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Importance of nutrition and host availability on oogenesis and oviposition of *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae)

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Abstract

A variety of host and non-host meals were tested for their potential in triggering oogenesis and oviposition in females of *Cephalonomia stephanoderis* Betrem, a synovigenic parasitoid of the coffee berry borer, *Hypothenemus hampei* (Ferrari). The consumption of non-host meals or meals composed of honey and crushed host eggs or pupae was insufficient to initiate oogenesis. The presence of suitable hosts for oviposition appeared essential for inducing oogenesis and oviposition in this parasitoid. Whereas females may host-feed on all developmental stages of *H. hampei*, these were not equally suitable in stimulating oogenesis and oviposition. In no-choice tests, oogenesis and oviposition were observed only in females supplied with fully-developed larvae, prepupae and pupae. Direct contact with hosts apparently stimulated egg maturation and egg-laying. Delaying the allocation of energy to egg production until suitable hosts are available for oviposition may be an adaptive attribute of a parasitoid of a concealed and patchily distributed host such as *H. hampei*.

Introduction

Among hymenopterous parasitoids, females of synovigenic species emerge with, at most, a fraction of their lifetime complement of mature eggs (Flanders, 1950; Jervis & Kidd, 1986). Autogenous species can mature some eggs without first feeding, whereas anautogenous species must feed during a variable pre-oviposition period to stimulate oogenesis (Jervis & Kidd, 1986). Although non-host food sources such as nectar, pollen or honeydew may be exploited in nature, host-feeding is widespread (Jervis & Kidd, 1986; Jervis *et al*., 1993, 1996). Females may consume the haemolymph and other tissues of their hosts to meet nutritional requirements and sustain oogenesis (Jervis *et al*., 1992, 1996; Heimpel & Rosenheim, 1995; Heimpel & Collier, 1996). Host feeding is frequently associated with the production of large anhydropic (i.e. yolk-rich) eggs, a limited egg storage capacity, and the ability to resorb eggs when hosts are scarce (Flanders, 1942; Jervis & Kidd, 1986). Both the quality and quantity of the ingested food influence egg production (Wheeler, 1996). Moreover, the egg content may vary according to the adult parasitoid diet, host materials being incorporated into lipoid and protein bodies that form the yolk (Le Ralec, 1995).

Cephalonomia stephanoderis Betrem (Hymenoptera: Bethylidae) is a solitary ectoparasitoid of prepupae and pupae of the coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae) (Koch, 1973; Abraham *et al*., 1990). Native to equatorial Africa, the borer has become the major pest of coffee worldwide (Le Pelley, 1968; Baker,

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1999). *Cephalonomia stephanoderis* was introduced from Africa to Mexico and other Latin American countries during the late 1980s and early 1990s to control the borer (Barrera *et al*., 1990; Benavides & Portilla, 1990). This parasitoid appears to have become established in some coffee growing areas but high control levels of borer populations have generally not been achieved (Delgado & Sotomayor, 1991; Barrera, 1994; Sponagel, 1994; Damon, 2000). In the field, *C. stephanoderis* females search for potential hosts inside coffee berries, where host availability is variable and intimately related to the phenology of the coffee tree (Baker, 1984). Moreover, foraging female parasitoids may encounter a variety of host stages inside the coffee berry as *H. hampei* eggs are laid in patches and adult and offspring generations overlap (Corbett, 1933).

The present paper focuses on the role of host availability, nutrition and mating on the reproductive biology of *C. stephanoderis* females. Female parasitoids are synovigenic, anautogenous and use hosts for both feeding and reproduction (Koch, 1973). The duration of the pre-oviposition period varies with the nutritional state of females and environmental factors such as temperature. It lasts a minimum of two to three days (e.g. Koch, 1973; Lauzière *et al*., 1999) and according to Koch (1973), *C. stephanoderis* females must feed on *H. hampei* pupae to initiate oogenesis. The objective of this study was to determine the influence of host developmental stage, host feeding and mating status on egg maturation and oviposition in *C. stephanoderis* females.

In Mexico, *C. stephanoderis* has traditionally been reared using infested coffee berries collected from coffee plantations. The cost of mass-reared parasitoids can be reduced by using supplementary diets as additional sources of carbohydrates, proteins and vitamins that have a marked influence on the fecundity and longevity of many laboratory reared parasitoids (Leius, 1961, 1962; Sandland, 1979; Jervis & Kidd, 1986). Rearing costs of *C. stephanoderis* could be reduced by establishing effective mass rearing techniques that would lessen the dependence on hosts for host feeding without compromising the parasitoid's quality. The effect of various host and non-host foods on egg maturation and oviposition behaviour was therefore also studied.

Materials and methods

Biological material

Parasitoids were obtained from a stock colony maintained at El Colegio de la Frontera Sur (Tapachula, Chiapas, Mexico) that was established in 1988 after the parasitoids were imported from Togo. Parasitoids used in the experiments were reared on prepupae and pupae from a colony of *H. hampei* maintained on a semi-artificial diet (Villacorta & Barrera, 1993). Parasitoid pupae (cocoons) were placed individually in gelatin capsules until adult emergence. Newly emerged females (< 6 h) of similar size were selected, allowed to mate for a 24-h period with young experienced males (< 48 h), and immediately used in tests. Unmated females were also isolated for 24 h prior to the tests in order to compare similar age mated and unmated females. Experiments were conducted at 28 ± 2°C and 75 ± 5% relative humidity under a 12L:12D photoperiod. Only female fully-developed larvae, prepupae, pupae and adults of *H. hampei* were used as hosts because females of the borer are significantly larger than conspecific males (Corbett, 1933).

Host acceptance for host feeding or oviposition

To determine which host developmental stages are used for host feeding and/or oviposition, eight mated and eight unmated *C. stephanoderis* females were placed individually in an experimental arena (two concave microscope slides placed against each other creating a 16 mm diameter and 1.6 mm depth arena) and provided daily with honey and a supplement of: (i) nothing (control); (ii) 20 eggs; (iii) 20 small (0.75–1 mm) larvae; (iv) ten fully-developed (2 mm) larvae; (v) ten prepupae; (vi) ten pupae; and (vii) ten adults of *H. hampei*. Preliminary observations showed that parasitoid females did not exhaust the food provided. The number of hosts used for feeding and oviposition was determined daily for a period of seven days. All hosts were visually examined under a stereomicroscope for wounds and surface deflation caused by host feeding and/or the presence of a parasitoid egg attached to the cuticle. Wounds inflicted by *C. stephanoderis* females to adult *H. hampei* were assessed by categorizing individuals as either 'paralysed' (host feeding uncertain) or 'decapitated' (borers undoubtedly fed upon). A two-way ANOVA (Systat, SPSS Inc., Chicago, Illinois) was used to compare numbers of hosts fed upon and parasitized, as well as the duration of the pre-oviposition period of unmated and mated females supplied with different host developmental stages. Means were separated using Tukey's HSD test.

To determine if the different host stages were equally effective in triggering oogenesis, all females were killed, dissected and the condition of their ovaries recorded after the seven-day observation period. In addition, one unmated and one mated female of each treatment were dissected daily over the entire experimental period. Female parasitoids were held in a drop of saline solution, their ovaries extracted from the abdominal cavity under a stereomicroscope (50×) and the number of developing and mature oocytes recorded using an ocular micrometer (400×). Since sperm can be seen under the microscope at 1000× with immersion oil, the content of the spermatheca, slightly crushed between a microscope slide and a glass cover, was also observed to confirm mating status.

Effect of feeding regimes on oogenesis and duration of the pre-oviposition period

To test the effect of food regime on oogenesis and on the duration of the pre-oviposition period of mated *C. stephanoderis* females, different host and non-host meal treatments were provided: (i) no food; (ii) honey; (iii) honey and five crushed *H. hampei* eggs; (iv) honey and a crushed pupa; (v) honey and fresh egg albumin; (vi) honey and brewer's yeast (ICN Biomedicals, Aurora, Ohio); and (vii) honey and four intact, healthy host pupae. Yeast and albumin were incorporated into honey in a 1:1 ratio. Females of treatments 1–6 were fed *ad libitum* with the corresponding diet for three consecutive days after which they were provided with four intact host pupae. Females of treatment 7 were offered host pupae from day 1. Three additional treatments (8–10) were included where female parasitoids were fed as in treatments 2, 4 and 6, but for five rather than three consecutive days. Twenty five females per treatment

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were used. Females were observed once every 6 h, once they had been provided with host pupae, until the first egg was laid in order to determine the duration of the pre-oviposition period (calculated from the day host pupae were introduced into the arena). The effect of food supplements on the duration of the pre-oviposition period was examined using ANOVA. To rule out possible effects of female size on oogenesis, the head width of females was measured after the observations with a stereomicroscope (50×) equipped with a micrometer eyepiece and used as a size index. There was no significant difference between treatments regarding female size (ANOVA, F = 1.37, df = 9, 236, $P = 0.08$). Females (n = 4) that did not oviposit or died within a ten-day period were not included in the statistical analysis.

Additional data on oogenesis were obtained by dissecting five recently emerged (< 6 h) females (control) and five females allocated to treatments 1–7 for a one to three-day period. Dissections were carried out as previously described and the number of developing and mature eggs was recorded.

Results

Host acceptance for host feeding or oviposition

Cephalonomia stephanoderis females fed on all developmental stages of *H. hampei* (table 1). From the beginning of the observation period, females were regularly observed feeding on eggs and on the haemolymph and other tissues of previously-paralysed older developmental stages of *H. hampei* (fig. 1). Feeding was difficult to determine on older host stages, especially adults, as it occurred through membranous areas such as between the pro- and mesothorax or between the sternites, with no signs of host feeding apparent. Unless the female parasitoid prolonged its attack, host feeding wounds on adults could not be differentiated from host stinging alone. Following prolonged or repeated feeding bouts, host tissues were consumed and only the empty cuticle of larvae, prepupae or pupae remained. As for *H. hampei* adults, in 1.4 % of cases (16/1120) the haemocoele was left empty as females 'decapitated' the host by tearing apart the pro- and mesothorax and consumed the soft, accessible host tissues. By contrast, 57% of adult hosts were stung and paralysed (644/1120). Non-concurrent host feeding (i.e. destructive feeding) was observed in the majority of the tests (99%, n = 336). Oviposition took place only on prepupae, pupae and on a few fully-developed *H. hampei* larvae (table 1). *Cephalonomia stephanoderis* females rarely oviposited on mature larvae (1%, n= 197), preferring those larvae that had transformed into prepupae during the 24-h period of exposure to the parasitoid (before hosts were replaced).

Numbers of hosts fed on by *C. stephanoderis* females differed significantly according to host developmental stage, but the mating status of parasitoid females had no influence (Two-way ANOVA, $F_{\text{host stage}} = 42.16$, df = 6, 98, $P < 0.001$; $F_{\text{mating status}} = 0.17$, df = 1, 98, $P = 0.69$) (table 1). There was no significant difference in the numbers of hosts parasitized by unmated or by mated *C. stephanoderis* females offered fully-developed larvae, prepupae or pupae (Two-way ANOVA, $F_{\text{host stage}} = 0.44$, df = 2, 42, $P = 0.65$; $F_{\text{mating status}} = 3.03$, df = 1, 42, $P = 0.09$) (table 1). Furthermore, the duration of the pre-oviposition period was not significantly affected by mating status of *C. stephanoderis* or by the stage of the host provided (fully-developed larvae, prepupae or pupae) though females provided with pupae began to lay eggs slightly earlier than females provided with prepupae or with fully-developed larvae (Two-way ANOVA, $F_{\text{host stage}} = 2.71$, df = 2, 42, $P = 0.08$; $F_{\text{mating status}} = 0.013$, df = 1, 42, $P = 0.91$) (table 1).

Dissection of newly emerged *C. stephanoderis* females (n = 14) showed that the ovaries of both unmated and mated females were undeveloped. The ovarioles (six in this species) were reduced, usually not clearly distinguishable, and without developing or mature eggs. Ovaries of females fed continuously with honey, eggs, small larvae or adults of *H. hampei* (n = 112) were also undeveloped and were devoid of mature eggs after the seven-day observation period. Oogenesis was initiated only in females supplied with fully-developed *H. hampei* larvae, prepupae or pupae. In these cases, developing oocytes were present in the ovaries of two-day-old females while mature oocytes were observed in females aged three days and older (fig. 2).

Effect of feeding regimes on oogenesis and duration of the pre-oviposition period

The pre-oviposition period lasted an average of 2.5 ± 0.75 days from the day *C. stephanoderis* females were offered host pupae (n = 246) and was not shortened by providing parasitoid females with an external source of carbohydrates or proteins (of non-host origin) prior to offering them suitable hosts for oviposition (ANOVA, F = 1.55, df = 9, 236,

Table 1. Daily host feeding and oviposition rates and duration of the pre-oviposition period (mean ± SD) of mated and unmated *Cephalonomia stephanoderis* females provided with different developmental stages of *Hypothenemus hampei* over a seven-day period.

Host stage	Unmated females*			Mated females*		
	Host feeding rate (hosts per day)	Pre-oviposition period (days)	Oviposition rate (eggs per day)	Host feeding rate (hosts per day)	Pre-oviposition period (days)	Oviposition rate (eggs per day)
Eggs	3.2 ± 2.6 c	–	–	3.1 ± 2.0 c	–	–
Small larvae	2.8 ± 2.5 c	–	–	3.5 ± 3.4 c	–	–
Fully-developed larvae	0.6 ± 0.9 ab	3.50 ± 1.07	0.91 ± 1.01	0.6 ± 0.9 ab	2.88 ± 1.64	1.36 ± 1.34
Prepupae	0.6 ± 0.7 ab	3.13 ± 1.73	1.21 ± 1.17	0.6 ± 0.7 ab	2.75 ± 1.04	1.41 ± 1.45
Pupae	1.0 ± 1.1 b	2.35 ± 1.19	1.16 ± 0.95	1.0 ± 0.9 b	2.00 ± 0.53	1.34 ± 1.23
Adults†						
decapitated	0.1 ± 0.3 a	–	–	0.2 ± 0.4 a	–	–
paralysed	5.7 ± 2.2 d	–	–	5.7 ± 2.5 d	–	–

*Means in the same column followed by different letters are significantly different (Tukey, $P < 0.05$).
†Decapitated: direct evidence of host feeding; Paralysed: no direct evidence of host feeding.

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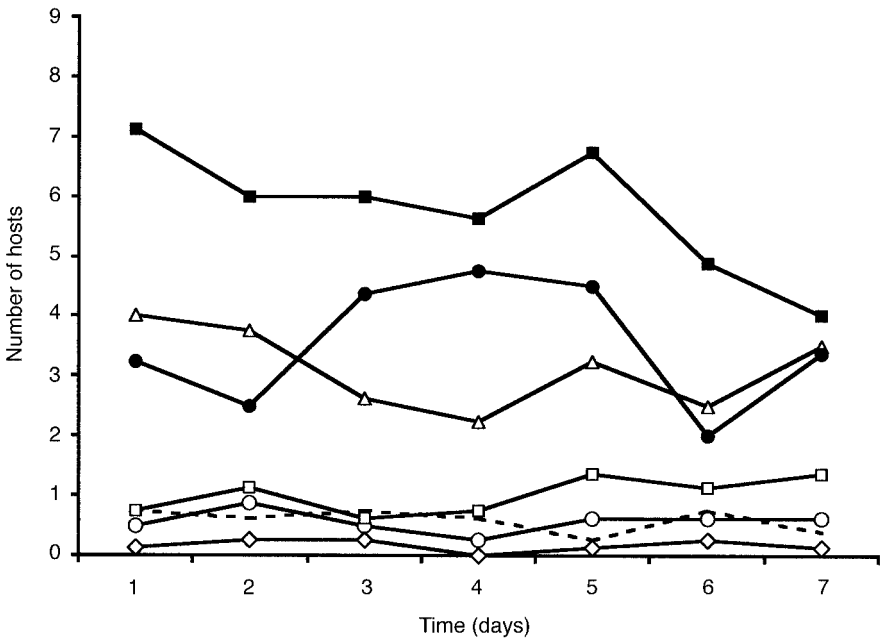

Fig. 1. Host feeding in *Cephalonomia stephanoderis* females. Numbers of hosts fed on or paralysed by females provided with different developmental stages of *Hypothenemus hampei* over a seven-day observation period (△, eggs; ●, small larvae; – – –, late larvae; ○, prepupae; □, pupae; ◇, decapitated adults; ■, paralysed adults). Decapitated adults: direct evidence of host feeding; Paralysed: no direct evidence of host feeding (see text for explanation).

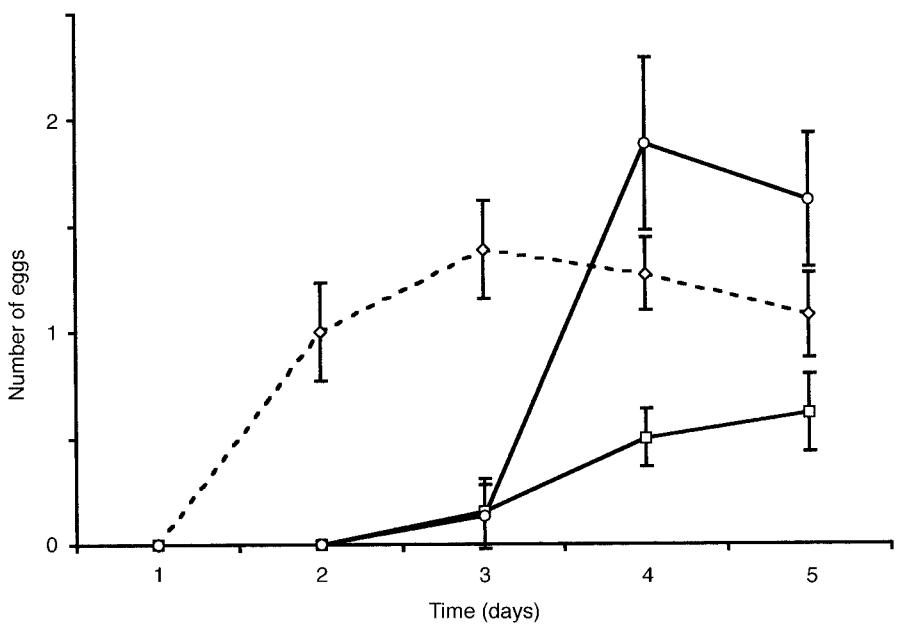

Fig. 2. Egg maturation in *Cephalonomia stephanoderis* females. Numbers of developing (◇) and mature (□) eggs and eggs laid (○) by females provided with *Hypothenemus hampei* pupae.

P = 0.13; table 2). Dissection showed that the liquid food supplements provided had no influence on egg maturation (even the host-based ones (treatments 3, 4 and 9)), although females were observed feeding on them. The development of ovaries of females from treatments 1–6 were very similar (after one, two or three days) to the ovaries of recently emerged females. Although the six ovarioles could be better distinguished, no developing or mature eggs were observed. Only the ovaries of females supplied with healthy, intact pupae (treatment 7) held, on average, 5.6 ± 0.9 (n = 5) developing oocytes after two days of exposure to the hosts and 4.8 ± 0.8 developing and 0.6 ± 0.5 fully-developed eggs on day 3 (n= 5). Indeed, three of the three-day-old females had already oviposited once at the time of dissections.

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Table 2. Duration of the pre-oviposition period (mean ± SD) of *Cephalonomia stephanoderis* females provided with different host and non-host diets over a three or five-day period prior to provision with healthy *Hypothenemus hampei* pupae.

Treatment	Feeding regimes	n	Regime period (days) *	Pre-oviposition period (days)†
1	No food	24	3	2.84 ± 1.61
2	Honey	25	3	2.60 ± 0.80
3	Honey + crushed eggs	25	3	2.54 ± 0.44
4	Honey + crushed pupae	24	3	2.52 ± 0.65
5	Honey + albumin	25	3	2.23 ± 0.14
6	Honey + brewer's yeast	24	3	2.55 ± 0.89
7	Honey + healthy pupae	25	0	2.58 ± 0.69
8	Honey	25	5	2.53 ± 0.42
9	Honey + crushed pupae	24	5	2.21 ± 0.34
10	Honey + brewer's yeast	25	5	2.35 ± 0.45

*Duration of feeding period prior to supplying female parasitoids with healthy, intact *H. hampei* pupae.
† Calculated from the day females were offered intact *H. hampei* pupae. Thus, total pre-oviposition period represents the sum of the feeding period and the observed pre-oviposition period. Means are not significantly different (ANOVA, $P > 0.05$).

Discussion

Host feeding by *C. stephanoderis* females may be an important factor affecting biological control programmes as it results in a significant reduction in the numbers of *H. hampei* (Lauzière *et al*., 1999). However, it poses a challenge for mass rearing since, as pointed out by Jervis & Kidd (1999), a larger number of hosts is required for destructive host-feeding parasitoids, than with non-destructive host feeders or with non-host feeders, in order to maintain an equivalent level of productivity. It is therefore important to determine the relationship between host feeding and host developmental stages, egg maturation and oviposition in *C. stephanoderis* in order to optimize mass rearing conditions.

The data indicated that under no-choice conditions, *C. stephanoderis* females fed on all host developmental stages and attacked several borers per day. This flexible host feeding behaviour is particularly important as host feeding is not only a means of acquiring nutrients necessary to sustain egg maturation but also of increasing adult longevity (Lauzière *et al*., 2000a). Furthermore, the fact that females may feed on any of the host developmental stages enables them to reserve prepupae and pupae, the more suitable and preferred host stages for oviposition, while feeding on the younger/smaller host stages or adults. In paired choice experiments, *C. stephanoderis* females fed preferentially, but not exclusively, on host stages not used for oviposition purposes (Lauzière *et al.*, in press), a behaviour exhibited by females of several other parasitoid species (e.g. Kidd & Jervis, 1991; Heimpel & Collier, 1996 and references therein; Lampson *et al*., 1996).

Dissections of newly emerged females confirmed that their ovaries were not developed, as had previously been reported by Koch (1973) and Pérez-Lachaud (1995). Dissections of older females indicated that all host stages were not equally efficient in triggering oogenesis. Females provided with eggs, first instar larvae or adults of *H. hampei* (i.e. host developmental stages not used for oviposition) failed to produce mature eggs, even though parasitoid females fed on these host stages for up to seven days (fig. 1). Females provided only with honey also failed to produce mature eggs. Oogenesis and oviposition were observed, however, in females provided with prepupae, pupae and, to a lesser extent, in those provided with fully-developed host larvae. Furthermore, females provided with crushed *H. hampei* pupae, but prevented from directly manipulating whole pupae, failed to develop mature eggs. The availability of additional sources of carbohydrates and proteins (honey, albumin, yeast) also failed to shorten the duration of the pre-oviposition period or trigger oogenesis in the absence of suitable hosts for oviposition. In fact, the ovaries of *C. stephanoderis* females provided with supplementary host or non-host diets, but deprived of hosts, never developed mature oocytes. These were observed only in the ovaries of females provided with suitable hosts for oviposition for at least two consecutive days. Unlike *C. stephanoderis*, females of *Microterys flavus* (Howard) (Hymenoptera: Encyrtidae) (Bartlett, 1964) and *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) (Collier, 1995; Heimpel & Rosenheim, 1995) respond to dietary supplements such as honey and haemolymph from small hosts not used for oviposition, and yeast or soy hydrolysates, by significantly increasing oogenesis and egg deposition, with a consequent reduction in production costs for mass-reared individuals. The usefulness of providing protein supplements together with suitable host stages for oviposition in reducing host feeding and enhancing fecundity, has not yet been investigated in *C. stephanoderis*.

The reasons for the lack of oogenesis in females provided with eggs, first instar larvae or *H. hampei* adults are not clear and several hypotheses might account for this: (i) the occurrence of significantly higher feeding rates on preferred hosts (prepupae, pupae and fully-developed larvae); (ii) eggs, first instar larvae and adults of *H. hampei* may be nutritionally inadequate for oogenesis; or (iii) the nutrients obtained from hosts not used for oviposition may be allocated to functions other than reproduction. The way the supplements were incorporated into the honey may also explain the lack of oogenesis in females provided with additional food.

Although the data obtained in the present study do not exclude any of the above proposed hypotheses, females fed with eggs, first instar larvae or adults of *H. hampei* were never observed exhausting their food supply (though biomass

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ingested could not properly be evaluated) and it was previously shown that eggs and first instar larvae of *H. hampei* were as effective as pupae in promoting survival of female *C. stephanoderis*, i.e. females lived more than 60 days (Lauzière *et al*., 2000a). Several other lines of evidence suggest that, in addition to host feeding, direct contact with hosts suitable for oviposition (i.e. host pupae, prepupae and mature larvae) may be required in order to trigger oogenesis in *C. stephanoderis*. Firstly, previous observations from videotaped oviposition sequences revealed that female *C. stephanoderis* spend a great amount of time examining hosts and sting-probe repeatedly *H. hampei* pupae both during the pre-oviposition and oviposition periods (Lauzière *et al*., 2000b). These observations suggest that essential chemical and physical cues from the host are perceived by *C. stephanoderis* females during contact with hosts, and are likely to be involved in triggering oogenesis and the whole host acceptance process. Secondly, data from videotape recordings showed that in a two-choice test, two out of nine *C. stephanoderis* females fed exclusively upon *H. hampei* eggs during the pre-oviposition period and reserved available host pupae for oviposition (I. Lauzière, personal observation). This indicates that the consumption of haemolymph from *H. hampei* pupae is not indispensable to initiate oogenesis in *C. stephanoderis*, as was initially suggested by Koch (1973), and that eggs may well be nutritionally adequate for oogenesis. Finally, oogenesis and oviposition in *C. stephanoderis* have been observed in females provided with prepupae and pupae (but not small larvae) of *Caulophilus oryzae* (Gyllenhal) and *Sitophilus* sp. (all Coleoptera: Curculionidae), two recently found factitious hosts (G. Pérez-Lachaud & I.C.W. Hardy, unpublished data).

The ability to regulate oogenesis according to host availability represents a favourable attribute of parasitoids such as *C. stephanoderis* that attack patchily distributed hosts. However, the specific nature of the stimuli that trigger and regulate oogenesis and egg-laying in this parasitoid species remains unknown and more studies are needed to understand the processes affecting nutrient metabolism and egg production. The development of a supplementary diet that would provide all of the nutrients required for egg maturation and general maintenance in females of *C. stephanoderis* would allow a reduction in the need for *H. hampei* hosts in breeding programmes and favour the development of efficient techniques for continuous rearing of this parasitoid.

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