The physiology of host-feeding in parasitic wasps: implications for survival

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Introduction

The nature of nutritional resources, and the rules governing the allocation of these nutrients in the organism, are arguably some of the most important and least understood elements in behavioural and evolutionary ecology (Boggs 1992). One of the systems where the connection between the ecological and physiological aspects of nutrition has been most explicitly made is in parasitoid wasps (Rivero & Casas 1999a). Parasitoids are excellent models for testing theories concerning the evolution of behaviour and life-history strategies (Charnov & Skinner 1984; Godfray 1994; Charnov & Skinner 1985; Quicke 1997) and for integrating such knowledge into multitrophic population ecology (Hassell 2000; Hochberg & Ives 2000). Females search the environment for hosts (usually other insects) in which to lay their eggs. In addition, in many species females must also feed from the host in order to obtain the nutrients necessary for egg production. Often, however, host-feeding is either incompatible with laying an egg or can reduce the quality of the host for the developing larvae (Jervis & Kidd 1986; Heimpel & Collier 1996). Host-feeding females are thus faced with a decision that epitomises the evolutionary trade-off between current and future reproduction: whether to use the host for egg-laying or for feeding.

Host-feeding in parasitoids has been the target of many theoretical studies that have aimed to predict the optimal physiological and environmental conditions under which a female should bypass an opportunity for current reproduction in order to feed from the host and increase her future reproductive opportunities (Jervis & Kidd 1986; Mangel 1989; Chan 1991; Kidd & Jervis 1991a; Houston *et al.* 1992; Chan & Godfray 1993; Collier *et al.* 1994; Collier 1995a; Heimpel *et al.* 1998). The predictions of these models, however, rely heavily on the nature and function of host-feeding. In particular, a key assumption of the models is whether host-feeding provides nutrients exclusively for egg production (Jervis & Kidd 1986; Chan & Godfray 1993; Collier *et al.* 1994; Heimpel *et al.* 1994), exclusively for maintenance (Houston *et al.* 1992; Chan & Godfray 1993), or both (Chan & Godfray 1993; Collier 1995a; Heimpel *et al.* 1998), with different assumptions rendering drastically different results in terms of behavioural decisions. The nature and allocation of nutrients also have implications for population stability and persistence (Briggs *et al.* 1995; Kidd & Jervis 1989; Kidd & Jervis 1991b). A drain of nutrients from the same pool of resources that produces eggs, for use in maintenance, is destabilising. On the other hand, a non host-food source, complementary to host-feeding, has stabilising effects (Briggs *et al.* 1995). By contrast, in

Kidd & Jervis' model (1989) host mortality inflicted by female parasitoid wasps through feeding overrides stabilizing (and persistence-promoting) processes. Thus, results of population dynamics models show that the rules of nutrient acquisition and allocation have important consequences for the dynamics of such interactions.

The experiments carried out so far have largely consisted of comparisons of egg production and longevity in host fed and unfed females (reviewed by Jervis & Kidd 1986 and Heimpel & Collier 1996). While the positive correlation between host-feeding and fecundity appears to be ubiquitous, these studies have, however, rendered ambiguous results about the effect of host-feeding on parasitoid longevity. In some species host-feeding has no effect on longevity, in some it does, while yet in others it does only if a sugar source is also available (reviewed by Jervis & Kidd 1986 and Heimpel & Collier 1996). While this disparity may partly be due to intractable differences in the experimental conditions (Heimpel & Collier 1996; Rivero & Casas 1999a), it is much more likely to reflect interspecific differences in the nature of the nutrients consumed.

Most studies assume that host-feeding parasitoids consume the host's haemolymph (Leius 1961; Jervis & Kidd 1986; Jervis *et al.* 1992; Rosenheim & Rosen 1992; Briggs *et al.* 1995; Collier 1995a; Heimpel & Collier 1996). This assumption, which is based on the highly proteinaceous nature of this substance (Chapman 1998) has, to our knowledge, never been tested experimentally. In fact, a wide range of feeding behaviours (from parasitoids which puncture the host and imbibe the fluids to those that consume the entire host), and host stages consumed (from eggs to pupae), are grouped under the common banner of "host-feeding" (reviewed by Jervis & Kidd 1986 and Heimpel & Collier 1996). Host-feeding may thus involve the ingestion of a wide spectrum of nutrients, which include not only proteins but also fat body lipids, sugars and trace elements. Studying the nature and function of these nutrients at a physiological level is essential in order to understand the adaptive nature of host-feeding decisions in parasitoids.

In this study, we carried out a detailed physiological investigation of host-feeding in *Eupelmus vuilletti* (Hymenoptera, Eupelmidae) a parasitoid that feeds and oviposits in third to fourth-instar coleopteran larvae. We aimed to: (1) determine the biochemical nature of the host-feeding fluids, (2) analyse and quantify their composition and (3) test directly the effect of these nutrients on female longevity. For this purpose we interrupted females while they fed and analysed biochemically the fluids extracted. The composition of the host-feeding fluid was then compared with haemolymph samples. We then separated, identified and quantified the main sugars in the host haemolymph using TLC coupled with colorimetric techniques. We

focus our attention on sugars because they are known to be critical in determining longevity in parasitoids and other insects (Jervis & Kidd 1986; Heimpel & Collier 1996; Chapman 1998). We then proceeded to test directly the role of these sugars in female longevity through a series of microinjections that allow us to precisely dose the sugars at the appropriate concentrations. Quantity of haemolymph consumed during host-feeding was also measured. Our approach allows us to test directly and unambiguously the physiological impact of host-feeding on life history traits in parasitoids.

Materials and methods

Eupelmus vuilletti (CRW) (Hymenoptera, Eupelmidae) is a tropical solitary host-feeding ectoparasitoid of third- to fourth-instar larvae of *Callosobruchus maculatus* (F) (Coleoptera, Bruchidae) infecting *Vigna unguiculata* (Fabaceae) pods and seeds. Females are synovigenic, i.e. they are born with some immature eggs and need to feed from the host in order to sustain egg production and maturation. Females, however, rarely use the same host for egg laying and for feeding (personal observation). Culturing and all experimental procedures were carried out in a controlled temperature room with a 13:11 light:dark photoperiod, a temperature cycle of 33ºC(light): 23ºC(dark), and a constant 75% humidity.

Extraction of host-feeding fluids

In this species, females feed from the host by puncturing its cuticle and creating a feeding tube with secretions from their ovipositor (Fulton 1933). The females then turn and use the feeding tube to extract the host fluids with their mouthparts. In this species, females host-feed an average of 18 times during their lives (personal observation). In this experiment, newly emerged females were deprived of hosts for 48 hours and were then placed individually in a small Petri dish (diameter 5.5 cm) with 3 hosts (fourth-instar *C. maculatus* larvae). Hosts had been previously extracted from the *V. unguiculata* seeds and placed inside a gelatin capsule following Gauthier & Monge (1999). This system allowed the observation of feeding behaviour and the extraction of the host-feeding fluids from the host-feeding tube. Once a feeding tube was constructed, the female was removed and a graduated micro-capillary connected to a manual pump was introduced inside the feeding tube. The liquid collected was immediately pumped out into a 1.5 ml Eppendorf tube placed on ice. In order to obtain a

sufficient quantity of fluid for biochemical analyses, extracts from several host-feeding events were pooled (about 10 host-feeding events per sample, 6 samples for lipid/sugar/glycogen analysis and 5 samples for protein).

Extraction of haemolymph

In order to compare the contents of the host-feeding fluids to those of haemolymph we extracted haemolymph directly from the host. Extractions of haemolymph were carried out using the same pumping system as above. For this purpose c.a. 0.7 µl of haemolymph was extracted from each host by inserting the micro-capillary in the mid-lateral side of their body. Haemolymph samples were analysed individually for each larva (33 samples for lipid/sugar/glycogen analysis and 32 samples for protein).

Whole host body extracts

60 hosts previously extracted from the *V. unguiculata* seeds were weighed (Supermicro Sartorius, Göttingen, Germany), and immediately placed individually into a 1.5 ml Eppendorf tube placed in ice where they were crushed with a micro-pestle. Whole body extracts were analysed individually for each larva (30 samples for lipid/sugar/glycogen analysis and 30 samples for protein). Results were expressed as µg/mg. For the ease of presentation and to be able compare these values directly with the values for the two other fluids (host-feeding fluids and host haemolymph compositions are expressed as µg/µl), we carried out a transformation assuming the density of whole body extract to be 1 mg/µl. This value is within the range of values for the insect body (0.915 mg/µl for lipids and 1.900 mg/µl for exoskeleton; Denny 1993).

Lipid, sugar and glycogen analyses

Quantification of the amount of lipids, sugars and glycogen in the host-feeding fluid (n=6), haemolymph (n=33) and whole host body extract (n=30) samples were carried out using a modification of the colorimetric techniques developed for mosquito analysis (Van Handel 1985a, 1985b; Van Handel & Day 1988). For this purpose, 40 µl of 2% sodium sulphate and 300 µl of chloroform-methanol (1:2) were added to each sample. After centrifugation at 180-200 g, the lipids and sugars remain dissolved in the supernatant, while the precipitate contains most of the glycogen.

For the lipid analysis, 150 µl of the supernatant was transferred into a borosilicate tube

(16x100 mm) and then placed in an ethylene-glycol heating block at 90°C to completely evaporate the solvent. 40 µl of 95% sulphuric acid were then added, and the tube re-heated at 95°C for 2 minutes. After cooling, 960 µl of vanillin reagent was added to the tube which was then left for 15 min (see Van Handel 1985b for details). Each sample was then transferred to a micro-cuvette and read in a spectrophotometer at 525 nm (DU®-64 spectrophotometer, Beckman, Villepinte, France).

For the sugar analysis, 150 µl of the supernatant was transferred into a borosilicate tube (as above) which was then placed in an ethylene-glycol heating block at 90°C to evaporate the solvent down to a few microlitres. After adding 1 ml anthrone reagent, the tubes were placed at 90°C for 15 min, then cooled and read in a spectrophotometer at 625 nm (see Van Handel 1985a).

The glycogen, adsorbed in the precipitated sodium sulphate, was washed with 400 µl of 80% methanol. Samples were then vortexed and centrifuged for 5 min at 180-200 g. Once the supernatant was eliminated, 1ml of anthrone reagent was added and the tubes were placed at 90°C for 15 min. After cooling, the samples were first filtered (Millipore®, diameter=0.45 µm), and placed in micro-cuvette and read in the spectrophotometer at 625 nm.

The calibration curves that allowed us to transform absorbances into concentrations were made with standard vegetable oil (for lipids) and glucose (for sugars and glycogen) following Van Handel (1985a and 1985b).

Protein analyses

Protein analysis was carried out using the Bradford dye-binding micro-assay procedure (Bradford 1976). Analysis of proteins cannot be made on the same samples as those used for lipids, sugars and glycogen determination and so it was carried on a separate set of samples (n=5 for host-feeding fluids, n=32 for haemolymph samples and n=30 for whole body extracts). 800 µl of physiological water (0.15M NaCl) containing 0.001% Triton X-100 (Sigma Aldrich) was added to each sample and then placed 5 days in the fridge to allow time for the Triton-X to dissolve the proteins. 200 µl of Bradford Reagent (Bio-Rad Laboratories, Munich, Germany) reactive were then added. Samples were left to react for 15 min and then read at 595 nm. Calibration curves were obtained using bovine serum albumin (Sigma-Aldrich, S^{t} Quentin Fallavier, France).

Identification and quantification of host haemolymph sugars

Thin layer chromatography (TLC) was used to identify the main sugar components of the host haemolymph. Sugars were purified from haemolymph samples (about 10 host per sample, 3 samples), which were obtained as described previously. In order to deproteinise the sample and remove all lipids, samples were mixed with 200 µl of 70% ethanol and then with 500 µl of a chloroform-methanol-water solution (2:2:1) and centrifuged at 10,000 g (Bligh and Dyer 1959).

The sugar standards (D-fructose, D-trehalose, D-glucose and sucrose) and the purified haemolymph samples were separated on 20 x 20 cm aluminum sheets pre-coated with 0.25 mm of silica gel 60 (Merck, Fontenay sous bois, France). Plates were impregnated with 0.2 M K_2HPO_4 to improve resolution (Ghebregzabher et *al.* 1976). Separations were carried out three times in the same direction with an acetonitrile : water (34:6) solvent system (Gauch *et al.* 1979).

After final development and drying, plates were impregnated with 2.5% vanillin in a sulphuric acid : ethanol (4:1) solution and then heated for 5 minutes at 120°C in a drying oven to visualise the sugars. Identification of the main host haemolymph sugars was carried out using comparisons between mobility (measured as movement relative to the solvent front -Rf- on TLC) of the standard and haemolymph samples.

Quantification of sugars using the colorimetric technique described above cannot be made on samples that have been previously treated with a vanillin reagent. Another TLC was therefore performed where the sugars were separated on the plates following the above procedure, but were not treated with the colored reagent. Instead, the positions of the sugar bands were located using the Rfs previously obtained. The individual bands of sugars were then scratched from the TLC plate, placed in borosilicate tubes and quantified using the colorimetric technique described above.

Quantification of haemolymph consumption

On the day of emergence, 50 females were weighed (Supermicro Sartorius, Göttingen, Germany) and immediately placed individually in a small Petri dish with three fourth-instar hosts (as above). Females were observed continuously until a host-feeding event took place. Females were weighted once more immediately after they finished feeding and the amount of food consumed was estimated by subtracting the weight before and after feeding.

The effect of sugars on female longevity

The TLC identified sucrose and trehalose as the main sugar components of the host's haemolymph (see results). The next step was to determine whether these disaccharides directly influence female longevity. For this purpose, different solutions were injected directly into the parasitoid haemolymph on the ventral abdominal side of newly emerged females using a micro-capillary connected to a manual pump. The extremity of the micro-capillary was introduced between the 4^{th} and 5^{th} sternite at a depth of 1.5 mm under the cuticle in order to avoid penetration of the major organs. In the injection experiments, females injected with water were used as the control group in order to ensure that the penetration of the micro-capillary was not a confounding factor. The volume of solutions injected was determined from the amount of food consumed during host feeding (see results) and in order to avoid a dramatically high mortality due to experimental manipulation. In the control group (group 1, n=20), females were injected with 1µl of pure water. Two other groups were injected with 1 µl of a sucrose (group 2, n=16) or trehalose (group 3, n=18) solution at haemolymph concentrations (4.6 and 10.6 µg/µl respectively, see results). A fourth group was injected with 1 µl of a mixture of these two sugars at haemolymph concentrations (group 4, n=26). In the last group, experimental females were injected directly with 1 µl of host haemolymph (group 5, n=15) which had been obtained from hosts following the protocol described above. Once injected, females were placed in small Petri dishes and kept at room temperature to allow the wound to heal. Females that 'bled' profusely after injection were immediately discarded. Female survival, without access to hosts or food, was recorded every day until all females died.

Statistical analysis

Most of the distributions of the sampled populations are not normal, requiring the use of non-parametric tests. Non-parametric tests reported were carried out using SPSS (SPSS Inc., Chicago, USA) or following Zar (1984). The extraction of fluids from the host-feeding tube is a very tedious and delicate exercise and many extractions from several tubes are required to obtain enough materials for a single analysis. This explains the difference in samples size between samples from the host-feeding fluid and the haemolymph and host body extract. Dunn non-parametric multiple comparisons tests (for unequal sample size and tied ranks, Zar 1984) were carried out to determine where the significant differences lay.

Results

The composition of whole body extracts, of host-feeding fluids and thehost's haemolymph differ widely in the amount of most of the biochemical constituents (Kruskal-Wallis test, proteins: H = 22.36, $p<0.05$; lipids: H = 50.62, $p<0.05$; sugars: H = 34.53, $p<0.05$; glycogen: H = 1.89, *NS*) (see also Fig. 1). There were no statistical differences in the amount of proteins, lipids, sugars or glycogen between the host-feeding fluid extracted from the feeding tube and the host's haemolymph (Dunn test for the difference between the components of the host-feeding fluids and the host's haemolymph, proteins: Q = 0.688, *NS*; lipids: Q = 0.686, *NS*; sugars: Q = 0.092, *NS*) (Fig. 1). In contrast, whole body extracts were widely different from the host-feeding fluids (Dunn test, proteins: Q = 2. 971, $p<0.05$; lipids: Q = 3.284, $p<0.05$; sugars: Q = 3.041, $p<0.05$) and from the host's haemolymph (proteins: Q = 4.347, $p<0.05$; lipids: Q = 7.029, $p<0.05$; sugars: Q = 5.101, $p<0.05$) (Fig. 1).

The two main sugars in the host haemolymph were identified as the disaccharides trehalose and sucrose (Table 1). Trehalose is the most abundant (mean±s.e = 10.58 $\pm$ 0.32 µg/µl), followed by sucrose (4.20 $\pm$ 0.44 µg/µl). Disaccharides thus constitute at least to 85% of the total sugars present in the haemolymph (61% trehalose and 24% sucrose). Preliminary experiments suggest that the remaining 15% sugars are more likely to come from other sugar types present at concentrations too low to be detected by the TLC, rather than to errors in the quantification of the target sugars.

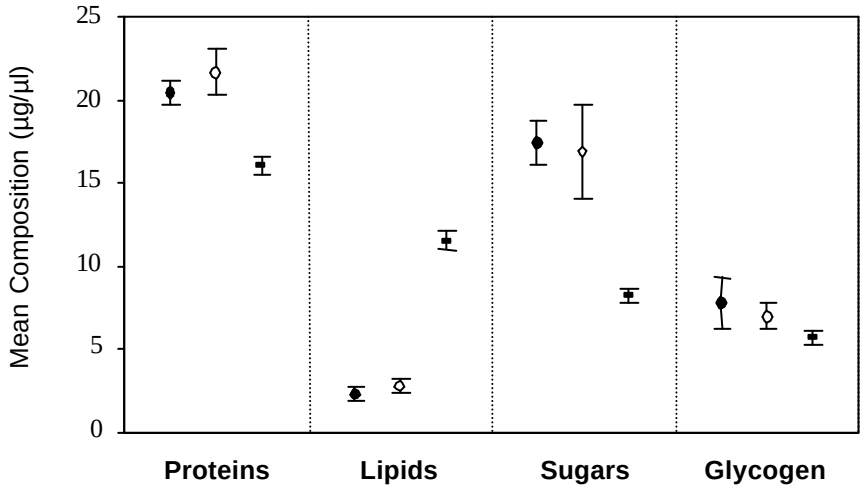

Figure 1. Mean composition of *C. maculatus (host)* haemolymph (●), host-feeding fluid consumed by the parasitoid *E. vuilletti* (○) and whole host body extract (▪). Mean composition of proteins, lipids, sugars and glycogen (mean $\pm$ error standard) are expressed in µg/µl.

Table 1. Identification of the main haemolymph sugars from Callosobruchus maculatus, using comparisons between mobility of sugar standards and main haemolymph sugars on Thin Layer Chromatography (mobility measured as movement relative to the solvent front, Rf).

Source	Sugar type	Rfs
Haemolymph samples	Sugar 1	0.05
	Sugar 2	0.11
Sugar standards	Trehalose	0.05
	Sucrose	0.11
	Glucose	0.21
	Fructose	0.27

Females gained an average of 0.2584 $\pm$ 0.1716 mg per host-feeding. The volume of solutions injected corresponds to the volume of fluid obtain from four host-feeding events and all solutions injected lead to a similar survival rate (about 85%). The injection of sugars into the female's haemolymph resulted in different female longevities (Fig. 2) (Kruskall-Wallis test, H=14.79, $p<0.05$). While single injection of either sucrose or trehalose at haemolymph densities did not increase survival (Dunn test between groups 1 and 2, Q=0.228, *NS*, and between groups 1 and 3, Q=0.695, *NS*), the simultaneous injection of sucrose and trehalose at haemolymph concentrations as well as the direct injection of haemolymph, increased survival significatively (Dunn test between groups 1 and 4, Q=2.810, $p<0.05$, and between groups 1 and 5 Q=2.926, $p<0.05$). Injection of trehalose and sucrose simultaneously, increased survival of females as much as injection of host haemolymph (Dunn test between groups 4 and 5, Q=0.557, *NS*). The simultaneous injection of trehalose and sucrose at haemolymph concentrations and the injection of host haemolymph lead to a mean survival gain of 1.27 and 1.61 days respectively, compared to the controls, which corresponds to an increase in longevity of 22% for 4 host-feeding events (see Fig. 2).

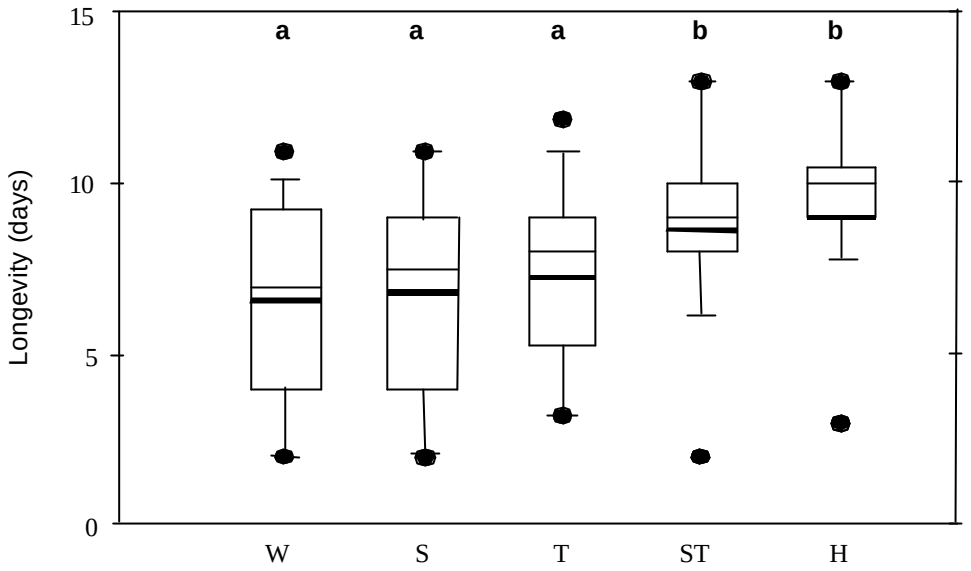

Figure 2. Effects of the injection of Water (**W**), Sucrose (**S**), Trehalose (**T**), Sucrose+Trehalose (**ST**) and host Haemolymph (**H**) on the longevity of the parasitoid *Eupelmus vuilletti*. The thin horizontal line of each box plot marks the median of the sample and the thick horizontal line marks the mean of the sample. Black dots correspond to the minimum and maximum longevity recorded for each treatment. Statistical differences between means are shown by letters (a, b).

Discussion

The lipid, sugar, glycogen and protein composition of the host-feeding fluid extracted from the feeding tube is not significantly different from the composition of the haemolymph extracted directly from the host. In contrast, whole body extracts differ widely in the amount of most of the above constituents, showing, in particular, a much higher level of lipids. These results provide strong evidence that *E. vuilletti* consumes the host's haemolymph during a host-feeding event. Females fed on average 18 times during their life (personal observation) and in each feeding event they ingested an average of 0.258µl of haemolymph (haemolymph density is roughly 1; Hoffman 1995).

The haemolymph of fourth-instar *C. maculatus* larvae was found to be high in sugars and proteins but low in glycogen and lipids. These results are highly consistent with previous studies where the haemolymph composition of insects has been quantified (Wyatt 1961; Florkin & Jeuniaux 1964; Mullins 1985; Chapman 1998). The disaccharides trehalose and sucrose were identified as the most abundant sugars in the host's haemolymph. Trehalose is known to be the main sugar in insects' haemolymph, where it is the key energy storage

molecule (Florkin & Jeuniaux 1964; Chapman 1998). The trehalose concentration we obtained (10.6 µg/µl) is also very consistent with that obtained in other Hymenoptera and in Coleoptera (*Apis mellifera* 10.4 µg/µl, *Tenebrio molitor* 15.5 µg/µl, *Periplaneta americana* 15.3 µg/µl, *Heliothis zea* 10.4 µg/µl; see Fell 1990 and Leta *et al.* 1996). The presence of sucrose seems less common but has also been reported in butterfly larvae (Bounias 1983).

Experiments in which the effect of different adult diets on fecundity and longevity are compared (reviewed by Jervis & Kidd 1986 and Heimpel & Collier 1996) suggest that, in general terms, the proteins obtained from host-feeding serve to meet the high amino acid demands associated with egg production. These results have been confirmed by direct tracking of the incorporation of radioactively labelled amino acids into the eggs (Rivero & Casas 1999b; Rivero *et al.* 2001). Far less clear is the role of other nutrients present in the haemolymph, particularly the highly concentrated disaccharides. Sugar is known to have a critical effect on longevity of most parasitoids tested so far (reviewed by Jervis & Kidd 1986 and Heimpel & Collier 1996). The emphasis of most studies has however been on sugars that occur naturally in nectar or honeydew such as glucose, sucrose and fructose. In addition, in most cases females have been fed *ad libitum*. In contrast, we decided to concentrate our attention on how the two main haemolymph sugars influence female longevity when injected into the females at precise concentrations.

The simultaneous injection of trehalose and sucrose at haemolymph concentrations significantly increased the longevity of the females. In addition, females directly injected with haemolymph showed the same longevity as those injected only with a combination of the two sugars. These results thus identify the haemolymph sugars trehalose and sucrose as the main resources responsible for the increase in female longevity in host-fed females. Other haemolymph constituents, such as glycogen, proteins, and lipids probably have no or a very limited impact in this species.

The nature of nutritional resources and the pattern of allocation of nutrients are both fundamental aspects of the life-history of organisms and, as such, have critical consequences for fitness (Roff 1992; O'Brien *et al.* 2000, Jervis *et al.* 2001, Rivero *et al.* 2001). The role of specific sugars in determining longevity either directly or indirectly is a widespread phenomenon in insects, including parasitoids (Quicke 1997; Chapman 1998; Olson *et al.* 2000). We have shown that in our system the host's haemolymph is a rich source of such sugars and that host-feeding provides key nutrients for maintenance; as little as three host-feeding events increase the lifetime by one day. This positive relationship between number of host-feeding events and longevity is linear across all feeding events occurring during the

animal's lifetime (unpublished data).

Our study is the first to identify the constituents of host-feeding meals and to provide a manipulative proof that hemolymph sugars are solely responsible for increased longevity in *E. vuilletti*. Further studies need to be carried out to know the exact composition of the host feeding meal in other parasitoid species and to correlate it with observed life history traits. Quantitative and qualitative differences in the host feeding diets could explain the disparity between the extent of host-feeding gain and female food choices between parasitoid species. In particular, we suggest that the presence of sugars at sufficient concentrations in the host feeding meal may be a strong predictor of whether female parasitoids need to embark on costly nectar foraging trips (Jervis *et al*. 1993; Sirot & Bernstein 1996). The fact that some species of parasitoids are not able to survive by feeding on the host alone could also be explained by differences in the composition of the feeding meal. *Aphytis melinus*, for example, is likely to feed mostly on the sugar-poor fat body of their host which may explain their incapacity to survive more than 3 days without an extra sugar source (Heimpel *et al.* 1997). A low level of haemolymph sugars could also explain the observation made by Heimpel & Collier (1996) and subsequently by Heimpel *et al.* (1997) in (*A. melinus*) where host feeding only had an influence in longevity if the parasitoid was also allowed to feed on sugar. However, differences in the ability of different species to utilize the ingested sugars should also be taken into account.

Here, we examined only one aspect of the relationship between nutrition and life-history - that between haemolymph sugars and longevity. Further studies need to be carried out to determine the relative contribution of the different host feeding components to egg production and longevity. Such information would allow us to make stronger statements regarding the role of nutrient acquisition in reproductive decisions such as the trade-off between current and future reproduction. In addition, the magnitude of the drain of nutrients towards maintenance and the slope of the relationship between the amount of reserves and mortality, can have consequences for the stability of host-parasitoid population dynamics (Briggs *et al*. 1995). While the estimation of the relative magnitudes of these two parameters is the object of current experiments, the unexpected high increase in life expectancy per host-feeding event is a strong incentive contributing to the development of realistic, physiologically structured host-parasitoid population models. Parasitoid systems illustrate how, although nutritional physiology, behaviour, life-history and population dynamics are often studied independently, their integration can be essential in order to understand an organism's ecology.