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Oviposition behaviour, influence of experience on host size selection, and niche overlap of the solitary *Leptomastix epona* and the gregarious *Pseudaphycus flavidulus*, two endoparasitoids of the mealybug *Pseudococcus viburni*

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Abstract

Oviposition behaviour and host size selection of the solitary parasitoid *Leptomastix epona* (Walker) and the gregarious *Pseudaphycus flavidulus* (Brèthes) [both Hymenoptera: Encyrtidae] were examined on five size classes of the mealybug *Pseudococcus viburni* (Signoret) [Hemiptera: Pseudococcidae]. The host size classes mostly consisted of one stage (first, second, third instar nymph, young adult and preovipositing adult) and were presented together to wasps of either parasitoid species. Both parasitoid species locate the host by drumming the surface of the patch with the antennae. *Leptomastix epona* seems to use mainly the antennae to examine the host but *P. flavidulus* may accept or reject a host for oviposition after antennation or insertion of the ovipositor. *Leptomastix epona* attempts oviposition in all the host stages from second instar nymphs but *P. flavidulus* includes first instar. Both parasitoid species select mainly larger hosts (>1 mm, third instar nymphs) to oviposit but *P. flavidulus* is able to parasitize more second instar nymphs compared to *L. epona*. Female wasps of *L. epona* may host feed on small mealybugs (second and third instar nymphs) that they do not use for oviposition. Oviposition experience of either parasitoid species for 24 hours does not influence host size selection on patches with hosts of similar mixed sizes. Oviposition decisions are independent of the host sizes of the preceding ovipositions. Implications about stability of a single parasitoid – host system and the success of biological control of the mealybug were discussed in respect of the developmental refugia of the two parasitoid species. Niche overlap of the two parasitoid species was discussed with a view to giving an insight into a single or multiple introduction.

Introduction

Hymenopterous parasitoids have to find and accept a host to complete their reproductive cycle. Once a parasitoid has physically contacted a potential host, evaluation follows to determine whether the host is the appropriate species and growth stage to use for its offspring development (van Baaren & Nenon, 1996). Selection by one parasitoid between hosts of different age (stages) or of different species is defined as host selection.

Because the relative abundance of the most suitable stages may vary both spatially and temporally, parasitoids have evolved behavioural, ecological and physiological adaptations to discriminate among, and utilize their hosts (Nechols & Kikuchi, 1985). Host examination and attack may include different steps such as host encounter, antennation (drumming), probing, oviposition and marking (Van Driesche & Bellows, 1996) and different stimuli may be necessary to elicit this chain of behaviour. Thus parasitoids may use movements and vibrations by the host, chemical cues, both on the outside and inside of hosts, as well as physical features of the host such as size, shape and texture (Vinson, 1977; Van Driesche & Bellows, 1996).

Aspects of oviposition behaviour may be associated with an extreme degree of stereotype and tend to be expressed even in the absence of experience (Mowry et al., 1989; Papaj, 1993). However, host stage or host size selection decisions may be affected over the searching time by gaining experience or other learning-based changes in the parasitoid's nervous system, the 'stochastic variation' in encounter rate which is related to the perception of the density and quality of available hosts, and the egg load (Mackauer, 1990; Rosenheim, 1993). Hence, host selection in parasitoids can be a learned rather than being only an instinctive behaviour.

Papaj & Rausher (1983) have suggested that learning may influence host preferences by generating changes either in the rank order of preferences or in the degree of preference. Parasitoid learning demonstrates that experience sometimes reduces moment-to-moment variability in insect behaviour and makes behaviour more consistent (Papaj, 1993). Egg load and perceived host availability are likely to generate changes in the degree of preference but unlikely to generate changes in the rank order of preference. Changes in the rank order of preference after exposure to different host types may reliably indicate the effect of learning. However, the effects of egg load and perceived host availability should still be taken into account in order to evaluate the magnitude of the learning effect (Rosenheim, 1993).

Knowledge of host selection contributes to an understanding of the population dynamics of the host (pest) and the parasitoid species and it is important for the development and successful application of biological control and IPM programmes. In a single parasitoid - host system, non vulnerable classes of the host result in refugia which may contribute to population stability (Hassell & May, 1973) or instability (Kistler, 1985). The longer the refuge period the fewer the number of hosts that will be available to the parasitoid at any time inducing a slower rate of increase for the parasitoid and a greater stability for the parasitoid-host population (Hassell & May, 1973). Developmental refugia longer than the life span of the adult parasitoid may cause instability because intense parasitism can deplete all vulnerable hosts during the parasitoid life span creating asynchrony between the host and parasitoid life cycles and eventual extinction of the parasitoid (Kistler, 1985).

Host size selection may determine whether two monophagous parasitoids which share the same host species are able to coexist or one species will become extinct if they are released together (Kakehashi et al., 1984; Hochberg, 1996). The superior strategy (single or multiple introduction) depends on the niche width of each parasitoid and the degree of niche overlap between the parasitoids as well as other parameters such as the intrinsic rate of increase of the host and the searching efficiencies of the parasitoids which affect the effectiveness in biological control and the stability of the equilibrium of the three species (Kakehashi et al., 1984).

This study investigated the components of the oviposition behaviour of the parasitoids *Leptomastix epona* and *Pseudaphycus flavidulus* and examined host size selection and the effect of experience on host selection of *Pseudococcus viburni*.

Pseudococcus viburni is a world-wide distributed mealybug and important pest on agricultural and horticultural plants, field crops, ornamentals and in protected crops in Northern Europe (Williams, 1962; Panis, 1986; Gonzalez, 1991; Phillips & Sherk, 1991; Ben-Dov, 1994). *Leptomastix epona* and *P. flavidulus* are two parasitoid species which parasitize *P. viburni*. *Leptomastix epona* is a European species geographically distributed within the Palearctic region in Czechoslovakia, Denmark, Finland, Hungary, Poland, Russia, Spain, Sweden, United Kingdom, West Germany while *P. flavidulus* originates in the Neotropical region (Argentina and Chile) (J. Noyes, pers. comm.).

Materials and methods

Mass cultures. The culture of the mealybug *P. viburni* was established in the laboratory from individuals collected in the glasshouses at Imperial College at Wye. The primary mealybug cultures were maintained on sprouted potatoes of the variety 'Desiree' in plastic sandwich boxes ($17.5 \times 11.5 \times 5$ cm) with net covered openings for ventilation. They were kept in a rearing room at 26 ± 1 °C, 50 – 65 r.h., L16:D8 photoperiod and 3.3 W m^{-2} light intensity.

The parasitoids *L. epona* and *P. flavidulus* were reared on *P. viburni* feeding on sprouted potatoes, in sandwich boxes in a rearing room which was similar to the one used for the host but with constant light.

Experiments. The oviposition behaviour of the parasitoids *L. epona* and *P. flavidulus* on patches of different sized hosts of the mealybug *P. viburni* was studied under laboratory conditions at 23 ± 1 °C and artificial light (7 W m^{-2}).

The arena for the parasitoid was a 6 cm diameter Petri-dish where a piece (5.5 × 4.0–5.5 cm) of a *Passiflora coccinea* (Passifloraceae) leaf was placed (lower surface upwards) on a layer of 8 g l^{-1} Bacteriological agar (No.1, Oxoid Ltd.) which had been previously autoclaved. Individuals of the pest were transferred from the mass culture on the leaf discs of *P. coccinea* up to 24 hours before the experiment. The host patches consisted of mealybugs of five distinct size classes which comprised mostly one stage according to sampled sizes of mealybugs measured after moults: 0.3–0.5 mm (crawlers), 0.5–0.9 mm (second instar), 1–1.66 mm (third instar), 1.83–2.33 mm (young adult), 2.33–3.33 mm (preovipositing adult). Only female mealybugs were used apart from the two small size classes where males and females could not be distinguished. Four individuals from each class were placed in each Petri-dish, hence the host density was twenty mealybugs. Members of each class were put as a group in distinct positions around the main vein of the leaf. The positions of the groups were determined with randomization for each replication in order to ascertain that the order of encounters of the parasitoid was not affected by the position of the host. However, the distribution of the different sized mealybugs changed during the experiment because the mealybugs were moving.

Freshly emerged females of *L. epona* or *P. flavidulus* were used. To obtain such female wasps, mummified mealybugs were collected from the mass cultures, put into glass vials (length 5 cm, diameter 2.5 cm), then kept in the incubator at 26 ± 1 °C under constant light and were checked twice per day at the same time for emergence. Experimental females of *L. epona* were observed until mating took place after a male was introduced in the vial. Females of *P. flavidulus* which had emerged from different hosts that bore gregarious broods with at least one male sibling, were assumed to have mated with their brother. After mating, the female wasps of *L. epona* or *P. flavidulus* were fed with 50% honey solution for 24 hours and then released individually in the Petri-dishes to gain experience of oviposition on hosts for another 24 hours. The feeding and release process was repeated in Petri-dishes with the same host classes as experienced before.

At the beginning of each release, the behaviour of the parasitoid was observed with a stereo-microscope (× 10) and the encounters with the hosts, as well as the reaction of the mealybugs were recorded with the help of a digital clock. Components of the oviposition behaviour such as the start of an encounter, antennation, antennal rejection, antennal acceptance, probing, oviposition, rejection after ovipositor insertion, failure of insertion of the ovipositor, and host feeding were used as defined by de Jong & van Alphen (1989) or van Lenteren (1976) and were recorded.

An ‘encounter’ started when the parasitoid touched a mealybug with her antennae. However, to consider it as an encounter, the parasitoid should continue with the ‘antennation’ of the mealybug. When the parasitoid left a mealybug and walked away after antennation, this was defined as ‘antennal rejection’. If the parasitoid turned around and tried to insert the ovipositor into the mealybug after antennation, this would be classified as ‘antennal acceptance’. ‘Probing’ occurred when the ovipositor was inserted into the host and might be followed by oviposition or by rejection of the host.

In the case of *L. epona*, insertion of the ovipositor was classified as ‘oviposition’ only when it was followed by a pumping movement of the host’s abdomen. The criterion was based on the finding with *Planococcus citri* parasitized by *L. dactylopii*, that when pumping of the abdomen had been observed, almost always an egg could be found at dissection (de Jong & van Alphen, 1989). Insertion of the ovipositor which did not cause this reaction from the host was classified as ‘rejection’. In the case of *P. flavidulus*, rejection after insertion of the ovipositor of the host was recorded when the wasp retracted her ovipositor after a probe (van Lenteren, 1976).

Ovipositor insertions that could not find their target, either because the ovipositor slid down the host’s cuticle or because the host moved away, were recorded as ‘insertion failures’. Puncturing of the host with the ovipositor resulting in the parasitoid feeding on the haemolymph (‘host feeding’) was also classified as rejection.

The same criteria as de Jong & van Alphen (1989) were used to end an experiment, thus when three out of the four hosts in a certain size class had been parasitized, the parasitoid left the leaf or did not resume searching for 5 min.

Experimental design and statistical analysis. The sequence of ovipositions by 27 female wasps of *L. epona* and 21 female wasps of *P. flavidulus* on different sized hosts were recorded when parasitoids were inexperienced and again after they had gained experience. The parasitoids and the different sized hosts were considered as a ‘physical system’ and the ovipositions in one host after another as different ‘states’ of the system (Anton & Kolman, 1978). The evolution of such a system is a ‘stochastic process’, as a future state of the system cannot be predicted with certainty and it is only possible to estimate the probability of its occurrence under certain assumptions (Anton & Kolman, 1978).

The time-series of ovipositions in the different host size classes were then considered as an ‘embedded Markov chain’ (‘process’) which defines that the occurrence of an oviposition does not depend on the host size of the preceding ovipositions (first-order dependence) or it depends on the host size of the immediately preceding oviposition but not on the host sizes of the ovipositions before the immediately preceding one (second-order dependence). The term ‘embedded’ defines the transitional behaviour of the system over unequal intervals of time (equal being the common) (Taha, 1976). The transition sequences of the parasitoid’s ovipositions from one host size class to another were analysed with the χ^2 test for first- against second-order dependency in frequency of ovipositions (Anderson & Goodman, 1963; Haccu & Meelis, 1994).

Based on the result that the process of ovipositions in the different sized hosts was a first-order dependent Markov chain, the ‘steady state’ probabilities of ovipositions were estimated. The ‘steady-state’ probabilities are the long-run absolute probabilities which tend to be independent of the initial ones as the number of transitions increases (Taha, 1976; Haccu & Meelis, 1994). They were calculated by multiplying the matrix with the probabilities of transitions from one host size to another for the oviposition of all the experimental parasitoids, repeatedly by itself until it reached a matrix with the same numbers on its rows.

Results

The components of oviposition behaviour of the parasitoid *L. epona* and *P. flavidulus* when foraging on mealybugs of mixed sizes of the host *P. viburni* are presented in Figure 1. Crawlers were not encountered by *L. epona* but were encountered by *P. flavidulus*. Encounters of female *L. epona* with small hosts resulted in ovipositions (antennation acceptance) or host feeding (antennation rejection) while after the encounters with large hosts followed oviposition but not host feeding. Encounters of female *P. flavidulus* with hosts of all sizes resulted in oviposition after acceptance by antennation or insertion of the ovipositor.

When the frequencies of ovipositions of *L. epona* in mixed sized classes of hosts over 30 min of observation were analysed using the χ^2 test for first- against second-order dependency in frequency of acts, no sequential dependency was found in the ovipositions which occurred from one host size class to another (for the inexperienced wasps $\chi^2 = 26.228$, d.f. $= 26$, and for the experienced wasps $\chi^2 = 20.297$, d.f. $= 17$ at 0.05 level of significance; critical values in Haccou & Meelis, 1994). Table 1 shows that the rank order of the steady ‘state probabilities’ of ovipositions in hosts of different size was: size class 5 $\geq$ size class 3 $>$ size class 4 $>$ size class 2. The rank order was the same in inexperienced and experienced parasitoids of *L. epona*.

Analysis of the frequencies of ovipositions of *P. flavidulus* in mixed sized classes of hosts over 60 min, using the χ^2 test for first- against second-order dependency of acts showed no sequential dependency in the ovipositions which occurred in the different host sizes (for the inexperienced wasps $\chi^2 = 29.665$, d.f. $= 48$, and for the experienced wasps $\chi^2 = 12.54$, d.f. $= 19$ at 0.05 level of significance; critical values in Haccou & Meelis, 1994). The same analysis on the recorded frequencies of host acceptances at antennation of the experienced wasps, showed no sequential dependency in the acceptances of the different host sizes ($\chi^2 = 27.913$, d.f. $=31$ at 0.05 level of significance). Table 1 shows that the rank order of the steady ‘state probabilities’ of ovipositions in hosts of different size was: size class 5 $>$ size class 4 $>$ size class 3 $>$ size class 2. The rank order was the same in inexperienced and experienced parasitoids of *P. flavidulus*.

Discussion

Oviposition behaviour and host size selection of the parasitoids. L. epona and *P. flavidulus* locate the host by drumming the surface of the patch with the antennae (antennal search mode, Vet & van Alphen, 1985). Therefore, the parasitoids can encounter hosts only on the surface of the host’s food medium (van Alphen & Jervis, 1996). Furthermore, antennations and antennal rejections of the host by *L. epona* may be due to tactile stimuli (measuring the size of the host) or in response to contact chemicals elicited by host kairomones. The latter is common in the Hymenoptera (Vinson, 1976) while their antennae contain many receptors utilized

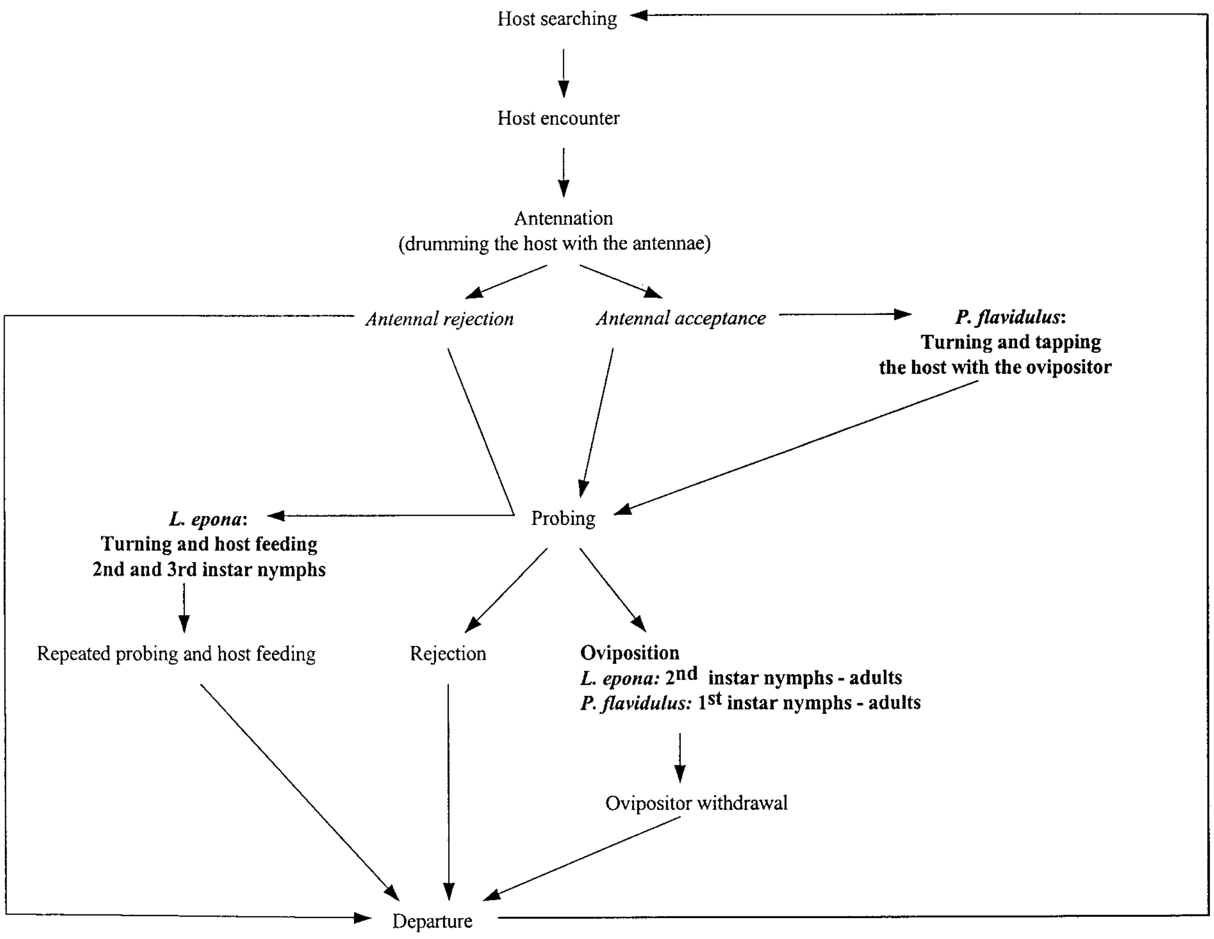

Figure 1. Components of oviposition behaviour of the parasitoids *Leptomastix epona* and *Pseudaphycus flavidulus* when foraging on mealybugs of mixed sizes of the host *Pseudococcus viburni* at 26 °C.

Table 1. Matrix with the 'steady state' probabilities of ovipositions in different host sizes for inexperienced and experienced wasps of the solitary parasitoid *Leptomastix epona* and the gregarious parasitoid *Pseudaphycus flavidulus*

	To host size class				
	1	2	3	4	5
From host size class: 2 or 3 or 4 or 5	Steady state probabilities for *L. epona*				
Inexperienced wasps	–	0.1122	0.2994	0.2245	0.3639
Experienced wasps	–	0.0076	0.3368	0.3270	0.3316
From host size class: 2 or 3 or 4 or 5	Steady state probabilities for *P. flavidulus*				
Inexperienced wasps	0.0225	0.1583	0.2291	0.2816	0.3086
Experienced wasps	–	0.0852	0.2550	0.2980	0.3619

in host detection (Slifer, 1969; Miller, 1972; Norton & Vinson, 1974).

Ovisposition behaviour and host size selection of the parasitoids. *Leptomastix epona* seems to use mainly the antennae to examine the host whereas *P. flavidulus* uses the antennae or the ovipositor (tapping the host with the ovipositor). Hence, acceptance or rejection of a host for oviposition may occur after antennation by *L. epona* and antennation or insertion of the ovipositor by *P. flavidulus*. Generally in the Hymenoptera, the ovipositor may be involved in host detection but is more important in host acceptance (Vinson, 1977).

Female wasps of *L. epona* may host feed on small mealybugs (second and third instar nymphs) that they do not use for oviposition. Jervis & Kidd (1986) have reviewed host feeding strategies in hymenopteran parasitoids, which may be of a biological significance from the point of view of the suppression of the pest.

In a system with a single wasp of *L. epona* and a patch of mixed sized hosts (0.33–3.33 mm) the crawlers are not encountered at all. The second instar nymphs are parasitized in smaller numbers than larger hosts (> 1 mm). The probability of oviposition by the parasitoid *L. epona* in mixed size classes of the host *P. viburni* tends to be zero in crawlers; it is very small for hosts from 0.5 to 0.9 mm and it is almost equally distributed among the larger host size classes. Hence, oviposition behaviour of *L. epona* reflects the range of the host sizes parasitized successfully, which is justified in terms of sex allocation and future fitness of the offspring (Karamaouna, 1999).

The probability of oviposition by the parasitoid *P. flavidulus* in host sizes between 1–3.33 mm increases with host size. *Pseudaphycus flavidulus* appears to oviposit with a small probability even in crawlers (0.3–0.5 mm) but parasitism is not successful, possibly because the resources are not adequate for parasitoid development (Karamaouna, 1999).

Both *L. epona* and *P. flavidulus* parasitize mainly larger hosts (> 1 mm) of the mealybug *P. viburni*. However, *P. flavidulus* seems to be more able to parasitize smaller hosts (0.5–0.9 mm), namely second instar nymphs, compared to *L. epona*. Williams & Hails (1994) concluded that biological control is most successful when there is little refuge from parasitism, a notion which favours *P. flavidulus* that faces a shorter developmental refuge period (eggs) than *L. epona* (eggs and crawlers). *Leptomastix epona* has a slightly lower intrinsic rate of increase (r_m) than *P. flavidulus* in small hosts (0.07 and 0.08 female eggs/female/egg, respectively) and in large hosts (0.12 and 0.13 female eggs/female/egg, respectively) (Karamaouna, 1999). However, destructive host feeding on small hosts by *L. epona*, which is not measured in the calculation of r_m, increases the parasitoid's efficiency to control smaller (younger) hosts.

Longer refuge to parasitism by *L. epona* may contribute to a greater stability of the parasitoid *L. epona* – host populations compared with the *P. flavidulus* – host populations. The duration of the egg incubation period of *P. affinis* is 12.5 days on average (unpublished data) whereas the life span of an average adult parasitoid of *L. epona* is 14–16 days in small or large hosts and the one of *P. flavidulus* is 7 days in small hosts to 11–12 days in large hosts at 26 °C (Karamaouna, 1999). The developmental duration of crawlers has to be added to the developmental refuge of *P. affinis* from *L. epona* in order to understand the synchronization of the parasitoid *L. epona* – host system. However, the relatively longer duration of the egg incubation refuge period of *P. affinis* compared with the life span of an average adult parasitoid of *P. flavidulus* may have a destabilising effect in the parasitoid *P. flavidulus* – host system when only small hosts are available.

A multiple introduction of *L. epona* and *P. flavidulus* in the same host habitat would make them competitors since the two parasitoids exploit size ranges of hosts which overlap greatly. Niche overlap model (Kakehashi et al., 1984) predicts that single introduction is a superior strategy than multiple introduction if the niches of the two parasitoids overlap to a great extent. However, intrinsic rate of increase of the host and the searching efficiencies of the parasitoids influence the result. Since *L. epona* attacks a fraction of hosts that *P. flavidulus* attacks, a single introduction of *P. flavidulus* will be favourable if the searching efficiency of *L. epona* is worse or not so different than the searching efficiency of *P. flavidulus*. A multiple introduction of *L. epona* and *P. flavidulus* will be a sound strategy if the searching efficiency of *L. epona* is better than the searching efficiency of *P. flavidulus*. Furthermore, interactions of other factors such as intra- and inter-host discrimination or multiparasitism, external contest and intrinsic competition between the parasitoids should be considered. Lastly, female biased sex ratios of *P. flavidulus* in small hosts would favour the population built up of the parasitoid against *L. epona* (Karamaouna, 1999).

A possible niche segregation between the parasitoid species when searching together, in a way that *P. flavidulus* would restrict itself to smaller hosts and *L.*

epona to larger hosts, could also be investigated (May & Hassell, 1981).

Influence of experience on host size selection by the parasitoids. There is no evidence that a specific host size selection by the parasitoids *L. epona* or *P. flavidulus* in a system with a single wasp and mixed sized hosts presented simultaneously depends on the host sizes in which the wasp had oviposited before the selection. Moreover, the 'lack of memory' characteristic of a first-order Markov chain in host selection by *L. epona* or *P. flavidulus* implies that the probability of any particular future oviposition is not influenced by additional knowledge concerning the host sizes of past ovipositions by the parasitoid. Consequently, host size selection is an instinctive rather than a learned behaviour.

Experience of oviposition by *L. epona* and *P. flavidulus* in patches of different sized hosts does not influence host preference since the rank order of the host size classes according to the probability of oviposition by the parasitoids, did not change after wasps had gained oviposition experience. However, the degree of preference may vary. Probabilities of ovipositions by female parasitoids of *L. epona* were more equally distributed among the host size classes (1–3.33 mm) and probabilities of oviposition in larger hosts by female *P. flavidulus* were higher after the wasps had gained experience of oviposition. These variations in the degree of preference may be due to the perceived host availability or the egg load. Parasitoids may select the resource types that are available in the local area or during the given time period, so that they exploit hosts better. In the case of *P. flavidulus*, a heavy egg load may be responsible for the parasitoid ovipositions in larger hosts as they support the development of more offspring.

Oviposition sequence of the parasitoids *L. epona* and *P. flavidulus* in hosts of different sizes in a patch is random, e.g. female parasitoids do not exploit larger hosts that increase the fitness of the offspring per host and then deposit eggs in hosts of lower quality. However, parasitoid preference towards the most suitable hosts is a fixed characteristic. The possibility that the parasitoid ovipositions on different sized hosts are associated with the parasitoid fitness per patch could be further investigated.

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