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Dynamic host feeding by the parasitoid *Aphytis melinus*: the balance between current and future reproduction

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Summary

1. In many species of parasitoid Hymenoptera, adult females can use hosts either for oviposition or 'host feeding'. Oviposition is current reproduction and host feeding represents investment towards future reproduction.

2. We investigated the influences of egg load, diet, age, experience and host size on host-feeding behaviour in the aphelinid parasitoid *Aphytis melinus* attacking oleander scale *Aspidiotus nerii* (Homoptera: Diaspididae). Hosts were either rejected, used exclusively for host feeding, used for both oviposition and host feeding concurrently, or used exclusively for oviposition. When hosts were used for both oviposition and host feeding, parasitoid progeny did not develop to adulthood.

3. Behavioural records were analysed with the logistic regression model, a statistical tool for assessing the relative contributions of multiple, potentially correlated, variables.

4. Variation in egg load was obtained by (i) using diet and age treatments to manipulate the rate of egg resorption by parasitoids and (ii) taking advantage of size-related differences in egg load. Parasitoids with lower egg loads were more likely to host feed than to ovipost. This result is consistent with recently developed theory.

5. During their first-ever encounter with a host, parasitoids that had been fed a pure sucrose diet during their adult life were more likely to host feed than were parasitoids fed a sucrose diet supplemented with yeast.

6. Contrary to theoretical predictions, younger parasitoids were not more likely to host feed than older parasitoids.

7. Smaller hosts were (i) more frequently used for host feeding than were larger hosts, and (ii) less suitable for progeny development than were larger hosts.

Key-words: Aphelinidae, *Aphytis,* current vs. future reproduction, egg load, host feeding, parasitoids.

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Introduction

During the last decade, a growing body of theory has been developed to investigate the oviposition behaviour of insect parasitoids. Much of this theory has explored how investment in current and future reproduction is balanced to maximize lifetime reproductive success (Iwasa, Suzuki & Matsuda 1984; Parker & Courtney 1984; Godfray 1986, 1987; Begon & Parker 1986; Mangel 1987a,b, 1989a, b; Godfray & Parker 1991, 1992; Mangel, Rosenheim & Adler in press). The models have focused primarily on host choice and clutch-size decisions, in which the trade-off between current and future reproduction involves reproductive opportunity: eggs deposited now are not available for deposition later. A major theoretical conclusion has been that host selection and clutch-size decisions should be fundamentally dynamic. That is, decisions should vary in response to (i) conditions of the environment such as host quality, host availability and the risk of predation, and (ii) states of the insect such as current egg load, nutritional reserves, life expectancy and experience. Tests of the theory have involved mainly parasitoid Hymenoptera, but tephritid fruit flies and butterflies have been prominent in the literature as well. Host selection and/or clutch-size decisions in these and other taxa have been linked to host availability (e.g. Podoler, Rosen & Sharoni 1978; Podoler 1981; Waage & Ng 1984; Strand & Godfray 1989), host quality (e.g. Roitberg & Prokopy 1983; Charnov & Skinner 1984; Pilson & Rausher 1988; Mangel & Roitberg 1989; Völkl & Mackauer 1990; Rosenheim & Rosen 1991; Hardy, Griffiths & Godfray 1992; Nelson & Roitberg 1993), egg load (e.g.

Odendaal & Rausher 1990; Rosenheim & Rosen 1991; Tatar 1991; reviewed by Minkenberg, Tatar & Rosenheim 1992), life expectancy (e.g. Weis, Price & Lynch 1983; Harris & Rose 1989; Roitberg *et al.* 1992, 1993) and experience (e.g. Singer 1982; Mangel & Roitberg 1989; Rosenheim & Rosen 1991). The behavioural plasticity demonstrated by responses such as these presumably aids insects in balancing current and future reproduction so as to increase lifetime reproductive success.

The overall reproductive strategy of many species of parasitoid Hymenoptera includes a behaviour that is qualitatively different from host selection or clutch size. This is the decision to use a host for oviposition or 'host feeding', which is the consumption of host material by the adult female parasitoid. Since the primary role of host feeding is to secure nutrients necessary for egg maturation (reviewed by Flanders 1953; Jervis & Kidd 1986; van Lenteren *et al.* 1987), the host feed vs. oviposit decision epitomizes the trade-off between current and future reproduction: oviposition represents current reproduction and host feeding represents investment towards future reproduction.

Host feeding can cause high levels of host mortality in the field (DeBach 1943; Flanders 1953; Kidd & Jervis 1989) and has been described from over 140 parasitoid species in over 18 hymenopteran families (Jervis & Kidd 1986) as well as the dipteran family Tachinidae (Nettles 1987). Comparative data suggest that host feeding is often part of a suite of life-history traits that includes the continuous maturation of eggs after adult emergence ('synovigeny') and the deposition of eggs that do not absorb nutrients from the host ('anhydropic' eggs) (Dowell 1978; Jervis & Kidd 1986).

Recently, a number of dynamic state–variable models have been developed to investigate the influence of environmental and physiological factors on the outcome of the host-feed vs. oviposit decision. These models generated clear predictions that the tendency to host feed rather than oviposit should increase with (i) declining egg load (defined as the number of mature oocytes present within the ovaries) (Chan 1991; Collier, Murdoch & Nisbet 1994), (ii) declining nutritional reserves (Chan 1991; Houston, McNamara & Godfray 1992; Chan & Godfray 1993), and (iii) increased probability of survival (Chan 1991; Houston *et al.* 1992; Chan & Godfray 1993; Collier *et al.* 1994). To generate these predictions, the parasitoid's current fitness gain (through oviposition) is balanced against future fitness gain (through host feeding) to maximize lifetime reproductive success.

We chose to test predictions generated by these models using the aphelinid parasitoid *Aphytis melinus* DeBach. *Aphytis melinus* is well suited for studies of host-feeding strategies for two classes of reasons. First, the biology of this species satisfies assumptions made by some of the models cited above that are critical to the predictions that we tested. These assumptions are that (i) host feeding renders hosts unsuitable for the development of parasitoid progeny and (ii) the nutrients derived from host feeding are used for egg maturation, but do not appreciably increase parasitoid life span. As this study shows for second instar hosts, concurrent host feeding and oviposition on the same host renders hosts unsuitable for development of progeny (see below). Also, *Aphytis* spp. are known to require a carbohydrate source for extended longevity, even in the presence of hosts (DeBach & White 1960; Rosenheim & Heimpel, in press), suggesting that host feeding alone does not increase life span. Host feeding does, however, allow *A. lingnanensis* Compere, and probably other *Aphytis* spp., to mature oocytes (G.E. Heimpel and J.A. Rosenheim, unpublished results). Secondly, behaviours related to the decision to host feed or oviposit have been demonstrated to exhibit a plasticity that is consistent with balancing opportunities for current and future reproduction (Rosenheim & Heimpel, in press). Previous studies with various *Aphytis* spp. have shown that host selection and/or clutch-size decisions are responsive to host stage and size (Abdelrahman 1974; Luck, Podoler & Kfir 1982; Luck & Podoler 1985; Reeve 1987; Walde *et al.* 1989; Rosenheim & Rosen 1991, 1992), presence of conspecific larvae (van Lenteren & DeBach 1981) and the larvae of other parasitoid species (Yu, Luck & Murdoch 1990), host density (Podoler *et al.* 1978; Podoler 1981), order of host encounter (Reeve 1987; Rosenheim & Rosen 1991) and egg load (Rosenheim & Rosen 1991, 1992).

Here we used direct observations of *A. melinus* attacking oleander scale *Aspidiotus nerii* Bouché to test the hypotheses that (i) egg load, (ii) nutritional status, (iii) life expectancy, (iv) experience and (v) host size should influence the outcome of the host-feed vs. oviposit decision. We now frame the specific questions to be addressed for each of these five factors.

EGG LOAD

The general paradigm emerging from theoretical and empirical studies of the effect of egg load on oviposition strategies is that higher egg loads lead to behaviours favouring current reproduction (reviewed by Minkenberg *et al.* 1992). Increasing frequencies of host feeding as egg load declines would be consistent with this general prediction (Chan 1991; Collier *et al.* 1994). The demonstration of an influence of egg load on host-feeding decisions in *Aphytis* spp. remains elusive, however, in the face of two recent studies. Rosenheim & Rosen (1992) experimentally isolated the influence of egg load from confounding factors and failed to demonstrate an egg load effect for *A. lingnanensis*. Collier *et al.* (1994), however, reported increased host feeding by *A. melinus* as egg load decreased due to oviposition events, as predicted. Although this latter study demonstrated a behavioural response correlated with changing egg loads, the experimental protocol did not isolate potential influences of experience with hosts from those of egg load alone.

NUTRITIONAL STATUS

Dynamic optimization models predict that as nutritional reserves decline, the tendency to host feed should increase (Chan 1991; Houston *et al.* 1992; Chan & Godfray 1993). Nutritional reserves for adult parasitoids can come from reserves accumulated during larval development, from host feeding, or from non-host foods acquired as an adult (House 1976). For synovigenic parasitoids, nutritional reserves can presumably increase either egg production, life span, or both. We are concerned with the effect of non-host nutrients acquired during the adult stage that are used primarily for egg production. We tested the hypothesis that *A. melinus* females substitute proteinaceous non-host foods for host feeding, and that their behaviour reflects an interchangeability of these two food sources.

LIFE EXPECTANCY

Theory predicts that, as life expectancy decreases, current reproduction should be increasingly favoured over future reproduction (Weis *et al.* 1983; Parker & Courtney 1984; Begon & Parker 1986; Mangel 1987a, b, 1989a, b; Roitberg *et al.* 1992, 1993). Thus, for the case of host feeding, the tendency to oviposit rather than host feed should increase as life expectancy decreases (Chan 1991; Houston *et al.* 1992; Chan & Godfray 1993; Collier *et al.* 1994). Here we show that older *A. melinus* females have lower life expectancy than younger females and test the hypothesis that older *A. melinus* females are less likely to host feed than younger *A. melinus* females.

EXPERIENCE

Host-feeding theory predicts that as host availability declines, so should the propensity to host feed (Jervis & Kidd 1986; Chan 1991; Collier *et al.* 1994). Following this reasoning, we tested the hypothesis that oviposition should be more prevalent during the first host encounter than during the second host encounter. This test is possible with *A. melinus* since a full complement of eggs is matured during the first day of adult life on a diet of honey alone (Opp & Luck 1986). *Aphytis melinus* that are at least 1 day old and have had honey therefore do not need to host feed before depositing their first clutch of eggs (Abdelrahman 1974; Reeve 1987). Other studies of *A. melinus* have demonstrated increasing rates of host feeding with successive encounters with third instar *Aonidiella aurantii* (Maskell) (Reeve 1987; Collier *et al.* 1994), but these results could be due to concurrent changes in egg load.

HOST SIZE

When there is a positive relationship between host size and quality, it is expected that smaller hosts will be used for host feeding and larger hosts for oviposition (Kidd & Jervis 1991; Murdoch *et al.* 1992). The positive relationship between host size and host quality has been amply demonstrated in *Aphytis* spp. (Abdelrahman 1974; Opp & Luck 1986; Hare & Luck 1991; Rosenheim & Rosen 1991, 1992), and indeed smaller hosts are more frequently used for host feeding than are larger hosts (Flanders 1951; Abdelrahman 1974; Walde *et al.* 1989; Rosenheim & Rosen 1992).

Some of the factors discussed above can co-vary, and their separate effects may be difficult to disentangle. For instance, we tested separately for effects of diet, age, experience and egg load on behaviour, yet diet, age and experience can themselves have strong influences on egg load. Unfortunately, these difficulties are not easily avoided. Experimental manipulation of egg load in parasitoids, for instance, has not yet been achieved without simultaneously altering some other factor or factors (Rosenheim & Heimpel, in press). Similarly, host encounters that do not result in rejection are inextricably tied to either changes in egg load (through oviposition) or nutritional status (through host feeding). We coped with these difficulties by using logistic regression modelling and other statistical techniques that recognize the joint effects of the interrelated variables.

The amount of time that a parasitoid spends host feeding on a single host can vary and may be influenced by the factors discussed above. The decision of how long to spend host feeding will be especially important under three conditions. First, when a single host is used for both host feeding and oviposition ('concurrent oviposition and host feeding'), hosts fed upon for longer amounts of time may be less suitable for development of progeny. Sandlan (1979) found that the ichneumonid *Pimpla* (= *Coccygomimus*) *turionellae* (L.) host fed for longer periods of time when hosts were used exclusively for host feeding than when hosts were used for concurrent oviposition and host feeding. Secondly, when the extraction of materials by host feeding follows a pattern of diminishing returns, each host may be viewed as a 'patch' from which the optimal amount of resources to be extracted (and thus the amount of time spent feeding) may be dependent on factors such as the ones discussed above. Rosenheim & Rosen (1992) demonstrated that host feeding by *A. lingnanensis* on single California red scale second instars provides food at a diminishing rate. Thirdly, when the act of host feeding imposes a cost on the parasitoid, such as decreased time left for foraging, or increased risk of predation, shorter host feeding times may be advantageous under some conditions. In this study, we tested for effects of egg load, diet, age and experience on host-feeding times. We also compared host-feeding times for parasitoids that used hosts exclusively for host feeding and parasitoids that used hosts for concurrent oviposition and host feeding.

Materials and methods

NATURAL HISTORY AND LABORATORY CULTURES

Aphytis species (Hymenoptera: Aphelinidae) are synovigenic ectoparasitoids of armoured scale insects (Homoptera: Diaspididae), a group of sessile plant-sucking insects that secrete a waxy, protective covering over their body (Rosen & DeBach 1979; Rosen, in press). Host-choice and oviposition behaviours by *A. melinus* follow a stereotyped pattern described in detail by Luck *et al.* (1982); host-feeding behaviour in *Aphytis* spp. is described by Rosenheim & Heimpel (in press). Briefly, hosts are discovered and recognized by physical contact with the parasitoid's antennae. Host size is then assessed externally during a series of walking and turning movements. The host is then either rejected or probed with the ovipositor, which provides an internal assessment of quality (van Lenteren & DeBach 1981). Probed hosts may still be rejected, or they may be either parasitized or fed upon. In some cases, host feeding and oviposition may occur on the same host (Baker 1976; Rosenheim & Rosen 1991, 1992; this study). To oviposit, *Aphytis* females drill through the scale cover with their ovipositor, probe the scale body (possibly injecting a paralysing venom), which arrests development, and deposit one to several eggs between the scale insect body and its cover or underneath the scale body (Luck *et al.* 1982). The parasitoid offspring then develop under the scale cover. To host feed, *Aphytis* females drill through the scale cover, probe the scale body extensively, and then exude a viscous substance from the ovipositor. This substance spans the distance between the scale body and its cover and hardens to form a 'feeding tube', from which host haemolymph is imbibed (Rosenheim & Heimpel, in press).

Experiments were performed with *A. melinus* individuals from a population collected in Tulare Co. (CA, USA), in 1990 from a site without recent insectary releases, and cultured in the laboratory for approximately 25 generations. Laboratory cultures were maintained at 26·7 ± 1·5°C and a photoperiod of 14L : 10D. *Aphytis melinus* is a biparental species introduced into California from northern India and Pakistan in 1957 to control California red scale *Aonidiella aurantii* on citrus (Luck 1986). The host used to maintain laboratory parasitoid cultures and in all behavioural assays was a uniparental strain of oleander scale *Aspidiotus nerii* growing on butternut squash *Cucurbita moschata* Duchesne. Although oleander scale is probably not the principal host for *A. melinus* (DeBach & Sundby 1963; Luck & Uygun 1986), it is readily parasitized by *A. melinus* in the laboratory (DeBach & Sundby 1963; Baker 1976; Rosen & DeBach 1979; van Lenteren & DeBach 1981; Luck *et al.* 1982; G.E. Heimpel & J.A. Rosenheim, personal observation), and *A. melinus* has reportedly controlled oleander scale populations in the field (DeBach & Rosen 1976). Oviposition behaviour of *A. melinus* is the same on California red scale and oleander scale (Luck *et al.* 1982). Oleander scale insects undergo two moults, and therefore three instars, during their life and are invulnerable to parasitism and host feeding while undergoing the second (and possibly first) moult (Baker 1976; G.E.Heimpel, personal observation).

BEHAVIOURAL ASSAY

Our aim was to obtain groups of parasitoids differing in nutritional status and age, and then to perform direct observations on individuals in each group to assess the effects of these different parasitoid states on host-feeding decisions. The influences of parasitoid egg load, size and ovipositional experience were also assessed. Two diet treatments (sucrose and sucrose + yeast) and three age treatments (2 days, 5 days and 15 days) were fully crossed to obtain six experimental groups. The sucrose diet consisted of 50% pure sucrose in de-ionized water, and the sucrose + yeast diet consisted of the sucrose diet with 5% (by weight) yeast extract (BACTO^R Yeast Extract, Difco Laboratories, Detroit, MI, USA).

The treatments were prepared as follows: *A. melinus* pupae were isolated from beneath scale covers and placed individually in 3-ml vials provided with a streak of either the sucrose or the sucrose + yeast diet. These pupae were checked daily for emergence of adult parasitoids. Emerged females were then moved to vials modified to provide a constant water supply via a thin cotton wick, as well as the same food that the emerging individuals had received. Food was brushed onto the sides of the vials, with half of the parasitoids receiving the sucrose, and the other half receiving the sucrose + yeast diet. Parasitoids were held in these vials until the behavioural assay was performed (i.e. for 2, 5 or 15 days). Twenty-four to 36 h prior to the behavioural assays each female was mated by placing a young unmated male into the vial holding the female to be tested. *Aphytis* parasitoids have been reported to mate very readily when placed together in vials or other artificial substrates (Gordh & DeBach 1976, 1978; van Lenteren & DeBach 1981; Collier *et al.* 1994). We frequently observed mating immediately upon introduction of the male into the vial.

The observational protocol was similar to that used by Rosenheim & Rosen (1991, 1992). Observations were performed by confining individual *A. melinus* females, prepared as described above, within a small foraging arena (floor area = 33 mm^2) which contained a single second instar oleander scale growing on butternut squash. The foraging arena was formed by affixing a small glass dome to the surface of the squash directly over a single scale insect using an inert adhesive gum (UHU HOLDIT^{R} plastic adhesive, Faber-Castell Corp., Lewisburg, TN, USA). The parasitoid was observed continuously at 12 × magnification and illuminated with fibre-optic lighting until it left the host or until 30 min had elapsed without host discovery. Parasitoids discovering the first host were then immediately transferred to a fresh second instar scale insect for an additional observation period, which was performed in a manner identical to the first. Host to host transfers were accomplished by inducing the parasitoids to jump or walk onto the inside surface of the glass observation dome by gently touching them with a camel-hair brush, and then positioning the dome over the next host to be offered. Second instar scale insects were used because of the size-selective nature of the host-feed vs. oviposit decision in *Aphytis*. First instar oleander scale insects are too small to support progeny development and so are used exclusively for host feeding by *A. melinus*, while third instars are preferred for oviposition (G.E. Heimpel, personal observation). Second instar hosts, however, are less preferred for oviposition while still allowing for successful progeny development, making either host feeding or successful oviposition possible (see the Results). We alternated diet treatment, approximate host size and, in most cases, parasitoid age during the 4 months that observations were performed. To control for the possibility that decisions were constrained by an inability to oviposit (due to egg limitation or physiological defect), parasitoids were confined with a third instar host after the second host encounter. One of 95 parasitoids tested did not oviposit on the third instar host and was therefore excluded from the analysis. Thus, three sequential host encounters were observed per parasitoid, the first two involving second instar hosts, and the third involving a third instar host. Observations from this last host encounter produced results on clutch size and sex allocation patterns that will be discussed elsewhere.

During each observation the following information was recorded. (i) The decision of the parasitoid to either reject, host feed only, oviposit only, or oviposit and host feed concurrently on the same host. Oviposition was recognized by the characteristic pumping motions that typify egg deposition (Luck *et al.* 1982; Rosenheim & Rosen 1991, 1992), and parasitoids were assumed to be host feeding when their mouthparts touched the site on the scale cover that had been pierced by the ovipositor (see also Rosenheim & Rosen 1992). (ii) Time spent host feeding. The time spent feeding ('feeding bouts') was separated from time spent performing feeding-related activities such as searching for the puncture hole or reinitiating haemolymph flow through the feeding tubes ('inter-bouts'). A stopwatch was used to record times to the nearest second.

Immediately following the behavioural assay, scale size was assessed by measuring two perpendicular diameters of the scale cover, including the longest if apparent, to the nearest 0·01 mm. Scale covers are circular to ellipsoid, so scale cover area was calculated using the formula for the area of an ellipse: $(\pi/4)$(diameter 1 × diameter 2). Also, parasitoids were frozen in preparation for dissections later that day to quantify egg load and size. Parasitoid dissections were performed by holding parasitoids inside a drop of distilled water using a fine probe and then grasping and pulling the tip of the abdomen with a pair of fine forceps. By slowly pulling the abdomen distally from the thorax, the ovaries became exposed and the oocytes could be counted. Only oocytes that were deemed mature (i.e. positioned at the base of the ovarioles, not associated with nurse cells, and full size) were included in the egg load of dissected parasitoids. Egg load at any point during the behavioural assay was calculated as the sum of any eggs deposited afterwards and the dissected egg load. Parasitoids were then slide-mounted and one of the hind tibiae was measured at 100 × magnification to the nearest 0·01 mm as an index of parasitoid size.

To evaluate simultaneously the influence of variables that were continuous or approximately continuous (parasitoid hind tibia length and egg load, scale cover area) as well as categorical (diet treatment, parasitoid age, the history of prior host contact) on the parasitoids' decision to either reject the host, host feed only, oviposit and host feed concurrently, or oviposit only, we used step-wise polychotomous logistic regression, in which the decision variable was considered categorical (Dixon 1990). This statistical tool allowed evaluation of the relative contribution of a series of correlated variables. We evaluated the influence of the treatment variables as well as egg load, host size and parasitoid size on host feeding times using step-wise multiple linear regression. The influence of the diet and age treatments on egg load was assessed using two-way ANCOVA with parasitoid hind tibia length as a covariate. All means are reported ± 1 SEM.

DEVELOPMENT OF PROGENY

Hosts that were parasitized during the behavioural assay (i.e. hosts on which the parasitoid either oviposited only or host fed and oviposited) were monitored for progeny development. Immediately following the behavioural assays, oviposition was confirmed by gently lifting the scale cover with a fine probe and visually inspecting the scale body for eggs. The scale cover was carefully replaced by adhering it to the squash surface cover the scale body with a small amount of distilled water. Other studies of *Aphytis* parasitoids have successfully used this or similar methods of monitoring progeny development (Opp & Luck 1986; Yu & Luck 1988; Rosenheim & Rosen 1991). The parasitized hosts were then covered with the long end of a gelatin capsule (size 000) affixed to the squash using adhesive gum and held for at least 25 days at 26·7 ± 1·5°C and a photoperiod of 14L : 10D for progeny development to be completed. The hind tibia length of emerging parasitoids was measured as described above, and developmental mortality was recorded as occurring during the egg or early larval stage (i.e. no dead progeny visible), late larval stage (dead larva visible), or pupal stage (dead pupa visible). Step-wise polychotomous regression was used to test for effects of host size and clutch size on successful development of progeny.

INFLUENCE OF DIET TREATMENTS AND PARASITOID SIZE ON LONGEVITY

Theory predicts that life expectancy should have an effect on parasitoid foraging behaviour (Weis *et al.* 1983; Parker & Courtney 1984; Begon & Parker 1986; Mangel 1987a,b, 1989a,b; Roitberg *et al.* 1992, 1993). It was therefore important that we be aware of any effects of our experimental treatments on parasitoid longevity. To this end, over 250 *A. melinus* females were prepared as described above for the behaviour assays (i.e. receiving either the sucrose or sucrose + yeast diet in vials supplied with water at 26·7 ± 1·5°C and a photoperiod of 14L : 10D) and checked daily until they died. Longevity was recorded and parasitoid hind tibia length was measured as above as an index of parasitoid size. Mean longevity of the two diet groups was compared, and the age-specific life expectancy, e_x, for the two diet groups was calculated using standard techniques (e.g. see Southwood 1978). Since almost all progeny of observed females that completed development were males, the relationship between male size and longevity was obtained by rearing 88 males under the conditions described above, noting the age of death and measuring a hind tibia.

Results

INFLUENCE OF TREATMENTS ON EGG LOAD AND LONGEVITY

Egg loads of *A. melinus* (measured as the sum of eggs oviposited during the behaviour assay and mature oocytes found during the dissections) were significantly influenced by parasitoid age, hind tibia length, and an interaction between parasitoid age and diet (Table 1; two-way ANCOVA with age and diet as main factors and hind tibia length as a covariate). Younger and larger parasitoids had higher egg loads than older and smaller parasitoids (Fig. 1). Diet had no effect on egg load of the youngest parasitoids (Fig. 1a; ANCOVA, $F = 1·4$, $P > 0·25$), but exerted a significant effect on the two older age groups. At the age of 5 days, parasitoids fed sucrose had slightly lower egg loads than parasitoids fed the yeast solution (Fig.

Table 1. Results of two-way ANCOVA testing for effects of parasitoid age, diet and their interaction, as well as hind tibia length on the egg load of *A. melinus* used in the behavioural assays. Age was coded as an ordered variable with three states and diet as a categorical variable with two states

Independent variable	df	Mean square	*F*	*P*
Parasitoid age	2	142·6	48·3	<0·001
Diet	1	3·9	1·3	0·25
Age × diet interaction	2	23·2	7·9	<0·001
Hind tibia length	1	359·2	121·8	<0·001
Error	95	2·9		

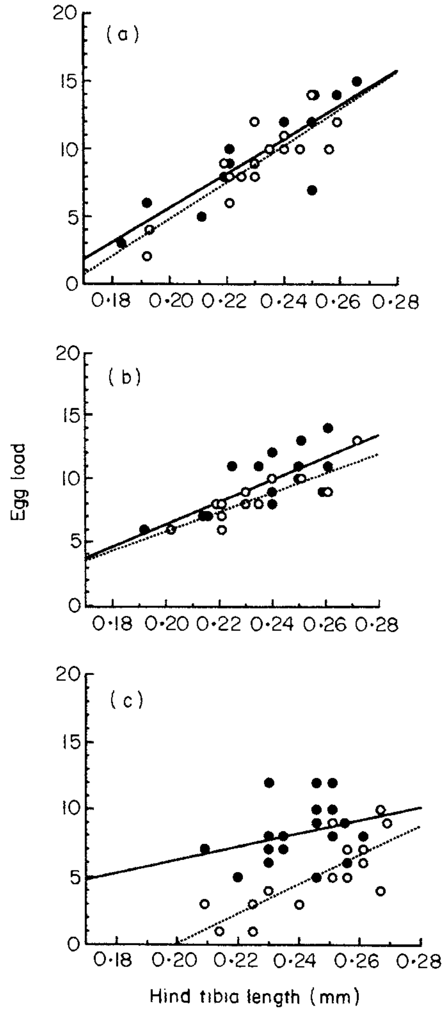

Fig. 1. Influence of hind tibia length (HTL) on egg load (EL) of *A. melinus* fed the sucrose (○, dotted line) and yeast (●, solid line) diets at three ages: (a) 2 days, (b) 5 days, (c) 15 days. Linear regression for 2-day-old parasitoids (a) fed sucrose: EL = 137·1(HTL) − 22·6, $r^2 = 0·75$, $P < 0·001$, and fed the yeast diet: EL = 127·5(HTL) − 19·8, $r^2 = 0·75$, $P < 0·01$. For 5-day-old parasitoids (b) fed sucrose: EL = 76·9(HTL) − 9·6, $r^2 = 0·71$, $P = 0·01$, and fed the yeast diet: EL = 89·2(HTL) − 11·5, $r^2 = 0·53$, $P = 0·07$. For 15-day-old parasitoids (c) fed sucrose: EL = 108·7(HTL) − 21·6, $r^2 = 0·60$, $P < 0·01$, and fed the yeast diet: EL = 49·4(HTL) − 3·6, $r^2 = 0·11$, $P > 0·5$.

1b; ANCOVA, $F = 4{\cdot}8$, $P = 0{\cdot}036$). At the age of 15 days, the egg loads of sucrose-fed parasitoids were substantially lower than those of parasitoids fed the sucrose+yeast solution (Fig. 1c; ANCOVA, $F = 33{\cdot}0$, $P < 0{\cdot}001$). Thus, the yeast diet maintained egg loads higher for a longer period of time than did the pure sucrose diet. These results suggest that (i) *A. melinus* are able to resorb oocytes ('oosorption'), and (ii) high rates of oosorption do not occur within the first 5 days of life under our experimental conditions.

Variation in egg load for the first host encounter was therefore obtained in two ways: (i) through size-dependent variation in egg load, and (ii) through oosorption by older sugar-fed parasitoids. During the second host encounter, egg loads varied due to these factors as well as in response to the number of eggs deposited on the first host.

Median longevity for parasitoids fed the pure sucrose diet ($9{\cdot}55 \pm 0{\cdot}51$ days; $n = 127$) was slightly shorter than that of parasitoids fed the sucrose+yeast diet ($10{\cdot}69 \pm 0{\cdot}68$ days; $n = 137$) (median test; $\chi^2 = 2{\cdot}7$, $P > 0{\cdot}1$). A log–rank test of survivorship (Dixon 1990) revealed a marginally non-significant effect of diet on survivorship (Fig. 2a; log–rank statistic = 3·61; $P = 0{\cdot}057$). Life expectancy, e_x, decreased with the ages used for testing and was about 1–2 days longer for 2- and 5-day-old parasitoids fed the sucrose+yeast diet than for parasitoids fed the pure sucrose diet (Fig. 2b). The life expectancy of parasitoids at age 15 days did not appear to differ across diet treatments (Fig. 2b). Male hind tibia length was not significantly correlated with male longevity ($r^2 = 0{\cdot}006$, $P > 0{\cdot}4$, $n = 88$).

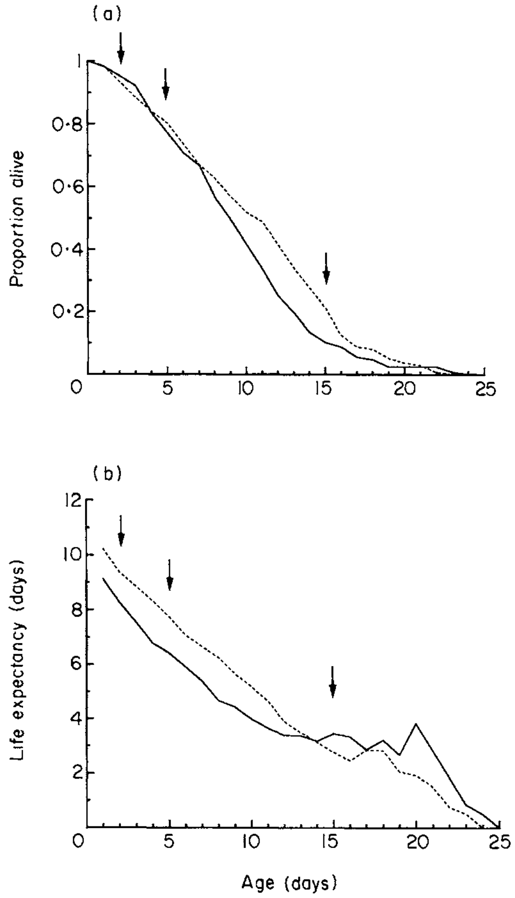

Fig. 2. Age-specific proportion of *A. melinus* females remaining alive (a) and life expectancies (b) when fed pure sucrose (solid line) and a diet containing sucrose and yeast (dotted line). Initial *n* was 127 for sucrose-fed parasitoids and 137 for parasitoids fed the yeast diet. Arrows indicate ages at which behavioural assays were conducted. Life expectancy, e_x, was calculated using the formula

$$e_x = \sum_{x}^{w} \left(\frac{l_x + l_{x+1}}{2} \right) \Big/ l_x$$

(Southwood 1978), where l_x is survivorship at age x days, and w is the day at which zero parasitoids remain alive.

OUTCOME OF THE HOST-FEED VS. OVIPOSIT DECISION

First host encounter

Out of 102 *Aphytis* observed from all treatments, 94 discovered the first host and oviposited on the third (third instar) host. The parasitoids performed one of four activities during the first host encounter: they either rejected the host ($n = 2$), host fed only ($n = 63$), oviposited and host fed on the same host ($n = 18$), or oviposited only ($n = 11$) (Fig. 3). In every case of concurrent oviposition and host feeding, oviposition preceded host feeding. Clutch sizes from these attacks were one in all but two cases, for which the clutch size was two. Parasitoids exclusively ovipositing laid clutches of one ($n = 4$), two ($n = 5$) or three ($n = 2$) during the first host encounter. Parasitoids exclusively ovipositing deposited significantly larger clutches than parasitoids ovipositing and host feeding concurrently (G-test of independence; $G = 9{\cdot}45$, $P < 0{\cdot}01$).

Step-wise polychotomous logistic regression identified parasitoid egg load and diet, but not age and size, as significant predictors of behaviour during the first host encounter (Table 2a). Eighty-seven per cent of the sucrose-fed *Aphytis* host fed without concurrent oviposition, compared with 49% for the parasitoids that had been fed the sucrose+yeast diet (Fig. 4a). Of the 11 *Aphytis* that oviposited only, 10 had been fed the yeast diet. The proportion of *Aphytis* host feeding without concurrent oviposition declined steadily with increasing egg load, while the proportion of *Aphytis* ovipositing, either exclusively or with concurrent host feeding, increased with egg load (Fig. 5a).

Since egg load was correlated with parasitoid size (Fig. 1), the possibility existed that an effect of parasitoid size was being masked by egg load (Rosenheim & Heimpel in press). However, when parasitoid size (i.e. hind tibia length) was forced into the regression model at the first step, the final model still identified egg load, diet and host size as the only significant factors; hind tibia length was rendered non-significant. Furthermore, when egg load was withheld from

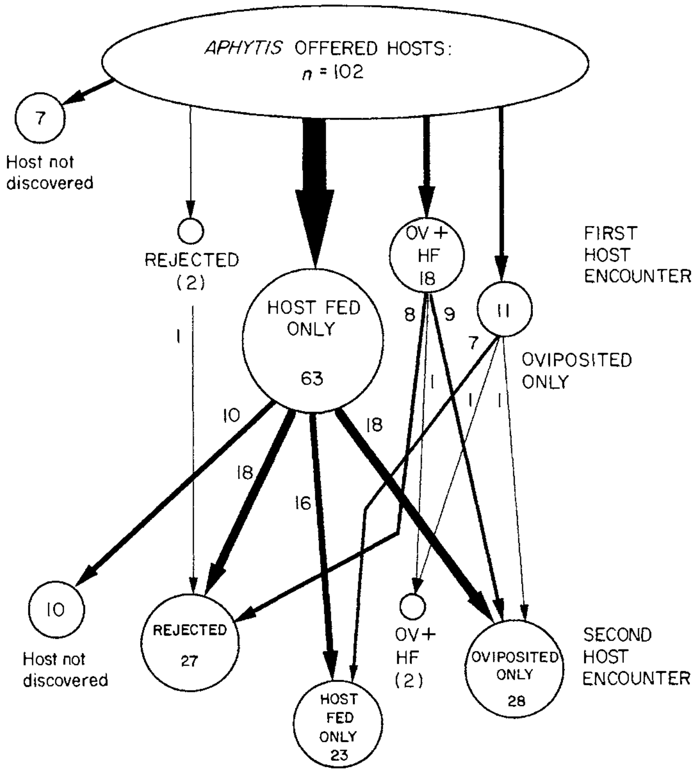

Fig. 3. Behaviour of *A. melinus* during two successive encounters with second instar oleander scale insects. Numbers refer to individual parasitoids. Arrow widths and circle areas are proportional to numbers of parasitoids performing behaviours during the two successive host encounters. OV + HF refers to concurrent oviposition and host feeding.

Table 2. Step-wise polychotomous logistic regression of factors potentially influencing the decision to reject, host feed only, host feed and oviposit concurrently, or oviposit only by *A. melinus* sequentially offered two second instar (i.e. suboptimal) hosts

Step number	Variable entered	df	Improvement χ^2	P
(a) First host, $n = 94$				
1	Egg load	3	18·75	<0·001
2	Diet	3	13·42	0·004
3	Host size	3	13·94	0·003
	Variables not entered	df	Approximate χ^2 to enter	P
	Parasitoid age	6	3·41	0·756
	Parasitoid size	3	0·38	0·945
Step number	Variables entered	df	Improvement χ^2	P
(b) Second host, $n = 80$				
1	Host size	3	20·72	<0·001
2	Egg load	3	22·42	<0·001
3	Experience*	9	33·57	<0·001
	Variables not entered	df	Approximate χ^2 to enter	P
	Parasitoid size	3	2·83	0·419
	Parasitoid age	6	4·79	0·571
	Diet	3	1·85	0·604

*The experience variable was coded to test for differences in behaviour during the second host encounter among parasitoids that had rejected, host fed only, host fed and oviposited, or oviposited only on the first host.

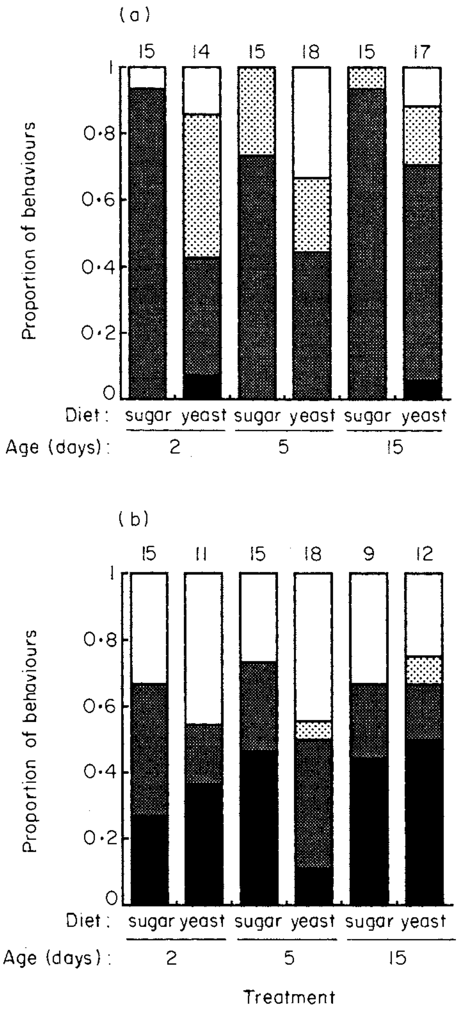

Fig. 4. Influence of two diet treatments (pure sucrose and sucrose + yeast) and three age classes on behaviour of *A. melinus* females during the first (a) and second (b) encounter with a single second instar oleander scale insect. *Aphytis melinus* either rejected the host (■), host fed only (▩), oviposited and host fed concurrently (▨), or oviposited only (□) during the host encounters. Numbers above columns are sample sizes.

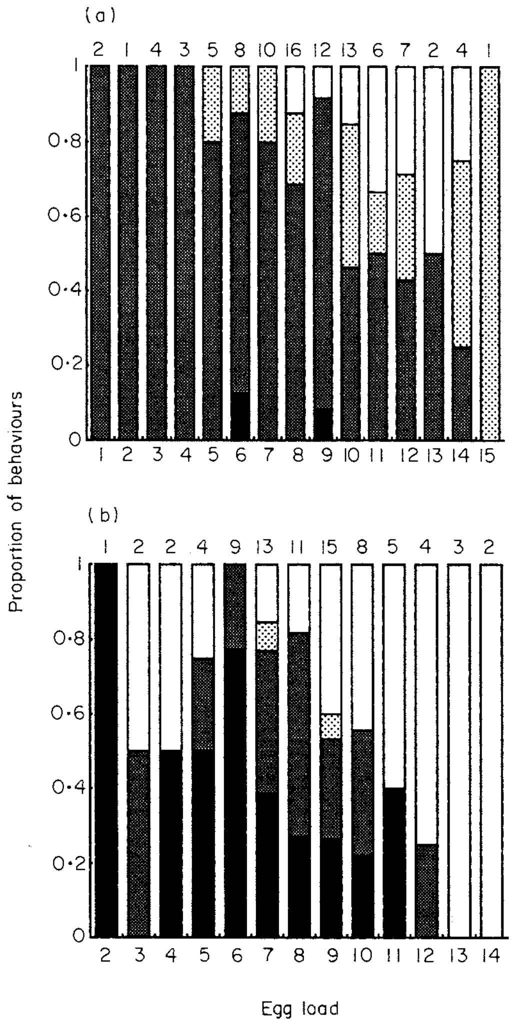

Fig. 5. Influence of egg load on behaviour of *A. melinus* females during the first (a) and second (b) encounter with a single second instar oleander scale insect. *Aphytis melinus* either rejected the host (■), host fed only (▩), oviposited and host fed concurrently (▨), or oviposited only (□). Data are pooled with respect to parasitoid age and diet. Numbers above columns are sample sizes.

the model, the effect of parasitoid size was still not significant.

Host size, however, did have a significant influence on host-feeding decisions (Table 2a), as has been found by other workers for *A. melinus* (Walde *et al.* 1989) and *A. lingnanensis* (Rosenheim & Rosen 1992). The smallest hosts were used primarily for host feeding or were rejected, and most oviposition occurred on the largest hosts (Fig. 6a).

Second host encounter

Ten of the *Aphytis* discovering the first host did not discover the second host, and in four cases the second host encounter was excluded form analyses because the scale was moulting (moult stage scale are not susceptible to either oviposition or host feeding; Baker 1976). For the 80 parasitoids encountering a susceptible second host, the same behaviours were noted as during the first host encounter. However, many more *Aphytis* oviposited exclusively ($n = 28$) and rejected the host ($n = 27$) during the second encounter than during the first encounter, while exclusive host feeding ($n = 23$) and concurrent host feeding ($n = 2$) were less prevalent (Fig. 3). During the second host encounter, egg load and host size once again had significant effects on behaviour, but diet now joined age and parasitoid size as non-significant factors (Table 1b; Figs 4b and 5b). As during the first host encounter, the proportion of *Aphytis* ovipositing increased with egg load (Fig. 5b).

We were interested in determining whether parasitoid behaviour on the second host was shaped by the previous experience on the first host. We did this first by comparing behaviour on the second host among individuals that had rejected, host fed exclusively, host fed concurrently, and oviposited exclusively

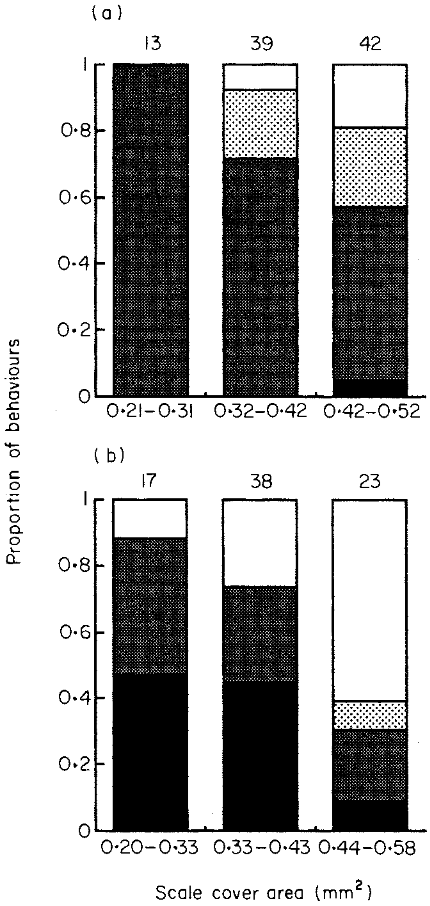

Fig. 6. Influence of host size on behaviour of *A. melinus* during the first (a) and second (b) host encounters. *Aphytis melinus* either rejected the host (■), host fed only (▩), oviposited and host fed concurrently (▨), or oviposited only (□). Numbers above columns are sample sizes.

during the first host encounter. The influence of the experience variable was highly significant (Table 2b). Host feeding on the first host led with approximately equal frequency to rejection, host feeding or oviposition on the second host (Fig. 3). Oviposition led in most cases to host feeding (Fig. 3), and concurrent host feeding led with approximately equal frequency to host feeding or oviposition (Fig. 3). When both encounters were considered together (with experience coded as 'no previous host encounter' vs. 'one previous host encounter'), experience entered the model as highly significant, as did egg load and host size (improvement χ^2 for experience = 65·8, for egg load = 34·3, for host size = 33·7, $P < 0·001$ for all variables).

As during the first host encounter, host size significantly influenced behaviour during the second host encounter (Table 2b); the smallest hosts were used primarily for host feeding or were rejected, and most oviposition occurred on the largest hosts (Fig. 6b).

TIME SPENT HOST FEEDING

During the first host encounter, parasitoids that oviposited and host fed concurrently spent significantly less time host feeding than parasitoids that host fed only (Fig. 7; step-wise multiple regression, F to enter = 15·2, df = 1, 76, $P < 0·001$). Diet, egg load, host size and parasitoid size did not significantly influence host-feeding times during the first host encounter ($P > 0·5$ for diet, parasitoid size and egg load, $P > 0·1$ for host size). However, feeding times of older parasitoids were significantly longer than those of younger parasitoids (for parasitoids host feeding exclusively: 2-day-old parasitoids, 3·7 ± 0·6 min; 5-day-old parasitoids, 4·0 ± 0·6 min, 15-day-old parasitoids, 5·6 ± 0·5 min; F to enter = 5·76; df = 2, 75, $P < 0·01$).

No significant effects on host-feeding times on the second host were found for diet, egg load, parasitoid size, host size or the behaviour on the first host (stepwise multiple regression, $P > 0·5$ for diet, parasitoid size and behaviour on the first host, $P > 0·1$ for egg load, $P > 0·05$ for host size).

DEVELOPMENT OF PARASITOID PROGENY

Five of 57 hosts receiving eggs that were monitored for progeny development were lost during experimental handling. Thirty-three of the 52 remaining hosts were used exclusively for oviposition and 19 were used for concurrent oviposition and host feeding. All 19 hosts used for concurrent host feeding yielded no adult parasitoid progeny. Mortality of offspring deposited on these hosts occurred during the egg or early larval stages in every case. Of the hosts used for oviposition only, 17/33 (51·5%) produced adult *Aphytis*. Clutches of both one (13/22; 59%) and two (4/9; 44%), but not three (0/2), produced adult progeny, but not more than one adult *Aphytis* developed successfully from any clutch. Of the 16 progeny that died during development, seven (44%) died during the egg or young

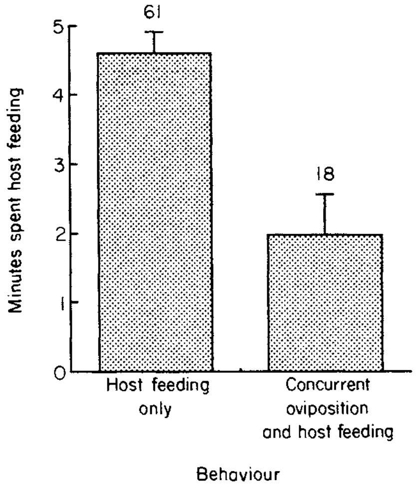

Fig. 7. Influence of behaviour (host feeding only vs. concurrent oviposition and host feeding) on time spent host feeding by *A. melinus* on a second instar oleander scale during the first host encounter (means ± SE). Only the time spent with the mouthparts touching the scale cover was included. Numbers above standard error bars are sample sizes.

larval stages, four (25%) died during the older larval stages, and five (31%) died during the pupal stage. The high rate of developmental mortality found in this study underscores the low quality of second instar hosts as oviposition sites for *A. melinus*. Rosenheim & Rosen (1992) reported similar values for *A. lingnanensis* developing on second instar *Aonidiella aurantii*. As was the case in the latter study, our experiments were designed to take advantage of the low quality of second instar hosts as oviposition sites to provide a more sensitive behavioural assay of the tendency to host feed vs. oviposit.

Among the hosts used solely for oviposition, we tested for effects of host size and clutch size on (i) successful development of progeny, (ii) developmental stage at death for those progeny not completing development, and (iii) size of emerging progeny. To avoid pseudoreplication in the analysis of survivorship of parasitoid offspring developing together on one host, survivorship to emergence for each host rather than each parasitoid egg was used as the dependent variable in polychotomous step-wise logistic regression. Successful development was more likely from larger than smaller hosts (Fig. 8; improvement $\chi^2 = 5{\cdot}2$, $P = 0{\cdot}023$). The effect of clutch size was marginally non-significant, although clutch size did enter the regression model (improvement $\chi^2 = 4{\cdot}7$, $P = 0{\cdot}093$). We believe that the lack of an effect of clutch size on progeny survivorship may have been an artifact of a small sample size. No effect of host size or clutch size was found on the stage at which progeny died before emergence (multiple logistic regression, $P > 0{\cdot}25$ for both variables).

Of the 17 adults that emerged, 16 were males and one was a female. (This highly male-biased sex ratio does not indicate that females were unmated; mated female *A. melinus* generally deposit male progeny on second instar hosts; G.E. Heimpel, personal observation). The single female emerged from the largest host yielding adult progeny and was herself larger than any of the emerging males. Host size had a marginally non-significant effect on the size of emerging male parasitoids (Fig. 9; $r^2 = 0{\cdot}22$, $P = 0{\cdot}070$); larger hosts yielded larger parasitoids. Hosts receiving a clutch of two or three eggs were not significantly larger than hosts receiving one egg (logistic regression, $P > 0{\cdot}15$), and the hind tibia lengths of the four adults emerging from hosts that had received two eggs were not different from those emerging from hosts in which one egg was laid (analysis of covariance with clutch size and host size as independent variables, t for clutch size $= -0{\cdot}19$, $P > 0{\cdot}5$).

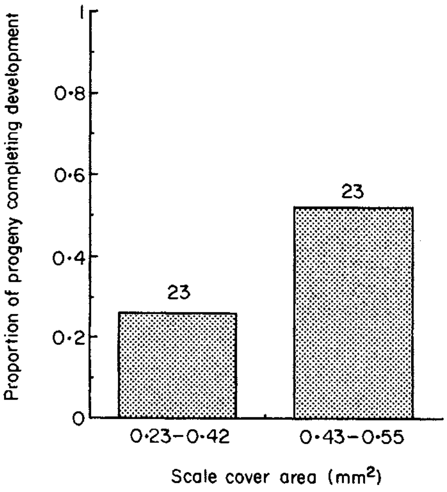

Fig. 8. Influence of host size on the proportion of *A. melinus* progeny successfully completing development. Numbers above columns are sample sizes.

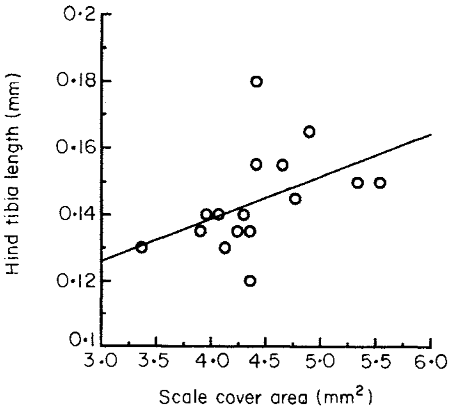

Fig. 9. Influence of scale cover area on hind tibia length of emerging male *A. melinus*. Regression equation: hind tibia length = 1·3 (scale cover area)+8·7. $r^2 = 0{\cdot}22$, $P = 0{\cdot}07$, $n = 16$.

Discussion

Godfray (1987) proposed for parasitoids that, '... a number of factors will influence the decision of whether to feed or oviposit: for example, energy reserves, life expectancy, and egg load'. In this study, we tested these predictions, which have since been formalized by Chan (1991), Houston *et al.* (1992), Chan & Godfray (1993) and Collier *et al.* (1994). We found support for an effect of nutrition and egg load, but not for life expectancy. In this section, we interpret our findings for the influences of egg load, nutritional status, life expectancy and host size on host-feeding strategies. We then discuss a paradox that emerged from our results and conclude by considering how host-feeding strategies exemplify the classical trade-off between current and future reproduction.

HOST-FEEDING STRATEGIES

Evidence has been mounting that egg load can be a major source of variability in insect foraging and oviposition behaviour (Minkenberg *et al.* 1992). The isolation of egg load from other variables that influence behaviour and that can co-vary with egg load, however, can be experimentally problematic (Rosenheim & Rosen 1991; Minkenberg *et al.* 1992;

Rosenheim 1993; Rosenheim & Heimpel, in press). In this study, egg load was manipulated by taking advantage of egg resorption in *A. melinus*. By withholding parasitoids from hosts and feeding some individuals a diet that allowed resorption to take place (the pure sucrose diet) and other individuals a diet that kept resorption to a minimum (the sucrose plus yeast diet), groups differing in egg load were obtained. This manipulation confounded egg load with diet and age. Multiple regression techniques, however, were able to separate the effects of these three variables. During the first host encounter, egg load and the diet treatment both influenced behaviour, and during the second host encounter egg load, but not diet, was a strong predictor of behaviour. Parasitoid age did not significantly influence the outcome of the host-feed vs. oviposit decision during either host encounter.

Another variable that covaried with egg load in our study was parasitoid size. In other studies, the hind tibia length of *A. lingnanensis* explained as much as 92% (Rosenheim & Rosen 1991) and 94% (Rosenheim & Rosen 1992) of the variation in egg load. In our study, hind tibia length of *A. melinus* accounted for between 11% and 75% of the variation in egg load, depending on the treatment. The strongest correlations were among the youngest parasitoids, and the sucrose diet led to stronger correlations than did the yeast diet. The stronger the correlation is between parasitoid size and egg load, the more difficult it is to distinguish between effects of these independent variables. By forcing parasitoid size into the statistical model at the beginning of a step-wise multiple regression procedure, and by withholding the egg load variable, our results demonstrated that parasitoid size was influencing behaviour only indirectly, through its effect on egg load.

The lack of a direct effect of parasitoid size on behaviour when egg load was included in the model was somewhat puzzling. Identical egg loads of two parasitoids differing in size represent different proportions of total egg capacity, a difference that could be expected to lead to differences in behaviour. The fact that the step-wise regression procedure did not find a significant effect of parasitoid size after accounting for egg load (Table 2) suggests that such an effect was not operating. To investigate more thoroughly the role of parasitoid size, we tested for an interaction between egg load and parasitoid size. No effect of such an interaction was found (step-wise polychotomous regression; approximate χ^2 to enter for the interaction = 0·79 for the first host encounter and 1·35 for the second host encounter, $P > 0{\cdot}5$ for both encounters). Rosenheim & Rosen (1992) found a positive correlation between hind tibia length and oocyte size for *A. lingnanensis*. A positive relationship between parasitoid size and egg size, if strong enough, could be responsible for the lack of an effect of parasitoid size on behaviour. The strong positive relationships between parasitoid size and egg load in both this study and Rosenheim & Rosen's (1991, 1992), however, demonstrate that the contribution of differential egg size in large vs. small parasitoids, if it exists, must be minor.

During the second host encounter, oviposition experience was another factor contributing to variation in egg load. By encountering hosts, parasitoids had the opportunity to assess host quality and availability, and when a host encounter leads to oviposition, egg load decreases. Both low egg loads and the perception of high host density are predicted to lead to increased levels of host feeding (Chan 1991; Chan & Godfray 1993; Collier, *et al.* 1994). In our study, however, there was less host feeding on the second than the first host; we suspect that this may have been due to satiation, or partial satiation, of parasitoids host feeding during the first encounter. Of the 29 parasitoids ovipositing during the first host encounter, 12 also oviposited during the second host encounter (see Fig. 3). This decline in the decision to oviposit could be attributable to either a decline in egg load or to an acquired perception of a higher host availability on the second vs. the first host. The results of the stepwise multiple regression suggest a complementary role for egg load and experience because the effect of experience is significant once the effect of egg load has entered the model.

The effect of egg load on host-feeding decisions has been explored recently in a few other empirical studies. Collier *et al.* (1994) reported higher rates of host feeding as egg loads declined, as was predicted, for *A. melinus*. In their study, variation in egg load was generated by allowing parasitoids to oviposit on a succession of hosts. These studies therefore demonstrated responses to changes in egg load that were associated with host encounters; they did not, however, isolate effects of egg load from the potential influence of experience with hosts. Rosenheim & Rosen (1992) used a protocol similar to the one employed in this study to isolate egg load effects from experience and found no influence of egg load on the outcome of the decision to host feed vs. oviposit in *A. lingnanensis*, a species closely related to *A. melinus*. For reasons that remain unclear, Rosenheim & Rosen's results are therefore at odds with the results presented here.

Parasitoids fed a diet of pure sucrose were more likely to host feed than parasitoids fed a sucrose diet containing yeast. This result is consistent with theory predicting that higher nutritional reserves should be linked to lower rates of host feeding (Jervis & Kidd 1986; Chan 1991; Houston *et al.* 1992; Chan & Godfray 1993). It also parallels work by Bartlett (1964), that provided evidence suggesting that *Microterys flavus* (Howard) females responded to the presence of yeast in their diet by choosing to oviposit rather than host feed. In our protocol we manipulated the presence or absence of nutrients required to mature oocytes (Fig. 1). The diet treatment covaried with egg load, but the fact that an effect of diet was found once the influence of egg load had been accounted for (Table 2) suggests a complementary role of these two variables.

Theory predicts that life expectancy should be positively correlated with the propensity to host feed, given the assumption that host feeding does not itself increase life expectancy (Chan 1991; Chan & Godfray 1993; Collier *et al.* 1994). Although the age treatments in this study successfully generated differences in parasitoid life expectancy, our results did not show an effect of age on the outcome of the decision to host feed vs. oviposit. To interpret properly laboratory results such as these, however, it is important to know the range of life expectancies found in the field. If field life expectancy is low, the lack of an age effect in the laboratory may not be surprising. Also, relaxing the assumption that host feeding does not increase life expectancy increases the range of conditions that favour host feeding over oviposition (Chan & Godfray 1993). Although *A. melinus* and *A. lingnanensis* only rarely reach ages beyond 1–3 days by host feeding alone (DeBach & White 1960; Rosenheim & Heimpel in press), it is conceivable that older parasitoids may increase their longevity by host feeding.

The use of smaller hosts for host feeding and larger hosts for oviposition has been demonstrated for many parasitoid species and is generally correlated with larger hosts being higher quality oviposition sites than smaller hosts (Kidd & Jervis 1991; Murdoch *et al.* 1992). Other studies have demonstrated within-instar size-selective host feeding by *Aphytis* spp. (Walde *et al.* 1989; Rosenheim & Rosen 1992), and a positive relationship between female size and lifetime reproductive success has been established for *A. melinus* under conditions of unlimited host availability (Luck 1990). Our results demonstrated a positive relationship between host size and the size of emerging male progeny, but the relationship between size and fitness of male *A. melinus* has not been established. In this study, no positive correlation between male size and longevity was found. This relationship, however, may be different in the field or in the presence of females. Also, larger males may have a higher rate of mating success than smaller males, independent of longevity considerations.

Our finding that the eggs deposited during concurrent oviposition and host feeding never developed successfully is paradoxical and is not predicted by any theory. Most of the cases of concurrent host feeding occurred during the first host encounter, and in each case oviposition preceded host feeding. Also, individuals host feeding concurrently deposited smaller clutches of eggs and spent less time host feeding than parasitoids host feeding exclusively (Fig. 7). The stereotyped nature of this behaviour suggests that it may have evolved under conditions not duplicated in this experiment. It is likely, for instance, that oleander scale, *A. nerii*, is not the natural (i.e. co-evolved) host for *A. melinus*. DeBach & Sundby (1963) considered oleander scale to be a suboptimal host for *A. melinus*, and Luck & Uygun (1986) found that *A. melinus* responded to contact kairomones found in the scale cover of the California red scale *Aonidiella aurantii*, but not in oleander scale (see also Hare, Millar & Luck 1993). Also, third-instar *A. aurantii* subjected to concurrent oviposition and host feeding by *A. lingnanensis* can result in the production of viable parasitoid offspring (J.A. Rosenheim, unpublished data). The evolutionary history of *A. melinus* host associations is unknown (Rosen & DeBach 1979), but it is conceivable that concurrent host feeding and oviposition on relatively small hosts results in successful development of progeny on a more suitable host species. Also, Hare & Luck (1991) have demonstrated significant host-plant influences on the quality of California red scale as hosts for *A. melinus*, suggesting that the host-plant may play a role in the suitability of hosts for concurrent oviposition and host feeding.

CURRENT VS. FUTURE REPRODUCTION

By host feeding, parasitoids acquire nutrients for egg maturation (Flanders 1953; Jervis & Kidd 1986; van Lenteren *et al.* 1987), and also in some cases for increased longevity (Jervis & Kidd 1986). As has been noted by Collier *et al.* (1994), the decision whether to host feed or oviposit in parasitoids is therefore a trade-off between current and future reproduction. To maximize lifetime reproductive success, parasitoids must sometimes renounce opportunities for current reproduction in favour of anticipated chances for future reproduction. For example, the rejection of suitable but low-quality hosts and the deposition of clutch sizes smaller than those maximizing fitness gain per clutch can each be optimal strategies when there is a high probability that there will be opportunity for future reproductive success (e.g. Godfray 1987; Mangel 1987b, 1989b). Conditions that favour opportunities for future reproduction for parasitoids include high host availability, long life expectancy and high egg loads. With respect to egg load and nutritional status, the behaviour of *A. melinus* in this study was consistent with that of foragers maximizing their lifetime reproductive success by balancing current and future reproduction. By host feeding, parasitoids were apparently giving up opportunities for immediate reproductive success in favour of 'anticipated' opportunities of future reproduction. The fact that host feeding was more prevalent when parasitoids had lower egg loads and nutritional reserves shows that the resolution of this trade-off was fundamentally dynamic, responding to the internal state of the parasitoid.

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