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The costs and benefits of host feeding in parasitoids

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Parasitoids are ideal organisms for testing theories concerning the trade-off between current and future reproduction. Upon encountering a host, a female has to decide whether to lay an egg, and thus invest in her current reproduction, or feed on the host to invest in her future reproduction. Theory predicts that the optimal female decision will depend on the costs and benefits of host feeding. The benefits of host feeding are well understood, but there is a lack of data on the associated costs. Models developed so far have assumed costs to be fixed: a host used for feeding cannot be used for egg laying and thus represents zero returns in terms of future reproduction. We investigated the costs and benefits of host feeding in *Nasonia vitripennis*, one of the many parasitoid species that can feed and lay eggs on the same host. Host feeding increased egg production but had no effect on the longevity of females; it also reduced the fitness of female offspring by significantly decreasing their size at emergence (no equivalent effect was found in male offspring). Female offspring size was negatively correlated with the extent of host feeding that had taken place in the host from which they emerged. The costs of host feeding in this species are therefore not fixed but vary according to the amount of nutrients extracted from the host.

The trade-off between current and future reproduction is one of the cornerstones of many areas of behavioural and evolutionary ecology (Clutton-Brock 1991; Roff 1992; Stearns 1992). Traditionally defined as a reduction in the potential for future reproduction induced by a current reproductive effort, this trade-off is essential for understanding the evolution of reproductive investment. Specifically, how much time and energy an organism invests in the current batch of eggs or young is expected to depend on its chances of reproducing in the future, which in turn will be determined by a combination of physiological (e.g. age, nutrition) and environmental factors (e.g. resource availability).

Some of the best examples of how organisms balance the trade-off between current and future reproduction come from parasitoids that mature eggs during their adult life (termed synovigenic; Jervis & Kidd 1986; Mangel 1989b; Houston et al. 1992; Chan & Godfray 1993; Godfray 1994; Collier 1995a, b; Heimpel et al. 1998). Parasitoids lay their eggs in or on the bodies of their hosts (usually other insects), whose tissues the parasitoid larvae consume as they develop. The host is, however, also the main source of nutrients for the foraging adult female (Jervis & Kidd 1986; Heimpel & Collier 1996). Host feeding, which consists in the consumption of the host's body fluids or tissues, provides the nutrients crucial for egg production (Jervis & Kidd 1986; Heimpel & Collier 1996). Synovigenic parasitoids are typically born with a limited number of mature eggs (Jervis et al. 2001) and thus their fitness is strongly dependent on the number of further eggs they can produce during their adult life (Rosenheim 1996). Upon encountering a host, female parasitoids are therefore faced with a decision: whether or not to bypass the opportunity to lay an egg (current reproductive opportunity) in order to feed on the host (thus boosting its chances of reproducing in the future).

Theory predicts that the probability with which a female parasitoid should feed or lay eggs on a host depends qualitatively and quantitatively on the costs and benefits of host feeding (Mangel & Clark 1988; Mangel 1989a; Houston et al. 1992; Chan & Godfray 1993; Clark 1993; Collier et al. 1994; Heimpel et al. 1994; Collier 1995a). The benefits of feeding are relatively well understood, with a number of studies showing that host feeding can lead to an increase in longevity or egg production (Jervis & Kidd 1986; Heimpel et al. 1994, 1997; Collier 1995b; Heimpel & Collier 1996; Giron et al. 2002, 2003). However, in contrast to this, there is a lack of data on the costs of

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host feeding. This lack of knowledge means that theoretical models have been constrained to adopt an all-or-nothing rule, with hosts being used for either feeding or oviposition (but see Heimpel et al. 1994). In many cases this is unrealistic, because almost half of the known host-feeding parasitoid species feed and lay eggs on the same host ('concurrent' host feeders, Jervis & Kidd 1986). Within these species, the costs of host feeding could have very different forms that could qualitatively alter the predictions of theory (Godfray 1994). For example, if the main cost of host feeding was due to changes in the host that would render it less suitable for parasitoid development, such as the use of a paralysing venom (Quicke 1997), then host feeding would have a fixed cost. The only model developed so far (to our knowledge) that allows for concurrent host feeding has indeed assumed costs to be fixed (75% decrease in host quality per host-feeding event, Heimpel et al. 1997). However, if the main cost of feeding was due to a decrease in the nutrients available for the developing offspring (resource limitation), then host feeding would have a variable cost, proportional to the amount of nutrients extracted from the host. The nature of these costs will therefore determine whether the key decision for a female parasitoid is either whether to feed, or how much to feed.

We investigated the costs and benefits of host feeding in *Nasonia vitripennis*, a concurrent host-feeding parasitoid of fly pupae (Whiting 1967). Although concurrent host feeding is the main strategy, *N. vitripennis* can also feed nonconcurrently under certain circumstances, such as when the females have no eggs in the ovarioles or when the host is unsuitable for oviposition (Edwards 1954). We measured the benefit of host feeding by determining the consequences of feeding for egg production and longevity, as has been done in studies on other species (reviewed in Jervis & Kidd 1986; Heimpel & Collier 1996). To quantify the form of the cost of host feeding it is necessary to manipulate experimentally the amount of feeding on a host. We did this by using the fact that food deprivation severely limits energy reserves in this wasp (Rivero & West 2002). Consequently, by varying experimentally the hunger levels of females, we were able to manipulate the amount of host feeding they did when provided with a host: hungrier females fed more. To decouple host feeding from oviposition we used two laboratory strains of *N. vitripennis* that differed in their eye colour. Red-eyed mutant females were used for host feeding, while the black-eyed wild type was used for the subsequent oviposition. This allowed us to control for any eggs laid by the host-feeding (red-eyed) female. By creating hosts that had been fed upon to different extents, we were able to determine both whether host feeding reduces the quality of the host for the developing offspring, and whether the reduction in offspring fitness is dependent on the amount of nutrients extracted from the host.

MATERIALS AND METHODS

Nasonia vitripennis (Hymenoptera: Pteromalidae) is an ectoparasitoid of dipteran pupae in birds nests (Whiting 1967). Females are gregarious, laying several eggs on the same host, which results in the larvae having to compete for resources within the host. The small flightless males emerge before the females and mate with them as they emerge. Females are winged and need to disperse after mating to find new, suitable hosts in which to lay their eggs. Females are born with a very limited number of mature eggs in their ovarioles but can produce and mature further eggs provided they have sufficient nutritional resources available (i.e. they are 'synovigenic', Flanders 1950). These nutritional resources can come from the reserves accumulated as a larva and carried-over to the adult stage (Rivero & Casas 2001) or from the consumption of the host's fluids (Jervis & Kidd 1986; Heimpel & Collier 1996). Larval reserves become quickly exhausted, even in sugar fed individuals (Rivero & West 2002), and thus host feeding is an essential component of the female's reproductive success. Host feeding in this species takes place in the same host which is used for oviposition (Whiting 1967).

Two different stocks of parasitoids were used in these experiments, both kindly provided to us by Prof. Beukeboom (Leiden University): a wild-type (black-eyed) stock (LBII) and a red-eyed stock (STDR). Both stocks of parasitoids were reared in the laboratory by placing 10–15 female parasitoids with about 30 fly pupae (*Calliphora vicina*, Diptera: Calliphoridae) in specimen tubes (7.5 cm long, 2.5 cm in diameter). Cultures and experiments were carried out at the same temperature (25 °C) and photoperiod (16L:8D).

Host-feeding Manipulation

Our aim in this experiment was to manipulate the extent of host feeding by females. For this purpose, LBII (black-eyed) females were allocated to one of the three experimental regimes, on the assumption that the time spent feeding correlates with the amount of resource extracted from the host. Females received a host either: (1) immediately after emergence ('newly emerged'); (2) after a 48-h ad libitum honey solution regime ('48 h honey'); or (3) after a 48-h water-only regime ('48 h water'). We predicted that the frequency or duration of host feeding would be highest in the 2-day-old food-deprived females and lowest in the newly emerged females. These predictions are based on previous experiments in which females emerged with a large amount of reserves which became severely depleted after a 48-h food deprivation period (Rivero & West 2002). The availability of sugar during this 48-h period, however, slowed down the depletion of larval reserves (Rivero & West 2002).

We obtained experimental females by dissecting parasitized hosts and isolating 12-day-old female parasitoid pupae individually in glass tubes (7.5 cm long, 8 mm diameter). Tubes were kept under standard temperature and light conditions and checked every 2 h. On emergence (day 0), females were immediately haphazardly allocated to one of the three treatments. Females allocated to the newly emerged treatment were observed within 2 h of emergence. No food source was provided before the

observation. Females allocated to the 48 h honey treatment received a small piece of filter paper soaked in honey solution for 48 h before the behavioural assay took place (on day 2). Females allocated to the 48 h water treatment received a similar piece of filter paper soaked in water.

On the day of the behavioural assay, the females were transferred to a clean glass tube (7.5 cm × 8 mm) containing two randomly chosen hosts. The tube was positioned beneath a binocular microscope and the female's behaviour was observed continuously for 1 h or until 30 min had elapsed without contact between the female and the host. This technique allowed us to observe up to three females at a time (one of each treatment). We recorded a host-feeding event when the females pierced the host cuticle with the ovipositor and immediately turned round to lick the fluids emerging from the wound. For each female we recorded the number of host-feeding events and the total time spent host feeding, which we calculated by adding up the individual times of each host-feeding event. We observed 60 females in this manner, 20 for each experimental treatment. At the end of the observation we dissected the hosts to determine whether any oviposition had taken place. The females were kept in the tubes until they died to determine the potential longevity benefits from host feeding (see below). At death, we estimated their size by measuring the length of their hindtibia.

Benefits of Host Feeding

The potential benefits of host feeding in parasitoids are an increase in fecundity or longevity (Jervis & Kidd 1986; Heimpel & Collier 1996). To quantify the longevity benefits of host feeding in *N. vitripennis*, we recorded the survival of the host-fed females used in the behavioural observations (see above). For this purpose, at the end of the observation, we extracted the host and left the females in the tubes with only a small piece of filter paper soaked in water and no food. In addition, we set up two control, nonhost-fed, groups concomitantly, one where females had no food from the day of emergence, and another in which females received a rich honey solution for 48 h. The five experimental treatments are summarized in Table 1. At the end of the experiments the hindtibia length of females was measured as an estimate of size.

To quantify the fecundity benefits of host feeding, on the day of emergence (day 0) 40 females received a host for 1 h (treatment B1, Table 2), while 40 others were host deprived (but given a filter paper soaked in water, treatment B2). We counted the eggs 48 h later, after freezing the female to kill it, by dissecting it under a binocular microscope. Only mature eggs were counted (Whiting 1967). We added two additional treatments to determine whether the egg load effect of host feeding depends on the timing and nutritional condition of the females (as we know to be the case in most parasitoid species, Jervis & Kidd 1986; Heimpel & Collier 1996; Rivero & Casas 1999). In one of these treatments, the females were first food deprived for 48 h before being allowed to host feed on day 2 (treatment B3); in the other, females received honey solution first and then the host (treatment B4). We dissected the females 48 h later (on day 4) to count the eggs. The four experimental treatments are summarized in Table 2.

Costs of Host Feeding

In this experiment we quantified the costs associated with laying eggs in a host that had already been used for host feeding. For this purpose, black-eyed females (LBII) were allowed to oviposit in clean hosts or in hosts that had been fed on by either a newly emerged, 48 h honey or 48 h water red-eyed (STDR) female. These different types of host varied in the extent of feeding that had taken place in them (Table 3).

Female parasitoid pupae of the black-eyed stock were isolated in small tubes (7.5 cm × 8 mm) which we checked daily for emergences. On the day of emergence (day 0) females first received a clean host (randomly chosen from our laboratory cultures). This was done to limit the amount of feeding carried out by the females on the experimental hosts. The following day (day 1) the host was removed and the female received a paper soaked in honey solution for a further 24 h. On day 2, the black-eyed females were haphazardly allocated to one of four treatments. Females were either given a randomly chosen clean host (treatment C1 or control females, $N = 81$), a host previously used for host feeding by a newly emerged red-eyed female (treatment C2, $N = 73$), a host used for host feeding by a 48 h honey red-eyed female

Table 1. Host-feeding manipulation and longevity benefits of host feeding

	Treatment breakdown						
Treatments	Day 0	Day 1	Day 2	Day 3→death	Total HF time (min)	HF events (number)	Longevity (days)
Newly emerged	Host fed	(w)	(w)	(w)	4.73±1.57 (20)	0.85±0.18 (20)	3.38±0.42^{a} (20)
48 h honey	Honey	Honey	Host fed	(w)	9.66±1.93 (20)	1.15±0.22 (20)	5.71±0.28^{c} (20)
48 h water	(w)	(w)	Host fed	(w)	12.89±0.12 (20)	1.25±0.12 (20)	4.75±0.27^{b} (20)
Honey control	Honey	Honey	(w)	(w)	—	—	5.87±0.15^{c} (40)
Water control	(w)	(w)	(w)	(w)	—	—	4.48±0.12^{b} (40)

Columns denote the mean ± SE number of host-feeding (HF) events, mean feeding time, and longevity of females allocated to each treatment. Letters (^{a,b,c}) in the longevity column denote grouping of treatments using Tukey–Kramer multiple comparison tests ($\alpha = 0.05$). (w) denotes a period of food deprivation during which the female received only water. Sample sizes are given in parentheses.

Table 2. Egg load benefits of host feeding

Treatment	Treatment breakdown					Egg load
	Day 0	Day 1	Day 2	Day 3	Day 4	
B1	Host fed	(w)	Dissect	—	—	40.95 ± 4.59^{c} (40)
B2	(w)	(w)	Dissect	—	—	20.80 ± 1.92^{b} (40)
B3	(w)	(w)	Host fed	(w)	Dissect	13.65 ± 2.23^{a} (40)
B4	Honey	Honey	Host fed	(w)	Dissect	36.32 ± 3.60^{c} (40)

Mean ± SE total number of eggs produced by females allocated to each of the four experimental treatments (raw data). Letters (^{a,b,c}) in the egg load column denote grouping of treatments using Tukey–Kramer multiple comparison tests ($\alpha = 0.05$). (w) denotes a period of food deprivation during which the female received only water. Sample sizes are given in parentheses.

(treatment C3, $N = 80$), or a host used for host feeding by a 48 h water red-eyed female (treatment C4, $N = 79$). The experimental protocols used to obtain the different types of host were the same as those used above (see Host-feeding manipulation). Owing to the high number of replications, however, red-eyed females were allowed to host feed for 1 h but no behavioural observations were carried out during that time. The red-eyed female was then removed (size was not recorded) and the host immediately allocated to the appropriate treatment. The red-eyed stock was used to control for egg laying by the host-feeding females (see below).

Black-eyed females were allowed to lay eggs in the experimental host for 24 h after which time (day 3) we killed them by freezing and measured their hindtibia as an estimate of size. Hosts were left at the standard temperature and photoperiod for the offspring to develop. Once all the offspring had emerged (days 18–20), they were counted and their hindtibia length measured as an estimate of size. For each ovipositing female we obtained four separate measurements of fitness: brood size, brood sex ratio (proportion of males), mean female offspring size and mean male offspring size. Tubes in which red-eyed offspring were found ($N = 29$) were omitted from the analysis.

Statistical Analysis

The data were analysed using general linear modelling techniques available in the JMP statistical package (version 3.2.2, SAS Institute Inc., Cary, NC, U.S.A.) Each response variable was modelled by fitting all possible explanatory variables and their interactions into the model. The maximal model was simplified by stepwise deletion, with the sequential elimination of nonsignificant terms and interactions (Crawley 1993). After the minimal adequate model (the model including only significant terms and interactions) was obtained, we tested its appropriateness by inspecting a plot of the residuals against the fitted values. Response variables were transformed to account for non-normal errors: binomial data (sex ratio) was arcsine square-root transformed, and Poisson data (number of offspring, number of eggs) were square-root transformed (Sokal & Rohlf 1981). Longevity data were analysed using gamma errors and the reciprocal link (Crawley 1993) using the GlmStat statistical package (GLMSTAT, V. 5.75., www.glmstat.com). The significant values given in the text are for the minimal model, and nonsignificant values are those obtained before the deletion of the variable from the model. When appropriate, multiple comparisons within a treatment were carried out using the Tukey–Kramer test ($\alpha = 0.05$, Sokal & Rohlf 1981).

RESULTS

Host-feeding Manipulation

As we had predicted, the mean time spent host feeding was highest in 48 h water females, intermediate in 48 h

Table 3. Costs of host feeding

Treatment	Brood size	Sex ratio	Male offspring size (mm)	Female offspring size (mm)
C1 (control)	10.27 ± 1.04 (66)	0.24 ± 0.03 (43)	0.58 ± 0.01 (n=41)	0.58 ± 0.01 (n=41)
C2	9.29 ± 0.93 (72)	0.13 ± 0.01 (n=50)	0.58 ± 0.01 (n=40)	0.58 ± 0.01 (n=50)
C3	12.07 ± 0.95 (79)	0.17 ± 0.01 (n=63)	0.57 ± 0.01 (n=60)	0.56 ± 0.01 (60)
C4	10.08 ± 1.11 (67)	0.20 ± 0.02 (44)	0.57 ± 0.01 (n=40)	0.55 ± 0.01 (43)

Mean ± SE total number of offspring, sex ratio, and male and female offspring size produced by females allocated to each of the four experimental treatments (raw data). Note that in *N .vitripennis* the allometric relation between hindtibia length and body size is different for males and females: males' tibias are larger in proportion to body size. Treatments were as follows (see Methods for details): C1: females oviposited on a clean host (control); C2: females oviposited on a host previously used for feeding by a newly emerged red-eyed female; C3: females oviposited on a host used for feeding by a red-eyed female given honey for 48 h; and C4: females oviposited on a host used for feeding by a red-eyed female given only water for 48 h. Sample sizes are given in parentheses.

honey females, and lowest in newly emerged females (Table 1). This treatment effect was statistically significant and dependent on the size of the females (interaction size∗treatment: $F_{2,54} = 3.93$, $P = 0.02$). As female size increased, host-feeding time increased in 48 h water females (feeding time $= -12.87 + 4.57$ size) and decreased in newly emerged females (feeding time $= 17.83 - 2.2$ size), although this decrease was not statistically significant ($F_{1,54} = 1.33$, $P = 0.250$). The host-feeding time of 48 h honey females was independent of size (feeding time $= 12.23 + 0.45$ size). As a consequence of the differences in the slopes, differences in host-feeding time between the treatments were largest in the larger females (Fig. 1).

The total number of host-feeding events was higher in 48 h water females than in 48 h honey and newly emerged females (Table 1), although this difference was not statistically significant ($F_{2,57} = 1.84$, $P = 0.167$). Consequently, the difference in total amount of feeding was due to feeding for longer times rather than more often.

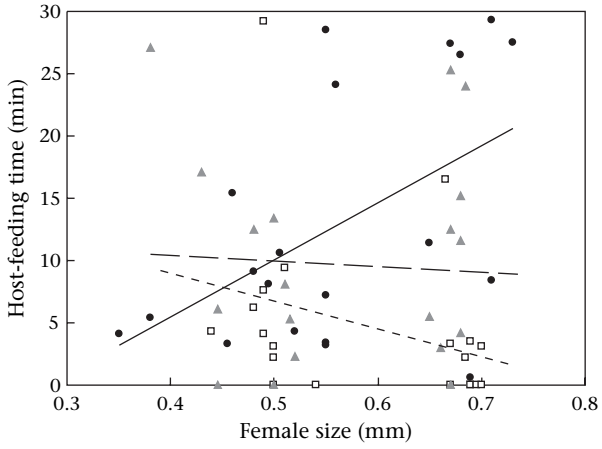

Figure 1. Regression of host-feeding time on female offspring size (length of hindtibia) for each of the three treatments: newly emerged females (□, – – –, $Y = 17.83 - 2.2X$), 48 h honey females (▲, ———, $Y = 12.23 - 0.45X$), and 48 h water females (●,———, $Y = -12.87 + 4.57X$). Regression lines obtained from the minimal adequate model containing size, treatment and the interaction size∗treatment ($r^2 = 0.25$).

Benefits of Host Feeding

The host-feeding treatment had a significant effect on the longevity of the females ($F_{4,136} = 21.64$, $P < 0.0001$). However, a Tukey–Kramer multiple comparison test ($\alpha = 0.05$) revealed that a single host-feeding event after 48 h water only (48 h water) did not significantly increase the life span of females with respect to females that were not allowed to host feed (water control; Table 1). Similarly, a single host-feeding event after a 48 h honey-feeding period (48 h honey) did not significantly increase the life span of females with respect to nonhost-fed females (honey control). The largest determinant of longevity was the presence of honey, as honey-fed females (48 h honey and honey control) lived 1–2 days longer than females in the other three treatments. The shortest life span was found among females that fed on a host on the day of emergence (newly emerged).

Host feeding had a significant effect on the number of eggs produced by the females ($F_{3,155} = 80.79$, $P < 0.001$). The effects of host feeding on egg production depended on the timing of the host-feeding event as well as on the previous condition (unfed, honey fed) of the female (Tukey–Kramer multiple comparison test, $\alpha = 0.05$). Females that fed on a host on emergence produced the most eggs, roughly 20 more eggs in a 48 h period than females that did not feed on a host (compare treatments B1 and B2 in Table 2). Females food deprived for 2 days before feeding on a host had significantly fewer eggs than females that fed on a host on the day of emergence (compare treatments B3 and B1), and than females that received honey solution for 48 h before feeding on a host (compare treatments B3 and B4).

Costs of Host Feeding

There were no differences in brood size (total number of offspring) of females allocated to the hosts from the four host-feeding treatments ($F_{1,270} = 1.56$, $P = 0.212$; Table 3). The number of offspring produced was solely determined by the size of the ovipositing female, with larger mothers producing larger broods ($F_{1,270} = 9.60$, $P = 0.002$).

The brood sex ratio (proportion of offspring that were male) was also constant across treatments ($F_{1,189} = 0.01$, $P = 0.926$; Table 3). Sex ratio was explained only by the size of the ovipositing female (sex ratio decreased with female size; $F_{1,189} = 19.39$, $P < 0.001$).

Previous feeding in the host did, however, have a significant effect on the size of the female offspring. Female offspring size decreased linearly as the host decreased in quality because of previous feeding ($F_{1,189} = 6.94$, $P = 0.009$; Table 3, Fig. 2). The size of the ovipositing female was also a significant determinant of female

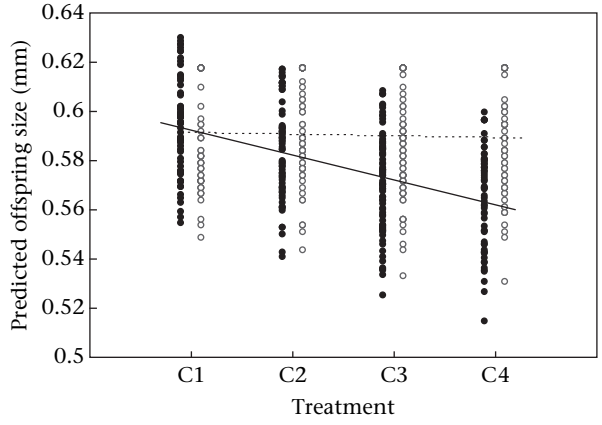

Figure 2. Regression of female (●, —) and male (○, – – –) offspring size on host-feeding treatment. See Table 3 for a description of the host-feeding treatments. Values shown are those predicted by the respective statistical minimal adequate models (see text for details).

offspring size (larger mothers produced larger female offspring; $F_{1,189} = 7.39$, $P = 0.007$), as was the total number of offspring in the brood (the size of female offspring decreased in larger broods; $F_{1,189} = 6.59$, $P = 0.01$).

In contrast, host-feeding treatment did not have a significant effect on the size of the male offspring ($F_{1,180} = 1.62$, $P = 0.204$; Table 3, Fig. 2), which was dependent only on the total number of offspring present in the brood (larger broods produced smaller males; $F_{1,180} = 11.70$, $P = 0.001$).

We explored our data further to determine why a decrease in the quality of the host as a result of previous feeding had an effect on the size of the female offspring whereas males were seemingly unaffected by it. In *N. vitripennis*, egg-to-adult development is shorter in males than in females by 24–48 h (personal observation). This adaptation, common across parasitoids that mate locally, ensures that males emerge before the females and that females are inseminated before they disperse (Godfray 1994). It can also result in an asymmetric competition for resources between males and females inside the host, as males can develop and emerge before resources become limiting, leaving the females to compete for what is left (Godfray 1994). Female offspring size may thus depend on the sex ratio of the brood in which they develop, with competition for resources being more severe for females when there is a higher proportion of (faster developing) males. We tested this hypothesis by including brood sex ratio in the model already containing the effects of treatment, brood size, and mother's size. When all broods were taken into account ($N = 194$), brood sex ratio did not have a significant effect on the size of the female offspring ($F_{1,189} = 0.06$, $P = 0.799$). However, when we restricted the data to broods of 11 or more individuals (11 being the median of the brood size distribution), i.e. to broods where competition between the offspring for resources is expected to be intense ($N = 146$), female offspring size decreased as the number of males in the brood increased ($F_{1,141} = 4.62$, $P = 0.03$). This effect was independent of the host-feeding treatment (interaction treatment∗sex ratio: $F_{1,140} = 0.04$, $P = 0.825$). In contrast, sex ratio did not have a significant effect on the size of the male offspring ($F_{1,173} = 0.14$, $P = 0.703$), even when the analysis was restricted to large broods ($F_{1,139} = 0.39$, $P = 0.528$).

DISCUSSION

We have shown that in *N. vitripennis*: (1) experimental manipulation of hunger level in female wasps provides a technique for manipulating the extent to which they feed on a host; (2) host feeding contributes to fitness because it increases egg production; and (3) host feeding also has a fitness cost because it decreases the size of female offspring developing on that host. Furthermore, the decrease in female offspring size was proportional to the extent of feeding that had taken place in the host from which they emerged, showing that host feeding has a variable rather then a fixed cost.

Benefits of Host Feeding

Our results show that host feeding has a very significant effect on egg production. Females allowed access to hosts for 1 h on the day of emergence produced up to 20 eggs more over a 48 h period than nonhost-fed females (compare treatments B1 and B2 in Table 2). These results are in line with those obtained in other parasitoid species (Jervis & Kidd 1986; Heimpel & Collier 1996). However, we also found that the benefits of host feeding vary with the nutritional condition and experience of the females. Females allowed to feed on a host after a 48-h feed deprivation period (B3 treatment) had the lowest egg load, probably caused by egg resorption being triggered by the long starvation (King 1963; Hopkins & King 1964; Whiting 1967; King & Richards 1968). As resorbed eggs leave no trace, we could not determine how many eggs were actually produced as a result of the feeding bout. Provisioning the female with honey for the first 48 h (B4 treatment) at least partly compensated for the lack of host nutrients, and females were able to produce almost as many eggs as females fed on the day of emergence. Although the sugars contained in honey are unlikely to be directly implicated in egg production (Engelmann 1970), they provide sufficient energy for body maintenance, thus probably limiting the need for egg resorption.

In contrast to other species (Jervis & Kidd 1986; Heimpel & Collier 1996), host feeding had no appreciable effect on longevity in *N. vitripennis*. Why some species derive clear longevity benefits from host-feeding fluids whereas others do not is not clear, but it may have to do with interspecific differences in the nature of the nutrients consumed and in particular with the amount of sugars present in the ingested fluids (Giron et al. 2002).

Costs of Host Feeding

Using the same host for host feeding and oviposition had a fitness cost for *N. vitripennis* females. Female offspring emerging from hosts previously used for feeding were significantly smaller than those that emerged from a nonhost-fed host. Furthermore, the decrease in female offspring size was a linear function of the host-feeding treatment (Fig. 2) which was a strong determinant of host-feeding time (Table 1). Host-feeding time, in turn, is known to correlate with the amount of nutrients extracted from the host, although the relation may not be linear (Giron et al. 2003).

In parasitoids, as in most other insects, female size is a strong determinant of fitness (Godfray 1994; Visser 1994; West et al. 1996; Ellers et al. 1998). In the present experiment, females that emerged from hosts that had been subjected to intense host feeding (C4 treatment) were on average 5% smaller than females that emerged from a fresh host. Field estimates of the size–fitness relation in other species suggests that this can decrease fitness by up to 30% (West et al. 1996). From previous laboratory experiments on *N. vitripennis* we know that such a reduction in size translates into 10 μg of lipid reserves less at emergence (day 0) and a significant

decrease in the number of eggs produced in subsequent days (two to three eggs less on day 1, and up to seven eggs less on day 2 if the female is food deprived; Rivero & West 2002). While the disadvantage in terms of mature eggs can be at least partly compensated through host feeding, the same cannot be said for the lipid reserves. Parasitoids, in contrast to other insects (Nayar & van Handel 1971; Brown & Chippendale 1974; van Handel 1984; Warburg & Yuval 1997), cannot synthesize lipids from the nutrients they obtain as an adult (Ellers 1996; Olson et al. 2000; Rivero & West 2002; Giron & Casas 2003). Consequently, lipids at emergence, which in insects are used for both maintenance and egg production (Nijhout 1994), are both essential and limiting for the adults.

In contrast, the size of male offspring was not affected by the host-feeding treatment. The most likely explanation for this is asymmetric competition for limited resources caused by differences in the speed of development between the sexes. Egg-to-adult development is shorter in males by 24–48 h (personal observation). While males develop faster in order to emerge earlier and ensure a maximum number of matings, females develop slower in order to emerge as larger adults (Godfray 1994). This can lead to the situation where competition for resources will be more intense for females, because males can obtain all the resources they need before resources become limiting. Consistent with this, we found that when hosts were heavily parasitized, the size of the female offspring decreased as the number of males in the brood increased. An alternative explanation for the lack of host-feeding effect on male offspring fitness is that the nutritional requirements of male and female larvae differ qualitatively, as seems to be the case in some other insect taxa (Stockhoff 1993; Telang et al. 2001, 2002, 2003; Dubois et al. 2002; Moreau et al. 2003).

To our knowledge, there is only one other study where the costs of host feeding have been quantified (Ueno 1997). Ueno found that hosts used for feeding by *Pimpla nipponica* (a solitary parasitoid of lepidopteran larvae) produced overall fewer offspring than hosts that were not used for feeding. We found no effect of host feeding on brood size (Table 3). Ueno's (1997) study, however, differs significantly from ours in several aspects. In his study, females fed on a host (for an unspecified amount of time) after an egg had been laid in it by a different female. Egg killing by the second female is a well-reported phenomenon (Arakawa 1987; Strand & Godfray 1989; Antolin et al. 1995), which cannot be discarded as an explanation for the decrease in offspring numbers. Furthermore, because the ovipositing and host-feeding females belonged to the same strain, Ueno could not determine to which of the females the offspring belonged. Thus, although Ueno's (1997) results also point to a cost of host feeding, they should be interpreted with caution.

In our study, we used host-feeding time as an approximation to the amount of nutrients extracted from the host. Further work is required that correlates directly the quantity and quality of nutrients extracted during a host-feeding bout with appropriate estimates of the resulting costs and benefits. Experimental extraction of a known amount of fluids from hosts before oviposition and the parallel injection of the same amount of host fluids into females (see e.g. Giron et al. 2002) would allow an accurate quantification of the costs and benefits associated with extracting a particular volume of nutrients. The shape of the cost and benefit function is also likely to depend on the quality of the nutrients extracted. Parasitoids that practise a less destructive type of host feeding (such as strict haemolymph feeders, Giron et al. 2002) will probably experience lower costs of host feeding than those that consume a large amount of tissues from the host.

To conclude, most models of parasitoid behaviour developed so far have predicted female decisions based on an all-or-nothing rule: a host used for feeding renders zero fitness in terms of current reproduction. However, we have shown that in *N. vitripennis* the costs of host feeding are not fixed but seem to be related to the amount of nutrients extracted from the host. In parasitoids that practise concurrent host feeding, the amount of host tissues or fluids ingested thus mediates directly the relation between the costs (decrease in female offspring size) and benefits (increase in egg production) of host feeding. The key decision for females balancing the trade-off between current and future reproduction will therefore not be when to host feed, as in classic feeding models (Mangel & Clark 1988; Mangel 1989a; Houston et al. 1992; Chan & Godfray 1993; Clark 1993; Collier et al. 1994; Heimpel et al. 1994; Collier 1995a) but how much to feed.

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