Entomologia Experimentalis et Applicata **83:** 305–315, 1997.

Adult feeding and lifetime reproductive success in the parasitoid *Aphytis melinus*

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Accepted: March 4, 1997

Key words: Aphytis melinus, biological control, host feeding, parasitoids

Abstract

The diet of adult females of the parasitoid *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae) includes host insects and sugar-rich foods such as nectar and honeydew. We compared the contributions of host feeding to longevity and fecundity in *A. melinus* females in the presence and in the absence of honey meals. First, we assessed the longevity of females that were not allowed to oviposit. While the longevity of females fed honey was significantly increased by host feeding (median ages were 30.5 days for host-fed females and 17 days for females not allowed to host feed), the lifespan of parasitoids not fed honey did not exceed 3 days for any individual and there was no effect of host feeding on longevity in this group. In the second set of experiments, we assessed the fecundity and longevity of females allowed to oviposit. We conducted two experiments, one in which honey was continuously available, and one in which honey was not available. In both experiments, daily observations were made of females that were either allowed to host feed or manually prevented from host feeding. In the presence of honey, host feeding significantly increased both fecundity and longevity, and in the absence of honey, parasitoids died within 2 days and host feeding had no significant effect on either fecundity or longevity. The lifetime fecundity of females fed honey but not hosts exceeded the initial egg complement by 60% on average. Approximately one host per day was used for host feeding whether honey was supplied or not, and each host-feeding meal contributed approximately 3.9 eggs to the lifetime fecundity of honey-fed females. In the last experiment, we compared the rate of egg resorption over a 36-h period in *A. melinus* females that were deprived of hosts and either fed honey or starved. While no egg resorption was detected in honey-fed females over this time period, starved females resorbed approximately 9 eggs. Thus, the availability of a sugar-rich food interacts strongly with host feeding in influencing longevity and fecundity and has a strong direct effect on egg resorption.

Introduction

The diet of adult female parasitoids can have important effects on lifetime reproductive success (e.g. Hagan, 1986; Jervis et al., 1996). Adult females of many species obtain materials required for egg maturation by feeding upon host insects ('host feeding'), and materials necessary for adult maintenance and survival are acquired by host feeding and/or by feeding upon any of a number of sugar sources (Jervis & Kidd, 1986, 1996; Heimpel & Collier, 1996; Jervis et al., 1996).

The availability of both hosts and sugar sources vary in natural and agricultural settings. Sugar sources for parasitoids in the field include floral and extrafloral nectar as well as honeydew excreted by homopteran insects (Rogers, 1985; Hagan, 1986; Evans, 1993; Jervis et al., 1993, 1996; Jervis & Kidd, 1996). A number of authors have noted that a lack of sugar availability may temporarily or permanently limit the reproductive success of parasitoids in agricultural systems (reviewed by van den Bosch & Telford, 1964; Powell, 1986; van Emden, 1990; Evans, 1993). Also, Toft (1983, 1984) has demonstrated that sugar limitation occurs for some dipteran parasitoids in nature. Thus, given that host availability can also vary within and among seasons, both sugar and hosts are potentially unavailable as foodstuffs for adult parasitoids.

Since any combination of sugar and hosts may be available to parasitoids in the field, both the separate and interactive effects of host and sugar feeding on parasitoid fecundity and longevity are of interest. Current knowledge of the effects of adult feeding on lifetime reproductive success is fragmented, however, both with respect to experimental conditions and the component of lifetime reproductive success that is measured. For instance, most studies have examined the relationship between sugar feeding and longevity (mostly under conditions of host deprivation) (e.g. Chumakova, 1960; Bartlett, 1962; Avidov et al., 1970), or the effect of host feeding on egg maturation (mostly under conditions of unlimited sugar availability) (reviewed by Heimpel & Collier, 1996). Collectively, these studies have shown that, for many host-feeding species, sugar meals increase longevity and host feeding provides materials used for egg maturation. One especially important question that has remained largely unaddressed, however, concerns the effect of host feeding on lifetime reproductive success in the presence versus the absence of sugar.

One reason for the paucity of information in this area is the difficulty of experimentally separating opportunities to oviposit from opportunities to host feed. This manipulation is necessary to obtain a ‘non-host-feeding treatment’ against which to evaluate the benefits of host feeding. Some researchers have separated host feeding from oviposition opportunities by placing physical barriers between the host and the parasitoid that allowed oviposition but not host feeding (Leius, 1961a,b, 1967; Bracken, 1965; Sandlan, 1979; House, 1980; Wardle & Borden, 1990). Leius (1961a,b) used this technique to compare the contribution of host feeding to lifetime reproductive success in the presence versus the absence of sugar meals for two ichneumonid species. In *Scambus boulianae* (Htg.), no eggs were produced without host feeding whether sugar was supplied or not, and while host feeding greatly increased the longevity of sugar-deprived females, it only slightly increased the longevity of sugar-fed females (Leius, 1961b). In *Itoplectis conquisitor* (Say), host feeding increased lifetime reproductive success both in the presence and in the absence of sugar meals (Leius, 1961a). However, *I. conquisitor* females did not host feed or oviposit until 7–10 days after emergence, and some sugar-deprived females died before beginning to host feed. Sugar-deprived females that survived the pre-host-feeding period and were allowed to host feed went on to live for 3–4 more weeks and laid significantly more eggs than females given only sugar (Leius, 1961a).

Here, we compare the contribution of host feeding to lifetime reproductive success in *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae), a parasitoid of the California red scale, *Aonidiella aurantii* Maskell (Homoptera: Diaspididae). *Aphytis* parasitoids feed on hosts (Rosenheim & Heimpel, 1994) and various forms of sugar, including honey, floral nectar, honeydew, and crystallized sucrose (Bartlett, 1962; Avidov et al., 1970; Heimpel & Rosenheim, 1995). Host fluids are imbibed through a ‘feeding tube’, which is secreted by the parasitoid ovipositor and spans the distance between the scale body and scale cover (Rosenheim & Heimpel, 1994). Larger hosts are preferred for oviposition, and smaller hosts are more likely to be used for host feeding (Walde et al., 1989; Rosenheim & Rosen, 1992; Heimpel & Rosenheim, 1995; Heimpel et al., 1996).

Aphytis melinus females emerge with zero or a few eggs (Opp & Luck, 1986; Collier, 1995; Heimpel et al., 1996), and mature approximately 8–12 eggs within 24–48 h if given sugar or honey and deprived of hosts (Opp & Luck, 1986; Heimpel et al., 1994, 1996; Collier, 1995; Heimpel & Rosenheim, 1995). This initial egg complement represents the maximum or near-maximum ovarial capacity of *A. melinus* (Collier, 1995; Heimpel & Rosenheim, 1995), but whether or not more eggs can be matured without host feeding is not known. Ovary dissections of honey-fed *A. melinus* and *A. lingnanensis* females that were either allowed to feed upon a single host or not allowed to host feed have shown that a single host-feeding meal leads to the maturation of approximately two eggs over a two-day period (Heimpel et al., 1994; Collier, 1995). Also, serial dissections of ovaries have shown that eggs of females deprived of hosts but given sugar meals are resorbed at a rate of one egg per day or less (Collier, 1995; Heimpel & Rosenheim, 1995).

The lifespan of sugar-fed *Aphytis* females varies between 2 and 6 weeks (DeBach & White, 1960; Bartlett, 1962; Quednau, 1964; Avidov et al., 1970; Gulmahamad & DeBach, 1978; Rosenheim & Hoy, 1988; Takagi & Ogata, 1990; Heimpel et al., 1994; Heimpel & Rosenheim, 1995; Collier, 1995). In contrast, the lifespan of sugar-deprived females rarely exceeds three days (Avidov et al., 1970), whether or not host feeding is allowed (DeBach & White, 1960; Heimpel et al., 1994). Thus, it appears that sugar-deprived females ‘starve to death’ even if host feeding is allowed. The possibility that host feeding may increase longevity when sugar is available has been addressed by Collier (1995), who showed that a single host-feeding meal late in life increased life expectancy of honey-fed *A. melinus* females. In conjunction with earlier studies, Collier's results suggest that host feeding may increase longevity in *A. melinus* only when females have access to sugar meals.

We conducted a series of laboratory experiments in which the contributions of host feeding to longevity and fecundity in *A. melinus* females were compared in the presence and in the absence of honey meals. We also compared rates of egg resorption in females that were either fed honey or starved.

Materials and methods

Insect cultures. *Aphytis melinus* was introduced into California, USA, from northern India and Pakistan in 1957 to provide control of California red scale on citrus (Luck, 1986). A laboratory colony was initiated with *A. melinus* females collected in Tulare Co., California in 1990 from a site without recent insectary releases. All females used in the experiments were isolated as pupae from a general culture parasitizing oleander scale, *Aspidiotus nerii* Bouche, growing on butternut squash, *Cucurbita moscata* Duchesne. Pupae were placed individually into $\frac{1}{2}$ dram shell vials covered with a perforated piece of parafilm which was supplied with 2–3 droplets of undiluted honey. Pupae and emerging adults were held in a growth chamber at 26.7 ± 1.5 °C, at a L14:D10 photoperiod, and r.h. of 65 ± 10%. Pupae were checked daily for adult emergence, and the parafilm and fresh honey were replaced daily after emergence. For all experiments, females were used on the second day after emergence; i.e. females were between 48 and 72 h old at the initiation of the experiments. We used 2-day old females because pilot studies had shown that parasitoids less than 24 h old are less likely to oviposit than females greater than 24 h old. In experiments in which females were allowed to oviposit, females were observed to mate with virgin males that were between 1 and 4 days old immediately preceding the initiation of the experiment.

We used virgin female third-instar California red scale insects growing on butternut squash for these experiments. To ensure virginity, second-instar female scale insects were covered with the short end of a gelatin capsule (size 00) affixed to the squash surface with an inert adhesive gum (UHU HOLDIT® plastic adhesive, Faber-Castwell Corp., Lewisburg, TN, USA).

Longevity without reproduction. In this experiment we quantified the contribution of host feeding to longevity of host-deprived *A. melinus* females in either the presence or absence of honey. Individual females were held in $\frac{1}{2}$-dram vials containing either no food, honey only (as described above), host only, or honey and hosts. In treatments which included hosts, scale bodies taken from the general culture without their associated covers were placed onto the inside surface of the fresh parafilm used to cover the vials. *A. melinus* females host feed, but do not oviposit, on hosts whose covers had been removed (Collier, 1995). Two second-instar hosts were offered per vial each day along with fresh honey. In the treatment in which both hosts and honey were offered, 2–3 droplets of honey were placed on the parafilm, and an additional drop of honey was used to adhere the scale bodies to the parafilm. For the hosts-only treatment, scale bodies were placed onto the parafilm without honey. In most cases, the scale insect bodies adhered to the parafilm for the entire 24-h period, but in some cases they became dislodged and fell to the bottom of the vial. Pilot studies as well as observations during the experiment confirmed that *A. melinus* females host fed, but did not oviposit, on hosts in both of these treatments.

Lifetime reproduction. In this pair of experiments, we obtained lifetime reproductive success of *A. melinus* females that were either allowed to host feed or not allowed to host feed. These experiments were repeated with and without honey. In both experiments, individual females were continually observed as they attacked a series of 3rd-instar California red scale hosts.

Observation arenas were similar to those described in Heimpel & Rosenheim (1995). Females were confined within a small foraging arena (floor area = 33 mm^2) which contained a single third instar, virgin female California red scale insect growing on butternut squash. Foraging arenas were formed by securing a glass dome to the surface of the squash directly over an individual scale insect using an inert adhesive gum (UHU HOLDIT® plastic adhesive). Parasitoids were illuminated with fibre-optic lighting and observed at 12× magnification.

The following procedure was carried out daily in the experiment in which parasitoids that were offered honey, and twice daily (every 10–14 h) in the experiment in which parasitoids were not offered honey. The rationale for the higher frequency of behavioral assays for parasitoids in the honey-deprived group was that previous studies had suggested that parasitoids offered hosts but not honey lived for a maximum of three days (DeBach & White, 1960; Heimpel et al., 1994).

For parasitoids that were allowed to host feed, hosts were offered in succession until two hosts in a row were rejected. Parasitoids were moved from host to host within the observational domes described above. Each host encounter was scored as oviposition, host feeding, or rejection. Oviposition was identified by a series of pumping movements by the female during the encounter, and confirmed by removing the scale cover immediately after the observation and counting the number of eggs on the host (Luck et al., 1982; van Lenteren, 1994; Rosenheim & Heimpel, 1994). *A. melinus* typically deposit between one and four eggs on 3rd instar California red scale (Luck et al., 1982; Rosenheim & Heimpel, 1994). Host feeding was identified by observing contact of the female's mouthparts with the scale cover following a characteristic series of movements by the ovipositor (Heimpel & Rosenheim, 1995). Rejection was defined as not probing a host after an encounter, or probing a host for less than 2 min and then quitting the host, and then not re-encountering the host for 5 more min (probes of < 2 min are typically not associated with oviposition [van Lenteren, 1994, personal observations]). Observations were also terminated if 60 min elapsed without a host encounter for the first host offered, or 30 min elapsed without a host encounter for any subsequent host offered.

For parasitoids that were not allowed to host feed, the same procedure was followed, except that parasitoids were prevented from host feeding by gently nudging them off of the host with an inset pin as the mouthparts were observed to make contact with the scale cover. Observations were terminated when host-feeding attempts were made on two hosts in a row. Oviposition by *Aphytis* tends to precede host feeding in a series of encounters with high quality hosts (Reeve, 1987; Rosenheim & Rosen, 1991; Collier et al., 1994; this study). As before, observations were also terminated when two hosts in a row were rejected, if 60 min elapsed without a host encounter for the first host offered, or 30 min elapsed without a host encounter for any subsequent host offered.

Between observations, parasitoids were held within the glass domes, which were covered with a perforated piece of parafilm, in a growth chamber set at 26.7 ± 1.5 °C, a L14:D10D photoperiod, and r.h. of 65 ± 10%. For the experiment in which parasitoids were offered honey, two droplets of undiluted honey were placed on the inside surface of the parafilm.

To determine whether failure to oviposit was due to egg depletion, five females that were treated identically to individuals from the no-host-feeding treatment were dissected before their natural death to obtain egg loads. These five parasitoids were frozen in preparation for dissections when two consecutive host feeding attempts were observed on the second consecutive day they failed to oviposit. Dissections were done later that same day as described by Heimpel & Rosenheim (1995); parasitoids were held ventral-side up within a drop of distilled water on a microscope slide using a fine probe, and the ovaries were exposed by gently pulling the ovipositor distally with a pair of fine forceps. This procedure exposed the parasitoid oocytes for quantification of egg load, which is defined as the total number of mature oocytes present in the ovaries.

To aid in the interpretation of fecundity data, we dissected a group of honey-fed, 2-day old *A. melinus* females (i.e., the age and nutritional status of females in the experiments at their first host encounter) to quantify egg load. Previous studies with *A. melinus* indicated that egg load at this age represents a full complement of eggs (Collier, 1995; Heimpel & Rosenheim, 1995).

Egg resorption. In this experiment, we compared the onset of egg resorption and the resorption rate over a 36-h period of *A. melinus* females that were either fed honey only or starved. As in previous experiments, females were fed honey for the first two days of their life. After this time, half of the parasitoids were deprived of honey by replacing the honey-supplied parafilm vial covers with blank pieces of parafilm. Females from both groups (honey-fed and starved) were then dissected to obtain egg loads 12 ± 2, 24 ± 2, and 36 ± 2 h after the honey was removed from females in the starved group.

Results

Longevity. Females fed both honey and hosts but not allowed to oviposit lived longer than those fed only honey (Figure 1; Median test, approximate $\chi^2 = 16.1$, $P < 0.001$; median ages: 30.5, 17 days respectively). In the absence of honey, parasitoids lived 3 days or less, whether they host fed or not, and there was no significant difference between longevity of the two groups (Figure 1; Median test, approximate $\chi^2 = 0.1$, $P > 0.5$). A 2-way ANOVA of square-root transformed longevit-

Table 1. Results of two-way ANOVA testing for effects of the presence or absence of honey and host meals and their interaction on square-root transformed longevity of *A. melinus* females deprived of hosts

Independent variable	df	Mean square	*F*	P
Honey meals	1	192.6	357.2	< 0.0001
Host meals	1	9.9	18.3	< 0.0001
Honey meals × Host meals	1	9.8	18.2	< 0.0001
Error	165	0.5		

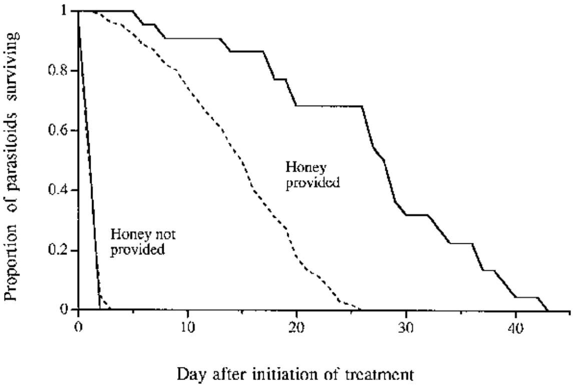

Figure 1. Survivorship of female *Aphytis melinus* allowed to host feed (solid lines), and prevented from host feeding (dotted lines). Treatments were applied to females allowed access to honey and to females deprived of honey. Sample sizes: host feeding and honey ($n = 22$), honey only ($n = 106$), host feeding only ($n = 17$), no food ($n = 21$).

ies revealed a strong interaction in the effect of host and honey meals on longevity (Table 1). The square-root transformation normalized distributions and equalized variances of the longevities of honey-fed females.

Lifetime reproduction. In the presence of honey, host-fed females laid more eggs than non-host-fed females during their lifetime (Table 2; Figure 2). Non-host-feeding females ceased ovipositing when egg reserves had apparently been depleted. Dissection of the 5 females treated identically to those prevented from host feeding had a mean egg load of 1.2 ± 0.2 (S.E.M.; range: 1–2) after refusing to oviposit for two days. This suggests that the cessation of oviposition in the non-host-feeding group coincided with the onset of egg limitation.

When parasitoids were given access to honey, the host-fed group lived significantly longer than the group prevented from host feeding (Table 2; Figure 2). When parasitoids were not given access to honey, neither fecundity nor longevity differed significantly between females that host fed and those prevented from host feeding (Table 2; Figure 3).

The average egg load of 2-day old, host-deprived, honey-fed females was 11.4 ± 0.6 (S.E.M.; $n = 36$). This value is similar to that found in other studies (Opp & Luck, 1986; Heimpel & Rosenheim, 1995; Collier, 1995) and represents the approximate maximum or near-maximum egg capacity of *A. melinus* females. The average lifetime fecundity of females offered honey but not allowed to host feed exceeded this value by a factor of 0.6, while the average fecundity of females offered honey and allowed to host feed exceeded this value by a factor of 5.7 (see Table 2). In the absence of honey, lifetime fecundity did not exceed the initial egg capacity whether host feeding was allowed or not (see Table 2).

Value of host-feeding meals. Parasitoids fed honey and allowed to host feed fed on hosts an average of 0.72 ± 0.07 times per day (S.E.M.; $n = 8$; range: 0.52 to 1.00; Figure 4). We can estimate the number of eggs matured per host-feeding meal for a given female, *i*, while correcting for the average fecundity without host feeding (18.1; see Table 2) as follows:

$$(\text{eggs matured per host-feeding meal})_i = \frac{(\text{lifetime fecundity})_i - 18.1\text{eggs}}{(\text{number of host-feeding meals})_i}. \quad (1)$$

Thus, a single host-feeding meal produced 3.9 ± 0.67 eggs (S.E.M.; range = 1.15 to 6.15). Similarly, the number of additional days of life gained per host feeding meal can be estimated as:

$$(\text{days gained per host-feeding meal})_i = \frac{(\text{longevity})_i - 11\text{days}}{(\text{number of host-feeding meals})_i}. \quad (2)$$

The average estimated number of days added to the lifespan per host-feeding meal was thus 0.61 ± 0.13 days (S.E.M.; range = 0 to 0.93). Since hosts were only offered once a day, it is conceivable that these values underestimate the value of host-feeding meals. However, since the average number of hosts fed on per day was less than one (see Figure 4), we doubt that much more host feeding would have taken place had parasitoids had continuous access to hosts.

Parasitoids deprived of honey fed on hosts an average of 0.95 ± 0.16 times per day (S.E.M.; $n = 7$; range: 0.33 to 1.50; Figure 5). Thus, although parasitoids

Table 2. Total number of eggs laid and median longevity of *A. melinus* females that were either given access to honey or not, and either allowed to host feed or not

Dependent variable	Adult feeding regimen					
	With honey			Without honey		
	With host feeding (n = 8)	Without host feeding (n = 7)	P	With host feeding (n = 7)	Without host feeding (n = 8)	P
Eggs laid ± S.E.M. (range)	76.4 ± 8.0 (30–106)	18.1 ± 8.5 (9-29)	0.0012[a]	9.4 ± 2.3 (3–22)	6.8 ± 1.0 (2–9)	> 0.5[c]
Median longevity in days (range)	20.5 (11–29)	11 (9–16)	0.023[b]	2 (1–3)	1 (1–2)	0.077[d]

[a] Wilcoxon's rank sums test, approximate χ^2 = 10.54.
[b] Median test, approximate χ^2 = 5.16.
[c] Wilcoxon's rank sums test, approximate χ^2 = 0.22.
[d] Median test, approximate χ^2 = 3.13.

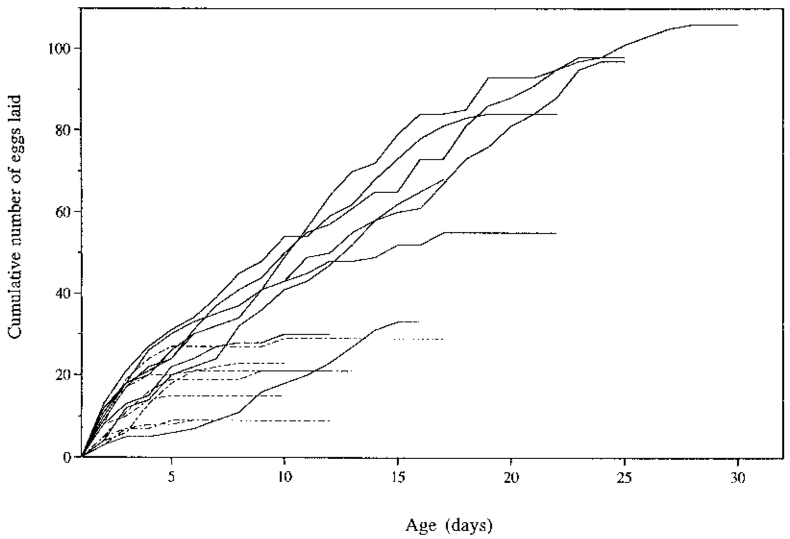

Figure 2. Cumulative number of eggs laid by *A. melinus* females given continuous access to honey that and either allowed to host feed (solid lines; n = 8) or prevented from host feeding (dashed lines; n = 7).

were offered hosts twice daily, host feeding occurred on average only once ever other exposure (see Figure 5). Since we did not detect a significant effect of host feeding on fecundity or longevity, we decline to calculate values of host feeding meals.

Egg resorption. Egg loads of host-deprived *A. melinus* females decreased drastically during the 36 h. following honey removal. In contrast, egg loads of females given continuous access to honey remained essentially constant during the same period (Figure 6). Effects of diet and age group on egg load were both significant, as was their interaction (Table 3).

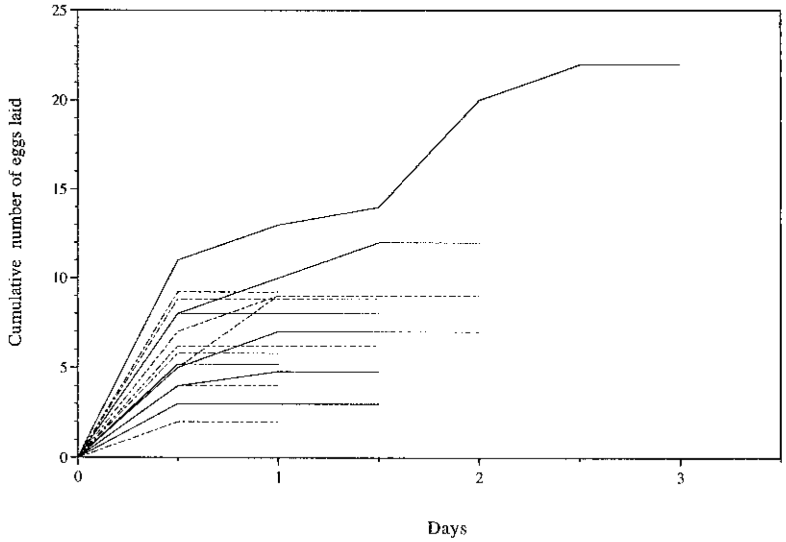

Figure 3. Cumulative number of eggs laid by *A. melinus* females deprived of honey that were either allowed to host feed (solid lines; *n* = 7) or not allowed to host feed (dashed lines; *n* = 8).

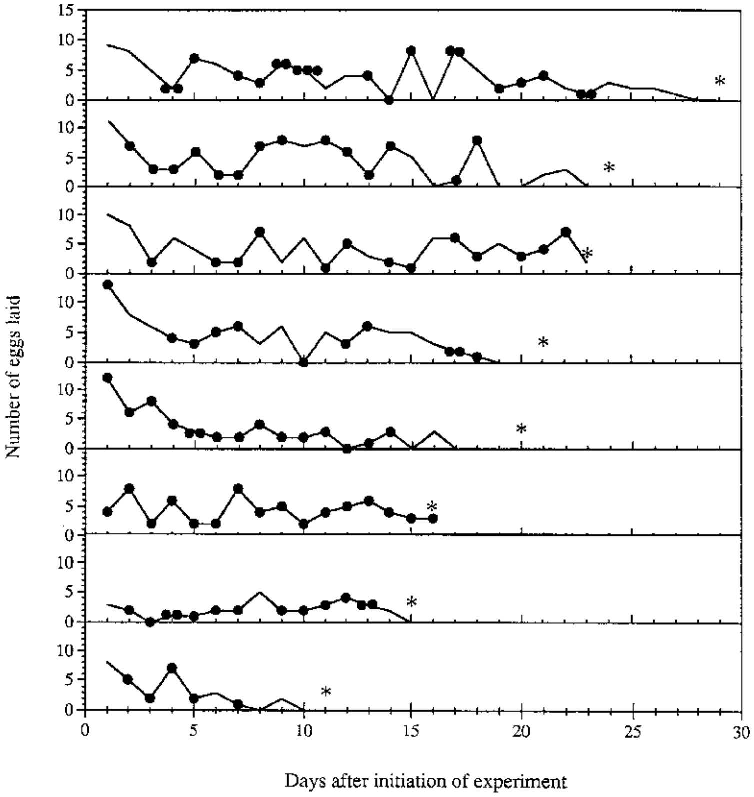

Figure 4. Daily number of eggs laid by eight individual *Aphytis melinus* females allowed continuous access to honey beginning at the age of 2 days. Each circle represents a single host-feeding meal, and asterisks denote the day of parasitoid death.

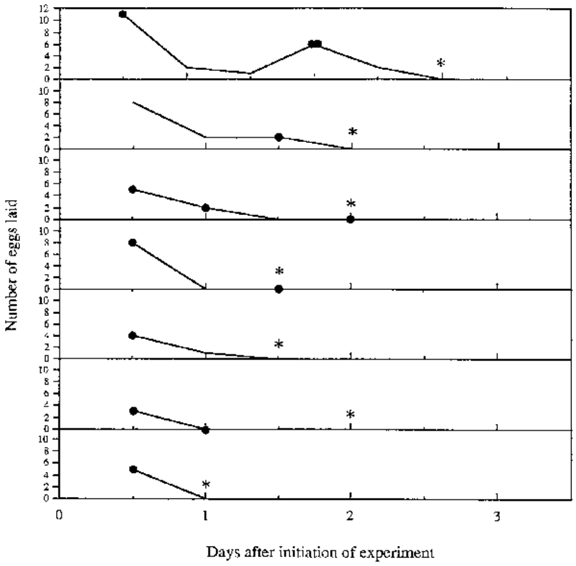

Figure 5. Number of eggs laid every 12 h by seven individual *Aphytis melinus* females deprived of honey beginning at the age of 2 days. Each circle represents a single host-feeding meal, and asterisks denote the day of parasitoid death.

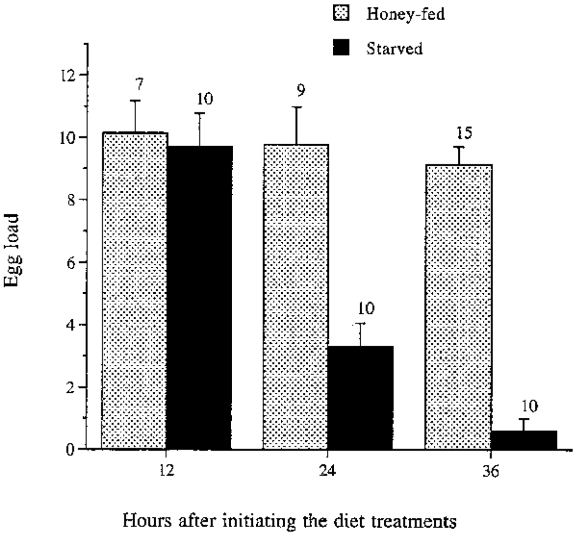

Figure 6. Mean egg loads (± S.E.M.) of *A. melinus* females that were either fed honey or starved 12, 24 and 36 h after individuals from the starvation group were deprived of honey (all females were fed honey for the first two days post-emergence). Numbers above standard error bars are sample sizes.

Table 3. Results of two-way ANOVA testing for effects of diet (honey vs. starvation) and parasitoid age group (number of hours after parasitoids in the starvation group were deprived of honey), and the interaction of these two factors on egg load of *A. melinus* females deprived of hosts

Independent variable	df	Mean square	*F*	P
Parasitoid age	2	125.7	17.6	< 0.0001
Diet	1	384.8	53.9	< 0.0001
Age × diet	2	82.4	11.5	0.0001
Error	55	7.1		

Discussion

Our results indicate a strong interaction between the influences of host feeding and honey feeding on lifetime reproductive success in *A. melinus*. Host feeding increased both fecundity and longevity of females, but only when honey was available. We also found that the rate of egg resorption was greatly increased by starvation.

Our most striking result was the extremely low lifetime reproductive success of females that were allowed to host feed, but not given access to honey meals. The implications of this result are that sugar-limitation in the field could have drastic effects on lifetime reproductive success of *A. melinus* regardless of host availability and the ability of females to host feed. A number of studies have shown low survivorship of host-deprived parasitoids held without honey or some other sugar source such as nectar or honeydew (e.g. Leius, 1961a, b; Syme, 1975, 1977; Lingren & Lukefahr, 1977; Foster & Ruesink, 1984; Idoine & Ferro, 1988; Idris & Grafius, 1995; Olson & Nechols, 1995). Many of these studies focused on non-host-feeding species, but for host-feeders, the caveat remained that host feeding might increase longevity in the absence of sugar. Some studies have answered this question in the affirmative; host feeding alone can promote the survival of a number of parasitoid species (Heimpel & Collier, 1996). A few studies, however, have suggested that females of some *Aphytis* and *Trichogramma* species 'starved to death' even when allowed to host feed (Hohmann et al., 1988; Heimpel et al., 1994; Heimpel & Collier, 1996). In this paper, we confirmed that host feeding alone is insufficient to maintain survival for more than 2-3 days in *A. melinus* females.

It has long been known that *Aphytis* parasitoids are synovigenic; i.e. females emerge with a fraction of the eggs that can potentially be matured during a lifetime. The evidence for synovigeny in *Aphytis* comes from (1) comparisons between initial egg loads (Opp & Luck, 1986; Rosenheim & Rosen, 1991, 1992; Collier et al., 1994; Heimpel et al., 1994, 1996; Collier, 1995; Heimpel & Rosenheim, 1995) with reports of lifetime reproductive success (Quednau, 1964; Gulmahamad & DeBach, 1978; Rosenheim & Hoy, 1988; Luck, 1990), and (2) dissections showing that egg maturation occurs after eggs have been laid (Heimpel et al., 1994; Collier, 1995). Previous studies have also shown that a single complement of eggs can be matured without host feeding (see refs. cited above). Whether or not host feeding is needed to mature more than a single complement of eggs was not known, however. We showed here that the lifetime fecundity of females fed honey but not allowed to host feed exceeded the initial egg complement by a factor of 0.6; the average egg load 2 days post-emergence was 11.4, while the lifetime reproductive success of females fed honey but not allowed to host feed was 18.1. Eggs produced without (or before) host feeding are presumably matured using materials obtained during the larval stage. The lack or near-lack of egg maturation by females more than 5 days old that were fed only honey suggests that honey supplies little, if any, materials used in egg production (see Figure 2).

The lifetime reproductive success of honey-deprived females did not exceed the initial egg complement. Females held without honey could therefore be considered ’functionally pro-ovigenic’. Although these females were presumably resorbing eggs during the experiment (see Figure 6), the lack of significant differences in fecundity between host-feeding and non-host-feeding groups suggests that (1) most oviposition took place before the onset of egg resorption (compare Figures 3, 6) and (2) host feeding did not lead to significant compensatory egg maturation.

Aphytis melinus females fed upon approximately one host per day whether honey was available or not. Previous studies with honey-fed *A. melinus* demonstrated that each host-feeding meal leads to the maturation of 2–3 eggs over a 1–2 day period (Collier, 1995; Heimpel et al., 1994). In this study, approximately 4 eggs were matured per host-feeding meal over the lifetime of honey-fed females. This suggests that, while some materials obtained by host feeding are used for egg maturation relatively quickly (i.e., within the first 24 h; Collier, 1995), other materials are stored for egg production later in life. The increased longevity of honey-fed females allowed to host feed showed that some nutrients obtained by host feeding are also used for somatic maintenance. Each host-feeding meal led to an average lifespan increase of approximately 0.6 days for honey-fed females. Whether these nutrients are used directly for somatic maintenance or come from resorbed eggs which were matured with host-fed materials is not clear. Collier (1995) found that a single host-feeding meal increased the lifespan of 20 day-old *A. melinus* females by approximately one day. Since Collier’s study used females that survived to the age of 20 days, and since our females were offered oviposition opportunities and Collier’s were not, our results can not strictly be compared with his.

In honey-fed, host-deprived *A. melinus*, egg resorption generally begins between 4 and 10 days post-emergence, and the rate of resorption is 1 to 2 eggs per day (Collier, 1995; Heimpel & Rosenheim, 1995). We showed here that starvation induces the early onset of rapid egg resorption (see Figure 6), as has been shown in other parasitoid species as well (Bell & Bohm, 1975). In our study, all but one mature oocyte was resorbed within 36 h of females being deprived of honey. Depletion of the entire complement of mature eggs therefore approximately coincides with the time that it takes starved females to die.

In summary, our results have shown that, while host feeding can increase both longevity and fecundity of *A. melinus* females, it can do so only when a sugar source is available. Both sugar and host meals are therefore necessary for maximum lifetime reproductive success. In the absence of sugar, lifetime reproductive success is extremely low, even if host feeding is allowed. We conclude that sugar limitation is a potential threat to *A. melinus* parasitoids in the field, regardless of host availability and the ability of this species to feed on hosts.

Acknowledgements

We thank Jane Adams for laboratory help. We also thank Timothy Collier, Marc Mangel, Paul Ode and an anonymous reviewer for advice on the manuscript. This work was supported in part by United States Department of Agriculture grant No. 92–37302–7855 to J.A.R., and a University of California Statewide IPM Project grant to G.E.H. and J.A.R.

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