMBERLAKE) (Hym.: Encyrtidae) (CLAUSEN, 1924).

In the present laboratory observations, conspecific superparasitism was regularly avoided up to two days after the previous attack. Competition for hosts may, however, become important, especially when hyperparasitoids become abundant at high CM and *E. lopezi* densities (NEUENSCHWANDER & HAMMOND, 1988; HAMMOND & NEUENSCHWANDER, 1990) and it is not known whether conspecific superparasitism occurs under these conditions.

In their search for hosts, female *C. hyalipennis* accept only mummified CM. These hosts are readily distinguished from both unparasitized and parasitized, but still living, CM by their hard integument. *C. hyalipennis* thereby differs in its choice from the other main hyperparasitoid in the CM biocenosis, *P. insolitus,* which - apart from mummies - probes also active mealybugs whether they are parasitized or not (GOERGEN & NEUENSCHWANDER, 1990).

The actual egg deposition requires one to several ovipositor insertions and is a distinct event accomplished on the same host that has previously been used for host feeding. Based on the few existing biological studies, these processes are apparently similar in other signiphorid species (QUEZADA *et al.,* 1973; AGEKYAN, 1968; WOOLLEY & VET, 1981; ROSEN *et al.,* 1992).

Female *C. hyalipennis* lay relative large yolky eggs. From the present study, the weight of each egg is estimated at 14-21% of the body weight. Once deposited, these eggs mature without further ingestion of host haemolymph. This form of ovigenesis is characteristic for lecithal (anhydropic) eggs and physiologically expensive for the parent (FLANDERS, 1950; GAULD & BOLTON, 1988). Because of their large size and high energetic demand few eggs develop simultaneously in the ovaries. Morphological studies conducted on other signiphorids indicate even lower numbers of available ripe eggs than in *C. hyalipennis* (WOOLLEY & VET, 1981). Such instantly limited availability of eggs was attributed to monootene ovarioles, in which only one egg develops at a given time (QUEZADA *et al.,* 1973).

The production of new eggs depends greatly on the ability of *C. hyalipennis* females to host feed. The female thereby devotes considerable time gaining access to its host and constructing a feeding tube for ingestion of host haemolymph. Host feeding thereby seems to have priority over oviposition. This attack sequence was found also in other signiphorid parasitoids (WOOLLEY & VET, 1981; ROSEN *et al.*, 1992). In the present study, females survived a few days only when deprived of honey, despite an opportunity for host feeding. Under the same conditions, the addition of honey prolonged longevity considerably. Unexpectedly, an exclusive honey diet without oviposition lowered the hyperparasitoid's longevity, despite the possibility of egg resorption. It is suggested that absorbed haemolymph is first allocated

to the production of eggs and plays a small role in maintenance. As carbohydrate sources are widely available in the field, the hyperparasitoid can thus survive temporal host scarcity.

In the laboratory, *C. hyalipennis* flew less, but was more often engaged in host feeding than other Hymenoptera of the CM complex. This resulted in lengthy 'patch times' (VAN ALPHEN & VET, 1986). It is interesting to note that, in the same ecosystem, the closely related *C. subaeneus,* which is more mobile than *C. hyalipennis*, is a solitary hyperparasitoid. Furthermore, in the laboratory, *C. hyalipennis* requires high host densities and fails to establish when it is confined to low CM and *E. lopezi* densities (GOERGEN & NEUENSCHANDER, 1992). By contrast, *C. subaeneus* readily invades cages with low *E. lopezi* populations (P. NEUENSCHWANDER, unpubl. results).

Since *C. hyalipennis* is rather polyphagous it can shift from one host species and/or host patch to another whenever conditions become unfavorable. This opportunistic behaviour makes it difficult to assess the ecological role of *C. hyalipennis*. Because this species feeds and oviposits on the same host, it can be classified as being a concurrent-destructive type of parasitoids, as defined by JERVIS & KIDD (1986). Based on the analytical model on host feeding strategies by these authors, an adaptation to high host densities is predicted for *C. hyalipennis.* This corresponds to field data that document a density dependent reaction of hyperparasitoids, i.e. particularly high population densities when primary and secondary host populations are high (NEUENSCHWANDER & HAMMOND, 1988).

The overall impact of hyperparasitoids on *E. lopezi*'s efficiency proved to be difficult to assess directly in field experiments (IZIQUEL & LE RÜ, 1989). Presently, the most extensive information is available from long-term field surveys which confirm that effective biological control by *E. lopezi* was achieved despite a substantial degree of hyperparasitism (NEUENSCHWANDER *et al.,* 1989; HAMMOND & NEUENSCHWANDER, 1990). Though *C. hyalipennis* comprised on average 31.9% of all hyperparasitoids of *E. lopezi* (NEUENSCHWANDER & HAMMOND, 1988), its potential for interference in the CM system is not clear and needs complementary field studies.

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