The relationship between host selection behaviour and offspring fitness in a koinobiont parasitoid

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Abstract. 1. When host quality varies, optimal foraging theory assumes that parasitic wasps select hosts in a manner that increases their individual fitness. In koinobiont parasitoids, where the hosts continue developing for a certain period of time after parasitisation, host selection may not reflect current host quality but may be based on an assessment of future growth rates and resources available for the developing larvae.

2. When presented with hosts of uniform quality, the koinobiont parasitoid *Leptomastix dactylopii* exhibits a characteristic host-selection behaviour: some hosts are accepted for oviposition on first encounter, while others are rejected several times before an egg is laid in them, a behaviour that is commonly associated with a changing host acceptance threshold during the course of a foraging bout.

3. The fitness of the offspring that emerged from hosts accepted immediately upon encounter was compared with the fitness of offspring emerged from hosts rejected several times before being accepted for oviposition.

4. The pattern of host acceptance and rejection was not related to any of the measured fitness parameters of the offspring emerging from these hosts (development time, size at emergence, sex ratio at emergence, and female offspring egg load).

5. While complex *post facto* adaptive explanations can be devised to explain the nature of such a time and energy consuming host selection process, it is suggested that physiological constraints on egg production or oviposition may provide an alternative, purely mechanistic, explanation for the results obtained.

Key words. Egg load, host quality, host selection, koinobiont parasitoids, offspring fitness.

Introduction

A classic problem in parasitoid behavioural ecology is the prediction of which hosts a female should attack and which it should ignore. Under a rate-maximisation criterion, the insect's decision should be based on whether quantity and quality of the nutrients that the host will provide outweigh the costs (i.e. time and energy expenditure) involved in handling it and ovipositing on it. In the simplest scenario, if the balance is positive the host will be accepted, if negative it will be rejected. Traditional foraging theory thus assumes implicitly that the host selection process reflects differences in the quality of the hosts present in the patch (Charnov & Stephens, 1988). Experimental evidence has shown, however, that in most cases

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host types above and below certain thresholds of acceptability (specific to each parasitoid) are not always accepted or always rejected (the zero-one rule), as predicted by classic average-rate maximisation models, but that their acceptability is also dependent on the physiological and informational state of the foraging insect (van Alphen & Vet, 1986; Collins & Dixon, 1986; Visser, 1995). Thus, the decisions taken by a parasitoid are dynamic, even at the time scale of a single foraging bout, depending both on the female's previous experience and hence perception of the environment, and on the predictions that the female has about its future, based on its current time and energy budget. Dynamic state variable models developed to predict the decisions of parasitoids exhibiting such *partial preferences* have given special attention to how patch depletion and changing egg reserves influence decisions (Iwasa *et al.*, 1984; Mangel, 1989a,b; Visser, 1991).

A behaviour often associated with the presence of a changing host-acceptance threshold in parasitoids is the initial rejection

of some hosts that will later be accepted for oviposition even within the same foraging bout (Visser, 1995). Hosts initially rejected are assumed to be of lower quality than those accepted immediately upon encounter. Testing such preference hierarchies, however, requires verification of the relative quality of the hosts present in the patch. For idiobiont parasitoids, in which the host stops growing after parasitisation and thus represents a fixed amount of resources, host quality can safely be associated with size, with larger hosts assumed to be of higher quality because they contain more resources for the developing larvae (Charnov *et al.*, 1981). Host age (King, 1990; Sequeira & Mackauer, 1992) and nutritional state (Boulétreau, 1986; Kouamé & Mackauer, 1991) have also been shown to influence parasitoid fitness. In koinobiont parasitoids, however, host quality is difficult to measure objectively as the hosts continue to grow and develop for some time after parasitisation (Askew & Shaw, 1986). The high rejection levels of apparently suitable hosts observed in certain koinobiont parasitoid species (Nell & van Lenteren, 1982; de Jong & van Alphen, 1989; Rivero-Lynch, 1994; Cadée & van Alphen, 1997) suggest that host choice may not reflect current host quality but may be based on an assessment of future growth rates and resources available for the developing larvae (Kouamé & Mackauer, 1991).

Leptomastix dactylopii Howard (Hymenoptera: Encyrtidae) is a koinobiont parasitoid that attacks third-instar and adult *Planococcus citri* Risso (Hemiptera: Pseudococcidae). When presented with a range of host sizes, the females have been shown to select the larger hosts for oviposition (de Jong & van Alphen, 1989). Females, however, exhibit a characteristic host-selection pattern when presented with hosts that appear to the experimenter to be of similar size, age, and nutritional status. While some of the hosts are accepted on first encounter, others are rejected one or more times before an egg is finally laid in them. Because there is no evidence that current quality varies among hosts, it is proposed that the observed behaviour is based on differences in female assessment of future potential of these hosts as a resource for their offspring. Females would thus accept immediately those hosts that with time would provide the best resources for the developing parasitoid while initially rejecting those of lower quality. The subsequent acceptance of the lower quality hosts would indicate a change in the future estimated fitness threshold during the course of the foraging bout. The only objective measure of host quality in koinobiont parasitoids is to determine the fitness of the offspring that emerge from the different host types. In the work reported here, therefore, several fitness components of offspring are compared between those emerging from hosts accepted on first encounter and those that have been rejected once or more before being accepted for oviposition. The starting hypothesis was that there is a quantifiable relationship between host acceptance behaviour and offspring fitness. Alternative hypotheses for the characteristic pattern of host acceptance observed are discussed.

Materials and methods

Hosts of uniform quality for the experiments were obtained by transferring mealybug egg masses onto potato sprouts and ensuring that mealybug density was approximately constant among the different sprouts through regular removal of excess individuals. Host patches consisted of a 2.5-cm leaf disc of bean plant *Phaseolus vulgaris* placed, underside facing upwards, on top of an agar base at the bottom of a plastic Petri dish (10.5 cm diameter). Ten third-instar and pre-ovipositing female mealybugs from the same cohort and of uniform size (mean ± SE: 2.25 ± 0.02 mm) were placed on the leaf disc 24 h before the parasitoid was released onto the patch.

To obtain virgin female parasitoids of known age, mealybug mummies were collected from the culture and placed individually in small glass tubes (5 × 1 cm) with a drop of honey solution as food. On the day of emergence (day 1), 20 females were placed individually with two males in a small Petri dish (5 cm diameter) containing a drop of honey solution, and left for 48 h to ensure mating. On day 3, females were allowed to search and oviposit for 24 h on patches that were identical to those to be used in the experiments. This procedure ensured that, on the day of the experiment, females had ripe eggs and were motivated to search and oviposit on the experimental patch. The following day, females were removed and placed in a small glass tube with a source of honey solution for 24 h. This allowed the female to replenish eggs before being released onto the experimental patch. On day 5, the females were released individually onto the experimental patch and their behaviour was observed continuously for 1 h. Upon encounter, the female parasitoid antennates the mealybug. If the host is accepted for oviposition, the female will turn round and insert the ovipositor. The whole action of antennation, turning, and egg laying is very rapid, lasting only a few seconds. The result is a single egg, which is laid inside the body cavity but remains attached to the derm by a long stalk that protrudes from the body of the host. This stalk can be observed easily under a binocular microscope by gently scraping off the white waxy coat that covers the mealybug body. A host is rejected when the female walks away from the host following antennation. The number of times that each female encountered and antennated each host before an egg was laid and the time at which each egg was laid were recorded using a hand-held Psion Organiser II (Model LZ64, Psion PKC, U.K.).

At the end of the experiment, females were measured (length of hind tibia) and dissected to count the number of eggs remaining in the ovarioles. Each parasitised host was transferred individually to an 8-cm diameter bean leaf disc placed over an agar base in a 9-cm diameter Petri dish. Hosts were left to emerge at 25 ± 2.5 °C, 70 ± 5% RH, and a LD 16 : 8 h photoperiod. The development time (to the nearest day), sex, and size of the emerged parasitoids were recorded. Female offspring were dissected and the number of eggs in the ovarioles counted. Hosts where no eggs where laid were discarded from the analysis.

The data were analysed with generalised linear modelling techniques (Aitkin *et al.*, 1989; Crawley, 1993) using GLIM (version 3.77, Numerical Algorithms Group, Oxford). A statistical model was built by fitting all explanatory variables and their interactions. The significance of an explanatory factor, in this case number of rejections before the host was accepted for oviposition, was assessed by deleting it from the

model and analysing the resulting change in deviance. The analysis was carried out using hosts as replicates and including the heterogeneity among females as an additional explanatory variable in the model. For this purpose, the main effect of female, and its surrogate variables, female size and egg load, as well as the interactions between these and other explanatory variables, were included in the statistical model. The choice of the appropriate error structure was made according to the nature of the response variable. The egg load of female offspring was analysed assuming Poisson errors. The appropriateness of this assumption was checked by comparing the residual deviance with the residual degrees of freedom after fitting the full model. The probabilities of the offspring emerging successfully and being male or female were assessed using binary errors, an abbreviated form of the binomial distribution in which the binomial denominator (i.e. the total sample from which each observation is drawn) is 1. With Poisson and binomial error distributions, the change in deviance attributable to a given factor is distributed approximately as χ^2. Offspring size was analysed using standard ANOVA once normal error variance was assessed.

Results

Of the total of 136 hosts parasitised by the 20 females, 83 (61%) adult parasitoids emerged. 6.8 ± 0.36 (mean $\pm$ SE) hosts were parasitised per female, and of these 4.14 ± 0.06 completed development and emerged successfully. The mean number of eggs left in the females' ovarioles at the end of the experiment was 14.20 ± 3.92. The pattern of host acceptance for oviposition is shown in Fig. 1. On average, females encountered each host twice (mean $\pm$ SE = 2.33 ± 0.23) before an egg was laid in it. The data, however, show an increasing trend with oviposition number. The first two hosts parasitised were uniformly accepted almost immediately upon encounter (i.e. not rejected) but further hosts were rejected up to an average of five times before an egg was laid in them. The time interval between consecutive ovipositions increased as ovipositions took place (Fig. 2), reaching an asymptote at 9–11 min from the fifth oviposition onwards.

Both the number of encounters with a host before an egg was laid in it and the interval between subsequent ovipositions were correlated significantly with the order in which that host was parasitised ($F_{8,133} = 16.62$, $P < 0.001$ and $F_{8,133} = 4.60$, $P < 0.001$ respectively; for number of encounters, the response variable was log transformed to correct the fan-shaped residuals obtained from fitting the untransformed variable), and explained a relatively high proportion of the variance (8.81% and 21.93% respectively). Female egg load did not have a significant effect on either the number of pre-oviposition rejections ($F_{1,126} = 0.06$, NS), or the time interval between ovipositions ($F_{1,126} = 2.33$, NS). Female size was relatively constant among females (mean $\pm$ SE = 1.14 ± 0.03) and did not have a significant effect on pre-oviposition rejection ($F_{1,126} = 2.51$, NS).

In order to test whether host rejections correlated with offspring fitness, hosts were divided into those that had been accepted immediately upon encounter and those that had been rejected once or more before an egg was laid in them. To allow for discrimination errors (Krebs & McCleery, 1984), the latter group was further divided into hosts that had been rejected once or twice before oviposition and hosts that had been rejected three times or more (maximum = 18 times) before being accepted (Table 1).

The pattern of host acceptance and rejection was not correlated with any of the offspring fitness parameters measured. Acceptance on first or subsequent encounters did not affect whether the offspring developing inside the host would complete its development successfully ($\chi^2_2 = 0.02$, NS) or indeed the developmental time (males $F_{2,31} < 0.01$, females $F_{2,50} = 0.15$, NS) or the sex ($\chi^2_2 = 0.06$, NS) of the parasitoids that did emerge. Furthermore, neither offspring size (males $F_{2,30} = 1.37$, females $F_{2,50} = 0.08$, NS) nor female offspring egg load on emergence ($\chi^2_2 = 0.99$, NS) could be predicted by the pattern of host acceptance by the female. Although hosts were initially of the same size, parasitoid females achieved a significantly greater adult size (mean $\pm$ SE = 1.25 ± 0.03 mm) than males (mean $\pm$ SE = 1.15 ± 0.03, $F_{1,82} = 8.48$, $P < 0.05$).

Discussion

Host size is the most easily measured, and therefore the most common, estimate of host quality found in the literature. In parasitoids developing in hosts that continue to feed and grow after parasitisation, however, host quality may vary independently of host size or total biomass (Sequeira & Mackauer, 1992). In these cases, it has been suggested that female parasitoids may not select hosts based on size alone but may use other qualitative criteria, which remain largely unknown. Hosts in the present experiment were of identical size and developmental stage at oviposition but some were rejected several times before an egg was laid in them, a behaviour that has often been interpreted as a change in the host acceptance threshold during the course of the foraging bout. The high rejection levels of apparently suitable hosts has been observed previously in this (de Jong & van Alphen, 1989; Rivero-Lynch, 1994) and another related (Nell & van Lenteren, 1982; Cadée & van Alphen, 1997) koinobiont species and has raised the prospect that host selection behaviour may be based on female assessment of future potential of hosts as a resource for their offspring rather than on current host quality. If repeated rejections are an indication of the lower potential quality of the host, the fitness of the offspring emerging from these rejected hosts would be expected to be lower, as larval growth and development can be affected profoundly by host quality (Scriber & Slansky, 1981; Mackauer, 1986), or else that proportionally more males should be laid in these hosts (Charnov *et al.*, 1981). In the present study, however, the fitness of offspring that emerged from hosts rejected several times was not significantly different from that of offspring emerging from hosts accepted immediately upon encounter, leading to the conclusion that the characteristic pattern of host acceptance and rejection found in *L. dactylopii* is not the result of differences in host quality. Alternatively, hosts may not differ in fitness benefits for the offspring but in the costs that
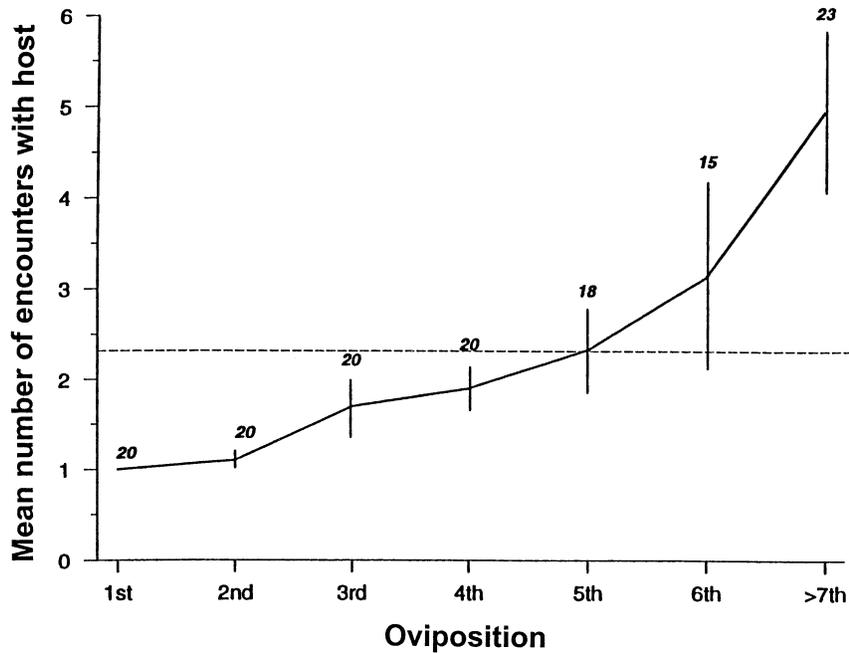
Fig. 1. Average number of encounters with hosts before an egg was laid in them. Hosts are numbered according to the order in which they were parasitised. The numbers above the standard error bars are the number of females. The dashed horizontal line represents the overall average number of encounters with hosts before oviposition occurred.
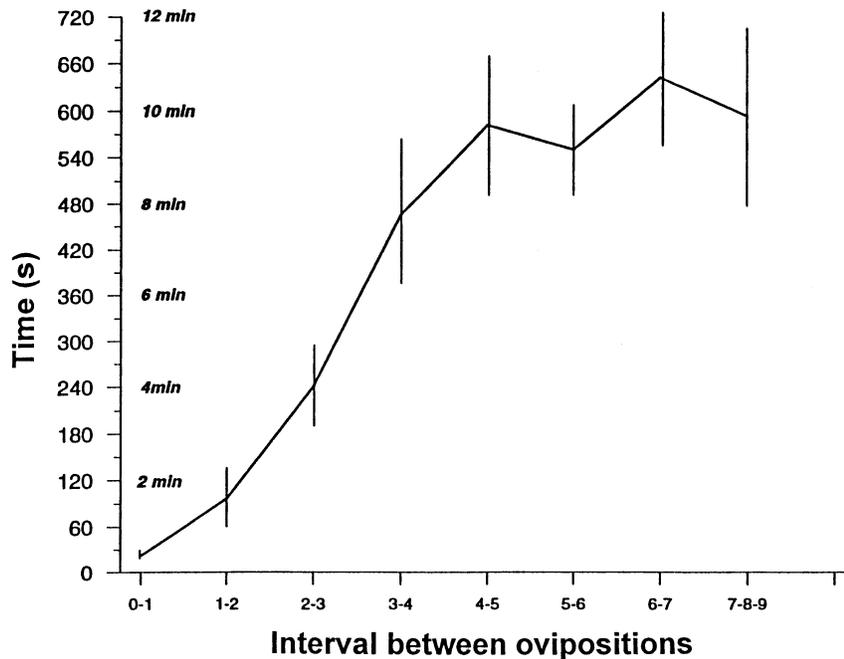

Fig. 2. Means and standard errors of the intervals between two consecutive ovipositions.

the female has to pay in order to lay an egg in them. When many *Callosobruchus chinensis* bruchids occur within an azuki bean, the bean is moistened and its tegument becomes softened. Virgin *Dinarmus basalis* females reduce the costs of oviposition, thereby expanding their lifespan, by laying eggs in these aggregated hosts (Nishimura, 1997). In the present system, where there are no physical barriers to oviposition, host-related differences in handling time could come about

Table 1. Number, sex ratio, mean developmental time, mean size, and mean egg load of the offspring that emerged from hosts accepted on first encounter (i.e. not rejected) or on second or successive encounters (i.e. rejected once or more).

	Number of host rejections		
	None	One or two	Three or more
Number (and percentage)	53 (61%)	16 (59%)	14 (61%)
of offspring emerged	($n = 87$)	($n = 27$)	($n = 23$)
Offspring sex ratio	39.6%	31.3%	42.9%
(% males)			
Male offspring			
(mean ± SE)			
Development time (days)	15.90 ± 0.15	16.00 ± 0.01	15.57 ± 0.20
Size (mm)	1.12 ± 0.04	1.25 ± 0.03	1.06 ± 0.04
	($n = 21$)	($n = 5$)	($n = 6$)
Female offspring			
(mean ± SE)	16.03 ± 0.10	16.00 ± 0.27	15.86 ± 0.40
Development time (days)	1.27 ± 0.04	1.21 ± 0.06	1.21 ± 0.08
Size (mm)	13.56 ± 1.42	11.33 ± 1.60	13.14 ± 3.44
Egg load	($n = 32$)	($n = 11$)	($n = 8$)

through differences in female size relative to host size. Between-female variation in size was, however, small and female size could not explain the results obtained.

There was therefore no evidence that hosts rejected several times for oviposition were of lower quality than those accepted on first encounter, and thus no ground for suggesting that females may be selecting hosts on the basis of their future potential as food for their offspring, or to reduce costs associated with oviposition. While several *post facto* adaptive explanations could be devised to explain the repeated rejection of apparently suitable hosts, there are inconsistencies that complicate the interpretation of the data. In synovigenic parasitoids such as *L. dactylopii* that have a limited number of mature eggs available at any one time, females are expected to become more selective as egg reserves become depleted. The increase in host rejection during the foraging bout may thus be interpreted as sampling the patch before oviposition decisions are taken, coupled with increased female selectivity associated with decreasing egg loads (Collins & Dixon, 1986). In this experiment, however, female egg load did not explain the pattern of acceptance and rejection of hosts. Furthermore, the acceptance towards the end of the foraging bout, when females have run out of about one-third of their available eggs, of hosts that had been rejected four or five times is difficult to explain in terms of increased female selectivity, unless patch depletion increases the value of the few remaining unparasitised hosts.

Physiological constraints in the egg-producing apparatus or in the ovipositing process could, on the other hand, provide a simple mechanistic explanation for the results obtained. Information relating to the role of ovarian dynamics on oviposition decisions is, however, vague. Current knowledge of the effect of egg load on behaviour in parasitoids is based on the assumption that all full-sized eggs lying at the bases of the ovarioles are mature and thus ready to be laid. Previous experiments with this (Rivero-Lynch, 1994) and other (Trudeau

& Gordon, 1989) species suggest, however, that factors such as ovulation or the rate of egg maturation may be more important in determining the rate of attacks than what is commonly measured as *egg load*. In the present experiment, the interval between consecutive ovipositions increased exponentially, levelling out at around 9–11 min from the fifth oviposition onwards (Fig. 2). Time wasted in host discrimination as the number of parasitised hosts increases cannot explain this result as the females handled on average less than one parasitised host between each oviposition (mean ± SE = 0.21 ± 0.06, ranging from 0.13 ± 0.09 hosts between the fifth and sixth oviposition to 0.40 ± 0.30 hosts between the second and third oviposition) and time invested in host discrimination is minimal (1–10 s; Rivero-Lynch, 1994). Such low encounter rates with parasitised hosts may be explained by the ability of this species to recognise parasitised hosts through olfactory stimuli alone (van Baaren & Nénon, 1996). Inter-oviposition times could therefore reflect at least partly differences in the maturation stages of the eggs lying at the bottom of the female's six ovarioles or in the time required to move the eggs from the lateral oviducts to the common oviduct and into the ovipositor (Quicke, 1997). Other factors essential for oviposition such as secretions from accessory glands may also set an upper limit to the number of eggs that can be laid per unit time. Similarly, because oviposition is likely to be a metabolically expensive endeavour, females may need to space oviposition events to rest the muscles or tissues associated with the reproductive tract or to replenish energy levels.

More work needs to be carried out on the physiology of egg production and oviposition in order to determine conclusively whether physiological constraints play a role in host selection behaviour in parasitoids. Host sampling during a *refractory phase* (*sensu* Mangel, 1993), when the female would be physiologically unable to lay eggs, may not be distinguishable from pre-attack rejection and may thus lead to erroneous

interpretations as to the adaptive nature of the behaviour. Such continued host searching and antennation may have obvious time-saving advantages for females attacking sessile hosts, particularly in environments that vary widely in quality. Only low host-searching and handling costs can, however, justify this continued search in preference to a sit-and-wait for the next egg to be ready behaviour once a suitable host is found.

In conclusion, while the existence of a changing acceptance threshold provides an attractive adaptive explanation for the host acceptance patterns observed during the foraging sequences of parasitoids searching in patches where hosts clearly vary in quality (Courtney *et al.*, 1989; Visser, 1991, 1995; Sirot *et al.*, 1997), problems arise when host quality is, effectively, unknown. In these cases, host quality should be assessed independently and not be inferred from the host selection behaviour of the female. There are indeed caveats associated with measuring fitness of offspring in the laboratory, and small fitness effects may be difficult to detect. Nevertheless, the results presented here suggest that the pattern of host acceptance of females may not depend exclusively on the acceptability of the hosts (Courtney *et al.*, 1989) but may be shaped partly by physiological constraints on the female.

Acknowledgements

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