

# Importance of host feeding for parasitoids that attack honeydew-producing hosts

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## Abstract

Insect parasitoids lay their eggs in arthropods. Some parasitoid species not only use their arthropod host for oviposition but also for feeding. Host feeding provides nutrients to the adult female parasitoid. However, in many species, host feeding destroys an opportunity to oviposit. For parasitoids that attack Homoptera, honeydew is a nutrient-rich alternative that can be directly imbibed from the host anus without injuring the host. A recent study showed that feeding on host-derived honeydew can be an advantageous alternative in terms of egg quantity and longevity. Here we explore the conditions under which destructive host feeding can provide an advantage over feeding on honeydew. For 5 days, *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) parasitoids were allowed daily up to 3 h to oviposit until host feeding was attempted. Host feedings were either prevented or allowed and parasitoids had ad libitum access to honeydew between foraging bouts. Even in the presence of honeydew, parasitoids allowed to host feed laid more eggs per hour of foraging per host-feeding attempt than parasitoids that were prevented from host feeding. The higher egg-laying rate was not compromised by survival or by change in egg volume over time. In conclusion, host feeding can provide an advantage over feeding on honeydew. This applies most likely under conditions of high host density or low extrinsic mortality of adult parasitoids, when alternative food sources cannot supply enough nutrients to prevent egg limitation. We discuss how to integrate ecological and physiological studies on host-feeding behavior.

## Introduction

Life-history theory deals with trade-offs that arise when limited resources need to be allocated among competing traits (Stearns, 1992). Two of the most studied life-history phenomena are trade-offs between current and future reproduction, and between reproduction and survival. In some Hymenoptera, such trade-offs are reflected in the decision of an adult female parasitoid to parasitize or feed upon a host (Heimpel & Rosenheim, 1995). When the female wasp parasitizes a host through oviposition, it invests in current reproduction, which is the most direct way to realize fitness. However, oviposition results in fewer eggs that can be used for future reproduction or survival through egg

resorption (Bell & Bohm, 1975; Jervis et al., 2001). Host feeding is the consumption of host hemolymph by the adult female parasitoid and provides nutrients that can be used to mature eggs (Jervis & Kidd, 1986; Heimpel & Collier, 1996). A single host feeding often yields more eggs in the future than can currently be laid in one host (Heimpel et al., 1994; Collier, 1995; Heimpel et al., 1997; Rivero & Casas, 1999; Giron et al., 2004). In some species, host feeding also increases longevity (Heimpel & Collier, 1996; Giron et al., 2002). Thus, an adult female parasitoid that feeds upon a host invests in both future reproduction and survival. However, at the same time, host feeding kills or reduces the quality of the host for oviposition (Jervis & Kidd, 1986). Hence, life-history traits are supported by different but competing host-handling behaviors.

Parasitoids could avoid the trade-off between current and future reproduction (or loss of opportunity to oviposit) by using an alternative food source that is equally nutritious

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as the host hemolymph but not as destructive to the host. Host-derived honeydew may have such quality. We argue that previous studies on the benefits of host feeding have ignored honeydew as the most realistic alternative, especially for parasitoids that attack honeydew-producing hosts. Most studies used honey or a sugar solution as control. Honey is not available in the field. Sugar solution is available in the form of nectar, but nectar generally lacks essential nutrients. In addition, searching for nectar reduces time available to search for hosts. Honeydew, on the other hand, is frequently exploited by insect parasitoids (Jervis et al., 1996; Wäckers, 2000; Heimpel et al., 2004). It contains amino acids in significant amounts (Gray, 1952; Auclair, 1963; van Vianen, 1982; Cochran, 1985; Crane & Walker, 1986; van Vianen, 1987; Byrne & Miller, 1990), which parasitoids need to sustain oogenesis. In cases of parasitoids attacking Homoptera, searching for honeydew does not reduce the time available to search for hosts (Wäckers, 1994; Takasu & Lewis, 1995), because honeydew is produced by the host and can be directly imbibed from the host anus (Vos, 1995; Zobelein, 1955; Jervis et al., 1996).

We previously addressed the question of the advantage of destructive host feeding over feeding on honeydew, which is innocuous (Burger et al., 2004a). We used *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae), which is a larval endoparasitoid and a non-concurrent destructive host feeder that is applied worldwide to control whitefly (Homoptera: Aleyrodidae) in greenhouses (van Lenteren et al., 1996). Honeydew excretion may result in growth of sooty mold on crops, which is one of the reasons why whitefly is an agricultural pest (van Lenteren & Noldus, 1990). *Encarsia formosa* parasitoids that were allowed to host feed neither had higher egg loads nor matured more eggs than parasitoids prevented from host feeding (Burger et al., 2004a). Parasitoids with access to honeydew, on the other hand, both had higher egg loads and matured more eggs than parasitoids without access to honeydew. In the presence of honeydew, host feeding did not increase survival. These findings suggested that feeding on honeydew could be an advantageous alternative to destructive host feeding, which raises the question how host feeding could have evolved as an adaptive behavior.

Our previous results might be explained by quantitative differences between the gain from a single host feeding and the ad libitum availability of honeydew. Moreover, other traits like egg quality could benefit more from host feeding than from feeding on honeydew. The aim of the present study was therefore to test the hypothesis that feeding on more than one host over a time span of several days has an advantage over feeding on honeydew regarding quantity or quality of eggs produced. Because parasitoids with yolk-rich eggs can also resorb eggs, a positive effect on

egg production might be counteracted by a negative effect on survival. To address this, we also measured the effect of host feeding on survival. Finally, we quantified egg-load dynamics of parasitoids with only access to non-host and host-derived food sources.

## Materials and methods

### Materials

Tomato plants, *Solanum lycopersicum* L. cv. Moneymaker (Solanaceae), were reared by Unifarm, The Netherlands, at 21 °C, 70% r.h., and L16:D8. Nymphs of the greenhouse whitefly, *Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae), were obtained from a whitefly culture reared under the same conditions on tomato at the Laboratory of Entomology, Wageningen, The Netherlands. Pupae of *E. formosa* parasitoids were obtained from Koppert Biological Systems, Berkel en Rodenrijs, The Netherlands.

### Effect of host feeding on oviposition, survival, and egg quality

*Encarsia formosa* pupae were allowed to emerge over a period of 24 h in a Petri dish containing honeydew. To collect honeydew, a whitefly-infested tomato leaflet was inverted on a piece of moist cotton wool in the bottom part of a Petri dish, which was then covered by Parafilm. Honeydew ejected by the whiteflies would accumulate on the Parafilm. The next day, the Parafilm containing droplets of honeydew was offered to the parasitoids. We continually observed individual foraging behavior of 0- to 1-day-old parasitoids on a whitefly-infested patch. The patch consisted of an inverted tomato leaflet on a piece of moist cotton wool and contained 25 fourth-instar whitefly nymphs. Nymphs were carefully removed from their original feeding site and transferred to the experimental arena prior to each experiment. We tested female nymphs from two treatments. In both treatments parasitoids were allowed to oviposit until host feeding was attempted. Individuals in one treatment ( $n = 28$  parasitoids) were prevented from host feeding by removing them as soon as host feeding was attempted (Heimpel et al., 1997). Individuals in the other treatment ( $n = 30$  parasitoids) were allowed to feed upon the host on which they attempted to host feed, and removed directly thereafter. Parasitoids were transferred back to their Petri dish containing honeydew either after the host-feeding attempt or after 3 h of foraging. Each parasitoid was allowed to forage in this way for five consecutive days. Within each observation period, we determined the number of ovipositions by nymphal dissection and scored foraging time (excluding host-feeding time), whether or not host feeding was attempted, and host-feeding time. As a measure of egg quality (Giron & Casas, 2003a), egg length and width were measured in

phosphate-buffered saline at  $400\times$  magnification for each egg laid ( $n = 15$  parasitoids prevented from host feeding and  $n = 18$  parasitoids allowed to host feed). After the fifth observation period, parasitoids were transferred to a Petri dish containing a piece of cotton wool pad drenched in a 10% (w/w) sucrose solution. We provided only a simple sucrose solution instead of honeydew to create a resource-poor environment. The sucrose solution was replaced daily and the parasitoids were kept in this Petri dish until they died ( $n = 25$  parasitoids prevented from host feeding and  $n = 28$  parasitoids allowed to host feed). Experiments were conducted at  $25^\circ\text{C}$ .

#### Effect of non-host and host-derived food sources on egg load dynamics

This experiment was designed to study how many eggs a parasitoid would have at its disposal by feeding only on non-host and host-derived food sources. In contrast to host feeding, the parasitoid can exploit these food sources without losing an opportunity to oviposit. *Encarsia formosa* pupae were allowed to emerge over a period of 24 h in a Petri dish containing water with or without a 10% (w/w) sucrose solution and with or without honeydew. Each diet was sprayed as droplets on a piece of Parafilm to equalize accessibility. Sucrose solution was replaced daily; water and honeydew were replaced twice a day because of higher rates of evaporation or crystallization. Honeydew was collected as previously described. Parasitoids were dissected and egg loads were measured 0 (before feeding), 2, 4, 6, 8, and 10 days after emergence. The sample size for newly emerged parasitoids that were dissected before they fed was 26. Sample sizes for parasitoids kept on water were 28 (2 days) and 18 (4 days). Sample sizes for parasitoids kept on food were 28 (2 days), 27 (4 days), 27 (6 days), 20 (8 days), and 17 (10 days) per treatment.

#### Statistical analysis

*Effect of host feeding on oviposition, survival, and egg quality.* Repeated measures were taken for each parasitoid, and the daily number of ovipositions could covary with daily foraging time, i.e., the time spent on the leaflet excluding host-feeding time, and with whether or not host feeding was attempted within the 3-h period. To overcome these difficulties, the total number of ovipositions per parasitoid was divided by the total foraging time and the total number of host-feeding attempts ( $n = 24$  parasitoids prevented from host feeding and  $n = 28$  parasitoids allowed to host feed). Effect of treatment (indicator variable  $h = 0/1$ , i.e., host feeding prevented/allowed) was tested on this response variable, i.e., number of ovipositions per hour per attempt, in a general linear model. Hind tibia length (htl) was used as covariate because it is a reliable measure of parasitoid size.

The effect of treatment ( $h$ ) on survival after 5 days of foraging was tested using Kaplan–Meier survival analysis.

Egg volume  $v$  ( $\mu\text{m}^3$ ) was estimated using the equation for a prolate spheroid,  $v = 4/3\pi*(l/2)*(w/2)^2$  (Blackburn, 1991; Otto & Mackauer, 1998), where  $l$  is egg length ( $\mu\text{m}$ ) and  $w$  egg width ( $\mu\text{m}$ ). Because for each parasitoid repeated measures were taken over time, the estimated volume of egg  $i$  laid by parasitoid  $j$  was regressed to time  $t$  ( $E\{v_{ij}\} = \beta_{0j} + \beta_{1j}*t_{ij}$ ). Parameter estimates for  $\beta_{1j}$  were used as response variable in a general linear model to test the effect of treatment ( $h$ ) on the estimated change in egg volume over time ( $\mu\text{m}^3$  per day), again using hind tibia length (htl) as covariate.

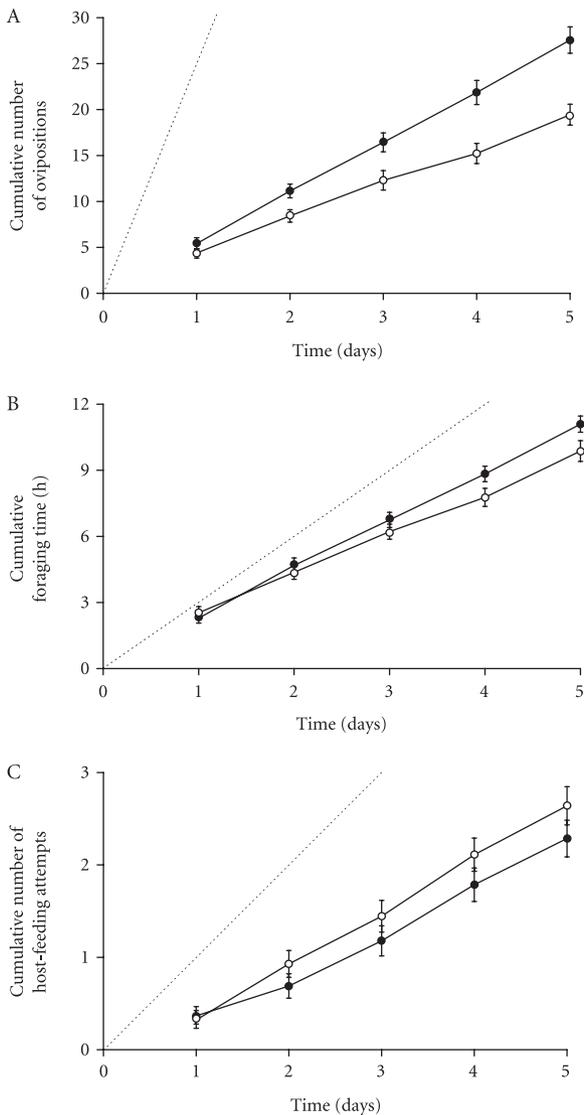
*Effect of non-host and host-derived food sources on egg load dynamics.* In this experiment, measurements over time were independent. A generalized linear model with Poisson distribution and log link function was applied using egg load as response variable, time ( $t$ ) as predictor variable and availability of sucrose solution ( $s = 0/1 = \text{absent/present}$ ) and honeydew ( $d = 0/1 = \text{absent/present}$ ) as indicator variables. For simplicity, we ignored the egg maturation period during the first two days.

*Model building: selection of predictor variables, indicator variables, and covariates.* To test which parameters differed significantly from 0, partial F tests (when Normal distribution assumed) or partial deviance tests (when Poisson distribution assumed) were used (Neter et al., 1996). A model with one parameter (the intercept) was tested against all possible models with two parameters. The model that gave the highest test statistic was tested against all possible models with three parameters, if its test statistic exceeded the critical value  $F(0.05; 1; n - p)$  or  $\chi^2(0.95; 1)$ . This was repeated until the test statistic became smaller than or equal to the critical value, or the full model was reached. If the test statistic became smaller than or equal to the critical value, the selected model with  $p$  parameters was tested against all possible models with more than  $p + 1$  parameters. If this resulted in a test statistic larger than the critical value, the analysis was continued using the better model with more than  $p + 1$  parameters. We present statistical results from the last step of the selection process. Models with interaction terms were only considered if associated main effects and lower-order interactions were also included.

## Results

### Effect of host feeding on oviposition, survival, and egg quality

In Figure 1, we compare the cumulative number of ovipositions, foraging time, and number of host-feeding attempts (mean  $\pm$  SE) between parasitoids allowed to host feed and parasitoids prevented from host feeding. This is for descriptive purposes; we will present a comprehensive statistical analysis in the next paragraph. Parasitoids



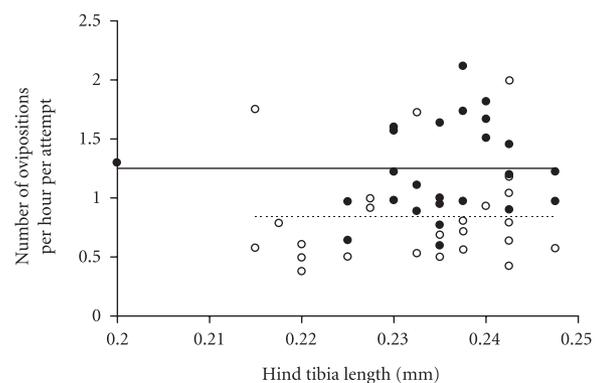
**Figure 1** Foraging behavior of *Encarsia formosa* parasitoids that were allowed to oviposit daily until host feeding was attempted, or until 3 h were spent foraging, during 5 days. Host feedings were either prevented (open symbols) or allowed (filled symbols). Mean  $\pm$  SE of (A) cumulative number of ovipositions, (B) cumulative foraging time (h), and (C) cumulative number of host-feeding attempts. Dotted lines show maximum values imposed by the experimental procedure (25 hosts per day, 3 foraging h per day, one host feeding per day).

allowed to host feed laid on average  $5.5 \pm 0.3$  eggs per day, 1.4 times the average oviposition rate of parasitoids prevented from host feeding ( $3.8 \pm 0.2$  eggs per day). After 5 days, the former had laid  $27.6 \pm 1.4$  eggs, the latter  $19.4 \pm 1.1$  eggs. Parasitoids allowed to host feed, however, also foraged on average 1.1 times longer than parasitoids prevented from host feeding ( $2.13 \pm 0.09$  vs.  $1.99 \pm 0.09$  h per day).

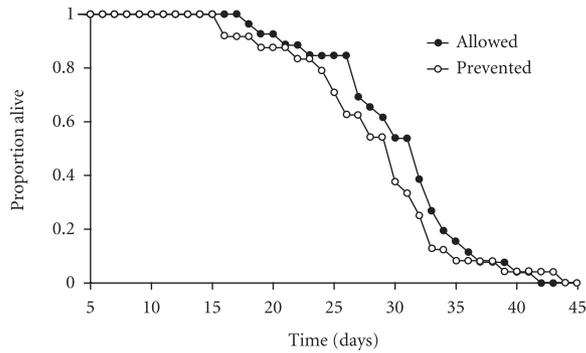
After 5 days, the former had spent  $11.1 \pm 0.37$  h foraging on the patch, the latter  $9.87 \pm 0.47$  h. In addition, the average proportion of parasitoids that attempted to host feed per day was slightly lower when host feedings were allowed ( $0.49 \pm 0.04$  attempts per day) than when host feedings were prevented ( $0.52 \pm 0.04$  attempts per day). After 5 days, parasitoids allowed to host feed had attempted  $2.3 \pm 0.2$  times to do so compared with  $2.6 \pm 0.2$  attempts by parasitoids prevented from host feeding. Parasitoids host fed on average  $21.5 \pm 2.25$  min across the 5 days.

Thus, host feeding had a positive effect on the oviposition rate, but also affected foraging time and the number of host-feeding attempts. Fortunately, we were able to statistically disentangle these multiple effects of host feeding. Figure 2 shows that even per hour of foraging and per host-feeding attempt, parasitoids allowed to host feed laid significantly more eggs ( $1.25 \pm 0.07$ ) than parasitoids prevented from host feeding ( $0.84 \pm 0.09$ ) ( $F_{1,50} = 13.26$ ,  $P = 0.0006$ ). This treatment effect was independent of hind tibia length ( $F_{3,47} = 0.19$ ,  $P = 0.902$ ).

After 5 days of foraging in a rich environment with hosts and honeydew, parasitoids were transferred to a diet of sucrose only. Although parasitoids allowed to host feed laid more eggs per hour per attempt (Figure 2), their survival was not significantly lower than parasitoids prevented from host feeding (Figure 3) (logrank = 0.68,  $P = 0.408$ ). Median longevity of parasitoids was 29 (host feeding prevented) and 31 (host feeding allowed) days. Thus, the increased oviposition rate in parasitoids allowed to host feed was not compromised by a decreased longevity.



**Figure 2** Number of ovipositions by *Encarsia formosa* per hour of foraging per host-feeding attempt plotted against hind tibia length (mm) when host feedings were either prevented (open symbols, broken line,  $h = 0$ ) or allowed (filled symbols, solid line,  $h = 1$ ). Lines represent most parsimonious general linear model:  $F_{1,50} = 13.26$ ,  $P = 0.0006$ ;  $y = 0.841 + 0.411 \cdot h$ . Statistical procedure is explained in the text.



**Figure 3** Survival of *Encarsia formosa* parasitoids after the first five days of life. During the first 5 days parasitoids were daily allowed to oviposit until host feeding was attempted, or until 3 h were spent foraging. Thereafter parasitoids had access to sucrose solution only. Host feedings were either prevented (open symbols) or allowed (filled symbols). Kaplan–Meier: logrank = 0.68,  $P = 0.408$ .

In Figure 4A we show estimated egg volumes per day (mean  $\pm$  SE) for exploratory purposes. Eggs laid by parasitoids allowed to host feed had an average estimated volume of  $111 \times 10^3 \pm 2.9 \times 10^3 \mu\text{m}^3$ , compared with  $109 \times 10^3 \pm 4.2 \times 10^3 \mu\text{m}^3$  by parasitoids prevented from host feeding. The change over time in estimated egg volume was not significantly different between parasitoids allowed to host feed ( $-3.2 \times 10^3 \pm 1.4 \times 10^3 \mu\text{m}^3$  per day) and parasitoids prevented from host feeding ( $-1.2 \times 10^3 \pm 2.1 \times 10^3 \mu\text{m}^3$  per day) (Figure 4b) ( $F_{3,29} = 1.32$ ,  $P = 0.288$ ). Thus, the increased oviposition rate in parasitoids allowed to host feed was also not compromised by a decrease in egg volume.

#### Effect of non-host and host-derived food sources on egg load dynamics

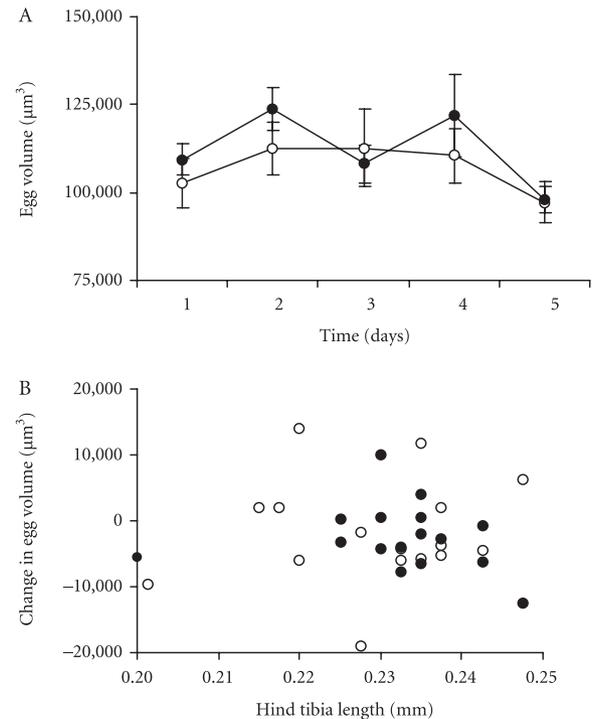
Figure 5 shows egg load dynamics of parasitoids with access to water only (control), sucrose solution, honeydew, or both sucrose solution and honeydew. Access to sucrose solution, honeydew, or both had a strong positive effect on egg load and survival compared with access to water only (d.f. = 1,  $\chi^2 = 97.69$ , control;  $P < 0.0001$ ). Parasitoids with only access to water quickly started resorbing eggs. Most of them had died after 4 days and none of them survived for 6 days. The average egg load of parasitoids with access to food initially increased to approximately 10 (sucrose), 12 (honeydew), and 14 (sucrose and honeydew) eggs at day 2. Between days 2 and 10, net oosorption was approximately 0.42 eggs per day, independent of food source.

#### Discussion

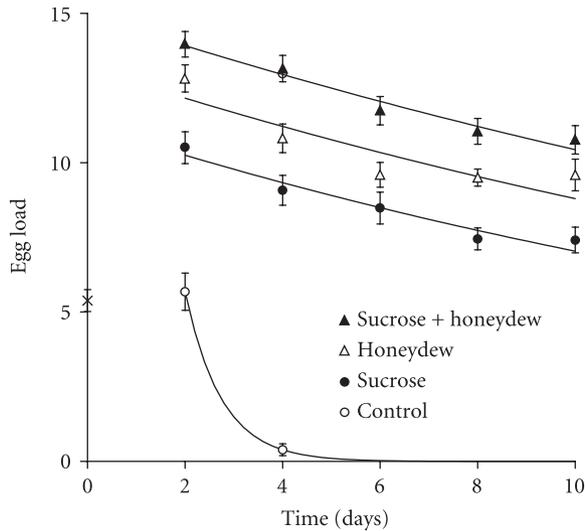
Even in the presence of honeydew, *E. formosa* parasitoids allowed to host feed laid significantly more eggs per hour

of foraging per host-feeding attempt than parasitoids prevented from host feeding. This higher oviposition rate was not compromised by survival or by change in egg volume over time. This suggests that the higher oviposition rate was actually realized by acquisition of nutrients from the host, rather than at the expense of the other two traits. Estimated egg volumes correspond well with the value of  $109 \times 10^3 \mu\text{m}^3$ , which we estimated from egg measurements by Agekyan (1981). Because parasitoids had ad libitum access to honeydew as a potential alternative to hemolymph during the 5-day period of foraging, results show that host feeding, although destroying an opportunity to oviposit, can provide a benefit over feeding on host-derived honeydew.

Previous studies have shown a positive effect of host feeding on fecundity or longevity. However, most studies used honey as a control (Heimpel et al., 1994; Collier, 1995; Heimpel et al., 1997; Ueno, 1999), which is an inaccessible



**Figure 4** (A) Mean  $\pm$  SE of estimated egg volume ( $\mu\text{m}^3$ ) over time in *Encarsia formosa*. Parasitoids were daily allowed to oviposit until host feeding was attempted, or until 3 h were spent foraging. Host feedings were either prevented (open symbols) or allowed (filled symbols). Average egg volume per parasitoid per day was used as replicate. (B) Change per parasitoid in egg volume over time ( $y$  in  $\mu\text{m}^3$  per day; estimated slope in linear regression) plotted against hind tibia length (htl) when host feedings were either prevented (open symbols) or allowed (filled symbols). Most parsimonious general linear model ( $E\{y_i\} = \beta_0 + \beta_1 \cdot \text{htl}_i$ ) did not perform better than the random model:  $F_{3,29} = 1.32$ ,  $P = 0.288$ .



**Figure 5** Egg load dynamics (mean  $\pm$  SE) of *Encarsia formosa* parasitoids without (open symbols,  $s = 0$ ) and with (filled symbols,  $s = 1$ ) ad libitum access to sucrose solution, and without (circles,  $d = 0$ ) and with (triangles,  $d = 1$ ) ad libitum access to honeydew. Lines represent most parsimonious generalized linear model with Poisson distribution and log link applied to data from day 2 onwards:  $\chi^2 = 97.69$ ,  $P < 0.0001$ ;  $\log(\gamma) = 4.418 - 1.341*t + 0.126*s + 0.284*d + 0.005*t*s + 0.011*t*d - 2.123*\min(s + d, 1) + 1.289*t*\min(s + d, 1)$ , where  $\gamma$  is egg load and  $t$  is time (days). Cross on y-axis indicates egg load (mean  $\pm$  SE) of newly emerged parasitoids before they fed.

food source in the field. Others used no control at all (Rivero & Casas, 1999; Giron et al., 2004) because the authors aimed to understand physiological rather than ecological processes. Here we show that host feeding can increase a parasitoid's oviposition rate compared with feeding on honeydew. To analyze the trade-off between current and future reproduction and to predict optimal host-feeding decisions (Heimpel & Collier, 1996; McGregor, 1997; Heimpel et al., 1998; Burger et al., 2004b), the costs and benefits, especially the host-feeding gain, need to be quantified. The increase in oviposition rate was approximately 0.41 eggs per hour of foraging per host-feeding attempt. Because parasitoids spent on average approximately 10 h of foraging during the 5-day period, our estimated host-feeding gain would be at least 4.1 eggs. Alternatively, parasitoids allowed to host feed laid on average 8.2 eggs more than parasitoids prevented from host feeding during the 5-day period. This corresponds to approximately 3.6 eggs per host feeding, because on average 2.3 hosts were fed upon during the 5-day period. These estimates are higher than in most studies (Szabo et al., 1993; Heimpel et al., 1994; Collier, 1995) because our time frame was longer and nutrients obtained from host feeding can be stored for

oogenesis later in life (Heimpel et al., 1997; Rivero & Casas, 1999; Rivero et al., 2001).

Using honeydew as a natural alternative, we previously found no positive effect of a single host feeding on fecundity or longevity (Burger et al., 2004a). We also found that sucrose or honeydew can provide the parasitoid with a fair amount of eggs (Figure 5; see also van Vianen & van Lenteren, 1986; van Lenteren et al., 1987). In addition, a dynamic state-variable model on optimal host-handling decisions (Burger et al., 2004b) showed that host feeding is maladaptive at the average host density described in *E. formosa*'s area of origin (Burger et al., 2004c). Ellers et al. (2000) showed that stochasticity in host encounter rate can lead to optimal egg loads exceeding the expected number of hosts encountered. Destructive host-feeding behavior may therefore have evolved as an adaptation to the aggregated host distribution that we also found in *E. formosa*'s native area (Burger et al., 2004c). Alternatively, the extra eggs could be reallocated toward longevity through oosorption to increase host-searching time (Bell & Bohm, 1975; Jervis et al., 2001). This would be useful only if the extrinsic mortality rate is not the sole determinant of adult parasitoid life span (Rosenheim, 1998).

Early studies on host-feeding behavior focused on ecological and evolutionary aspects, i.e., on the function of host feeding in terms of parasitoid fecundity and longevity and on when the host-feeding gain compensates for the loss of an opportunity to oviposit (Jervis & Kidd, 1986; Heimpel & Collier, 1996). During recent years, there has been major progress in the study of biochemical and physiological aspects of host-feeding behavior, i.e., the composition of host hemolymph and other sources, and the way nutrients are allocated (Rivero & Casas, 1999; Olson et al., 2000; Rivero et al., 2001; Giron et al., 2002; Giron & Casas, 2003a,b; Giron et al., 2004). The major gap in our understanding of host-feeding behavior is the link between these ecological and physiological processes (see Boggs, 1992; Chan & Godfray, 1993; Heimpel & Collier, 1996; Giron et al., 2004). These processes could be integrated by developing an optimization model that predicts how a parasitoid decides to obtain sugars, proteins, and lipids to maximize lifetime reproductive success. Parasitoids can acquire these nutrients from immature reserves, host feeding, feeding on non-host or host-derived food sources (most likely honeydew for parasitoids attacking Homoptera), or oosorption, and have to allocate these towards reproduction and survival. As mentioned previously, there is information for some but not all nutrient sources about their composition, quantity, and allocation. Gathering this information for a given species would provide the input data for the model. The decision about where to obtain the required resources will depend on the availability and

composition of the alternative nutrient sources (which can depend on environmental conditions) (Cox, 1970; Crafts-Brandner, 2002), the required nutrients for oogenesis and maintenance, the frequency of oviposition opportunities, and the parasitoid's extrinsic mortality rate in the field.

In conclusion, destructive host feeding can have an advantage over feeding on honeydew. This applies most likely under conditions of high host density or low extrinsic mortality of adult parasitoids, when non-host or host-derived food sources (nectar and honeydew) cannot supply enough nutrients to prevent egg limitation. We suggest that an optimization model should be developed to integrate ecological and physiological studies on host-feeding behavior. Such a model will help us to understand how a parasitoid acquires and allocates nutrients to achieve maximum lifetime reproductive success.

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