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Phoridae (Diptera) parasitizing *Coccinella septempunctata* (Coleoptera: Coccinellidae) select older prepupal hosts

GREGORY D.D. HURST*, FIONA K. McMEECHAN & MICHAEL E.N. MAJERUS

Department of Genetics, Downing Street, Cambridge CB2 3EH, UK

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Abstract. Phorids parasitizing *Coccinella septempunctata*, the seven spot ladybird, attend host prepupae and parasitize them at the point of ecdysis to the pupal stage. In this system, oviposition rates would be maximized through the choice of older pre-pupal hosts in preference to young ones. Field study revealed that old pre-pupal hosts were indeed more likely to be attended by phorids than young pre-pupae. We tested the hypothesis that this was due to a preference by simultaneously offering phorids an old and a young prepupal host in a choice test. The results suggest that phorids do indeed distinguish between host prepupae on the basis of age, choosing the older prepupa.

Introduction

Parasitoids face a world containing a variety of potential hosts in which to oviposit. Within this world, natural selection will favour (within the constraints of a time budget) individuals that distinguish between hosts, selecting the most suitable for oviposition. Empirical studies have shown an ability to differentiate between hosts of differing suitability for larval development, be this between different species of host (e.g. Kraaijeveld et al., 1995), between different developmental stages of the same host species (e.g. Luck et al., 1982), or between hosts differing in their status with respect to previous parasitization (e.g. Pijls et al., 1995). Further, parasitoids also exhibit adaptive choices between hosts within a particular life stage of their host species. *Asobara tabida*, for instance, selects early second instar *D. melanogaster* larvae in preference to late second instars, reducing the probability of encapsulation by the host (van Alphen & Drijver, 1982).

Parasitoids may also show preferences for host stages which maximize the rate of parasitization they achieve, rather than the quality of the hosts obtained. Van Alphen (1980) suggests the example of *Tetrastichus asparagi*, which preferentially oviposits in eggs rather than larvae, the larvae being suitable hosts for parasitoid development, but difficult to subdue. There are, however, fewer records for this type of preference, compared to those based on host suitability for larval development. One possible case is presented by the phorids *Phalacrotophora berolinensis* and *P. fasciata* (Diptera: Phoridae), which parasitize ladybird pupae (Coleoptera: Coccinellidae) (Klausnitzer, 1967). Parasitization by phorids is most successful if performed during or soon after the final larval ecdysis (Disney et al., 1994). Phorids therefore attend ladybird prepupae (larvae that have attached by anal cremaster and curled into the pupal position, prior to ecdysis to the pupa), waiting for them to ecdyse. If phorids are not egg limited, then their rate of parasitization would be maximized by the selection of older prepupae in preference to younger ones when presented with a choice between old and young prepupae.

In this paper we investigate this hypothesis, testing two of its predictions. First, we test whether older prepupae in the field are more likely to bear phorids than young ones. Such an observation is a necessary requirement of the hypothesis, but not sufficient evidence for acceptance of it; the observation is also compatible with a model where phorids select hosts randomly and thus build up to higher numbers on old

* Current address for correspondence: Department of Biology, University College London, 4 Stephenson Way, London NW1 2HE, UK; e-mail: g.hurst@galton.ucl.ac.uk.

prepupae, merely because they have been present for longer. The second prediction we tested is more discriminatory. This is that in a choice test, phorids should prefer old prepupae over young.

Field observations

Method

Prepupae of *Coccinella septempunctata* on *Urtica dioica* at Juniper Hall, Surrey UK (Grid Ref. TQ 174 524) were tagged during the evening of 22.vi.1995. The next morning, the presence or absence of phorids on these individuals was recorded, and the developmental stage of the individual noted (i.e. whether it had pupated). The individuals were surveyed again after 12 h, and the developmental stage of the individuals was noted.

Results

Fifty eight *C. septempunctata* prepupae were recorded on the morning of 23.vi.95. Ten of these carried phorids, and 48 did not. By the evening, nine of the ten individuals which carried phorids had ecdysed to the pupal stage. By this same time, fourteen of the 48 *C. septempunctata* individuals which did not bear phorids had ecdysed to this stage. There is a significant association between the possession of phorids in the morning and ecdysis to the pupal stage by evening. A greater proportion of *C. septempunctata* individuals bearing phorids ecdysed to the pupal stage during these 12 h than *C. septempunctata* individuals that did not bear phorids ($\chi^2 = 12.9$; 1 d.f.; $P < 0.001$).

Choice experiments

Method

Phorids were collected from host pupae in the field, brought into the laboratory, and stored in a cool place (15°C) for at least three hours, with an old pupa (more than two days from ecdysis) being provided to allow the phorids to feed (see Disney et al., 1994). Fourth instar *C. septempunctata* larvae were also brought into the laboratory from the field, and placed in 9 cm diameter petri dishes lined with paper. These were given aphids, and allowed to attach (become prepupae). When they had attached to the paper and entered the prepupal stage, the paper bearing the prepupa was cut out, and the time at which the individual entered the stage noted.

The choice test was performed in a well-lit laboratory in transparent boxes 25 cm × 15 cm × 15 cm. An "old" ladybird prepupa (more than 12 h elapsed since entering this stage) was placed at one end of the box, with a "young" prepupa (2–5 h after entering the stage) at the other end. The box was kept at constant orientation with respect to the environment, and the end at which young and old prepupa were placed was randomized, and was blind with respect to the observer. Phorids collected from a single host prepupa in the wild (groups containing one female, and either no, one or two males) were then placed into the box between the two prepupae, using carbon dioxide anaesthetic. The movement of the female phorid with respect to the prepupae was then observed over a period of one hour, or until she settled upon one of the prepupae. Settling was defined as occurring when an individual was positioned on a prepupa for more than five minutes. Within this definition, settling is equivalent to host choice for parasitism; observation shows that once this period has been reached, the phorid will remain on the prepupa until ecdysis unless physically disturbed. The choice experiment was repeated 30 times, over a period of 48 h, each group of phorid individuals being tested just once.

Results

Settling did not occur in the time span of the experiment in nine of the 30 trials. In the remaining 21 replicates, the female phorid settled upon the older prepupa on 17 occasions, and on the younger prepupa on 4 occasions. Where a choice was made, there was a significant preference for alighting on the older prepupa (Binomial test against no preference: $P < 0.01$).

Discussion

Phorids are found more frequently on old than young prepupae in the field. Laboratory experiments provide evidence that parasitoids distinguish between old and young prepupal hosts, preferring older hosts

to younger ones. This behaviour minimizes waiting time on the host and thus maximizes the rate at which hosts are located. If the phorid is not egg limited, then this behaviour will clearly maximize the rate at which eggs are laid in hosts. It will also minimize the time spent by the phorid on top of a prepupa, an exposed position that might be more dangerous to a phorid than other sites.

It is not known how the phorids distinguish between young and old prepupae, but it is likely that volatile chemicals emitted by the prepupae are used as a cue. The use of volatile host chemicals (kairomones) in host location has often been recorded for hymenopteran parasitoids and their use here is suggested in the host seeking behaviour of the phorid. In the choice test, female phorids were observed to sense the air with their antennae, and then move in a straight line to their host. However, whether this use of kairomones to detect hosts is also used to assess host suitability is unclear. Our observations included very few examples of phorids leaving the host upon which they had settled; the preference reflects the initial movement rather than rejection of unsuitable hosts following attraction to them.

The efficiency of the phorid in locating older prepupae may in part explain the high rates of parasitization observed in the field. During this experiment, collections of pupae from the field were made, and the number of pupae from which phorids emerged were scored. Parasitization rates on *C. septempunctata* exceeded 80% during the period of study.

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