Eur. J. Entomol. **95**: 571–579, 1998
ISSN 1210-5759

Differential parasitisation of adult and pre-imaginal *Coccinella septempunctata* (Coleoptera: Coccinellidae) by *Dinocampus coccinellae* (Hymenoptera: Braconidae)

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Braconidae, Coccinellidae, *Dinocampus coccinellae*, *Coccinella septempunctata*, host suitability, host recognition, host instar choice

Abstract. The parasitoid wasp *Dinocampus coccinellae* has been reported to parasitise adult, pupal and larval coccinellids. Field samples of larvae and pupae of *Coccinella septempunctata*, collected over 13 years in Britain, have failed to reveal any infected pre-imaginal individuals. The parasitisation rates of *D. coccinellae* into pre-imaginal and adult *C. septempunctata* were assessed in both choice and no-choice tests. Observations and test results revealed that British *D. coccinellae* have a strong preference to oviposit in adult coccinellids rather than larvae or pupae. This preference decreases as wasps age if denied oviposition opportunities.

INTRODUCTION

The wasp *Dinocampus coccinellae* (Schrank) exclusively parasitises coccinellids of the sub-family Coccinellinae (Ceryngier & Hodek, 1996). It is a solitary endoparasite, utilising mainly adult coccinellids (Ceryngier & Hodek, 1996). However, there are some reports of it ovipositing in pre-imaginal hosts, particularly when adult hosts are scarce (Smith, 1960; Maeta, 1969; David & Wilde, 1973; Filatova, 1974; Semyanov, 1978; Kadono-Okuda et al., 1995), in contrast to most members of its sub-family, the Euphorinae.

In Britain, the most common host of *D. coccinellae* is *Coccinella septempunctata* L. Although most authors report that *D. coccinellae* prevalence is greatest in adult coccinellids and host suitability is greater for adult than pre-imaginal coccinellids (e.g. David & Wilde, 1973; Obrycki et al., 1985), Sunderland (1978) reports that 29% of "old" larvae, 92% of pupae and 54% of adult *C. septempunctata* were parasitised in England in 1978. Yet, during 13 years (1984–1996) of work on coccinellids, involving the collection of many samples of larval, pupal and adult *C. septempunctata*, *D. coccinellae* has only been recovered from beetles collected as adults. (There is one unconfirmed report of *D. coccinellae* emerging from an adult *C. septempunctata* collected as a larva at Esher Common, Surrey, in July 1995 (Sloggett, pers. comm.). The mean proportion successfully parasitised, i.e. from which an adult wasp emerged, was 6.07% (n = 19,874), across all locations and seasons. No *D. coccinellae* emerged from individuals collected in the 2nd larval instar (n = 894), 3rd instar (n = 1,211), 4th instar (n = 1,532), or from those collected as pupae (n = 2980), returned to the laboratory and retained, at approximately 21°C, until at least 35 days

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after the adult beetles had emerged. This period should be sufficient to allow full development of *D. coccinellae* larvae at this temperature (Wright & Laing, 1978). Given the lack of *D. coccinellae* in these large pre-imaginal samples, and the exceptionally high prevalence of *D. coccinellae* in pre-imaginal *C. septempunctata* in Sunderland's data, the question arises as to whether *D. coccinellae* will parasitize pre-imaginal stages of *C. septempunctata* in Britain, except in extraordinary circumstances.

We here describe a series of experiments to address this question, with pre-imaginal stages of *C. septempunctata* being offered to *D. coccinellae*, either in choice tests with adult beetles, or in isolation.

MATERIAL AND METHODS

Stocks

Initial observations were conducted at the Scottish Crop Research Institute (SCRI), Invergowrie, Dundee, with formal choice and no-choice tests being carried out at the Department of Genetics Field Station (DGFS), Cambridge. Wasps were obtained by collecting samples of *C. septempunctata* in the Dundee and Cambridge areas, and feeding the ladybirds on *Acyrthosiphon pisum* (Harris) to allow wasp larvae to develop and emerge. On eclosion, wasps were kept in 9 cm Petri-dishes, with time and date of eclosion recorded, and fed on honey-water until used in tests.

Larval and pupal *C. septempunctata* used in the experiments were F_1 progeny of wild collected adults. Adults used at DGFS were also laboratory-bred F_1 progeny from wild collected adults. These adults were fed for 28 days on *A. pisum*, and were then overwintered in an unheated insectary. In the spring they were brought into the lab where they were fed *A. pisum* for between 14 and 21 days before tests. Adults used at SCRI were wild collected adults that had overwintered naturally, and had been kept in captivity at 20°C for over 45 days prior to use, to ensure that they did not contain developing parasitoids.

Initial observations

The reactions of wasps to different coccinellid stages were initially monitored by placing a single *D. coccinellae* female in a 9 cm Petri-dish containing five adults, or five 4th instar larvae, or five 2nd instar larvae of *C. septempunctata*, with a quantity of *A. pisum* as food for the coccinellids. Each stage was tested twice with different wasps. Observations were made continuously over 8 h, the wasp then being left in the dish for a further 16 h before removal. Coccinellid larvae were then reared to adulthood. Adults were subsequently dissected to assess parasitisation status.

Choice and no-choice tests

All tests were conducted at 21 ± 2°C with a 16L : 8D regime.

Choice between pre-imaginal and adult stages

A single individual of *D. coccinellae* was placed in a 9 cm Petri-dish with one immature (2nd, 3rd, or 4th instar larva or pupa) and one adult *C. septempunctata*, and approximately 20 *A. pisum*. A five-minute settling period was allowed. Thereafter, the Petri-dish was kept under observation for 60 min. All interactions between the wasp and the beetles were recorded. Behaviours observed were categorised (after Richerson & DeLoach, 1972) as: pursuance and investigation of host (PI), ovipositional stance (OS) (standing on mid and hind legs only with abdomen curled down and forward so that her ovipositor is held forward between her legs extending in front of her head), and ovipositional attack (OA) (jabbing the ovipositor into a host). Each pre-imaginal stage was tested against adults in 20 replicates. Wasps were used in tests between 24 and 48 h after eclosion. Because wasps have been noted to be more likely to detect mobile rather than immobile potential hosts (Balduf, 1926), larvae used had recently eclosed, and larvae and adults were starved for 6 h before the experiment, to reduce the chance of potential hosts remaining immobile throughout the tests. Pre-imaginal individuals and adults were dissected, under a dissecting microscope, within 72 h following the experiment to determine whether they had been parasitised. The thoracic and abdominal regions of dissected beetles were minutely examined and the number of individuals which contained parasitoid eggs and the number of eggs in each were recorded.

The number of interactions of the wasps with adult and pre-imaginal coccinellids were compared over all replicates using a Mann-Whitney test adjusted for ties.

Reactions of young and old wasps to pre-imaginal and adult host stages

The possibility that female *D. coccinellae* will oviposit more freely in pre-imaginal coccinellids if more suitable hosts (i.e. adult coccinellids) are not, and have not been, available previously, was investigated by two sets of no-choice tests. A single individual of *D. coccinellae*, that had eclosed 24–48 h previously (set 1), or 168–216 h previously (set 2), was placed in a 9 cm diameter Petri-dish with five coccinellids of a particular life-history stage (2nd, 3rd, 4th instar larvae, pupae, adults). Wasps used had been kept, at 21°C, and isolated from coccinellids since eclosion. Larval and adult coccinellids were supplied with an excess of *A. pisum*, and a small pad of cotton-wool soaked in honey-water was placed in the dish as food for the wasp. Monitoring of the interactions between the wasp and the coccinellids followed the same procedure as in the choice preference tests. Thereafter, the wasps were left in the Petri-dishes with the coccinellids for a further 23 h, and were then removed. For each coccinellid stage, the test was replicated five times. Coccinellid parasitisation status was assessed as for the choice tests.

Suitability of pre-imaginal and adult hosts

Because parasitisation was detected by dissection in both the choice and no-choice tests, full development of parasitoids was not observed in these tests. To investigate whether the parasitoid eggs deposited in pre-imaginal host stages could successfully develop into adults and, if so, to compare their rate of successful development with the rate for eggs deposited in adult hosts, an additional set of no-choice tests was run using 7–8 day old *D. coccinellae* with 4th instar larvae and adult hosts. The test protocol was as described above for the no-choice tests, with the exceptions that the wasps were left with the coccinellids for 48 h, and the larval and adult coccinellids were fed an excess of *A. pisum* following the tests, until a parasitoid larva emerged to pupate, or until 50 days after the test, or 50 days after eclosion, which ever was longer. This period substantially exceeds the time necessary for full egg and larval development of *D. coccinellae* at 20°C (Wright & Laing, 1978; Obrycki & Tauber, 1978; Obrycki et al., 1985). Only if adults died within this period were they dissected to assess parasitoid infection status. The tests were carried out on 20 adult and 20 4th instar larvae.

RESULTS

Initial observations

The reaction of wasps to adult *C. septempunctata* was to investigate and oviposit in them readily. Reaction to 4th instar larvae was much less positive. Wasps tended to ignore the larvae unless they moved, confirming that parasitoids detect potential hosts mainly by sight when they move, as noted by Balduf (1926). Once detected, 4th instar larvae were investigated, largely by circling and antennal stroking, but in no case was oviposition observed. Second instar larvae were almost totally ignored, the wasps interacting more with the aphids which were as large or larger than the coccinellid larvae.

On dissection, all coccinellids offered to wasps as adults were found to be infected. Four of these adults contained more than one *D. coccinellae* egg (one had 20, one had seven and two had two), the other six containing a single egg. None of the coccinellids offered as larvae were parasitised.

Choice between pre-imaginal and adult stages

The total, mean per replicate, median and range for each type of interaction observed (PI, OS and OA) with the pre-imaginal stage and adult in each test type, are given in Table 1. The number of adult individuals parasitised in each test, and the number of parasitoid eggs recorded are given in Table 2. No pre-imaginal individual was found to have been parasitised.

TABLE 1. Summary data of number of interactions of *D. coccinellae* with pre-imaginal and adult *C. septempunctata* offered in choice tests. Totals for each type of interaction (PI – pursuance/investigate; OS – oviposition stance; OA – oviposition attack) are given for the 20 replicates, with the mean, median and range of observed interactions per replicate, also given.

	Pre-imaginal stage			Adult		
	PI	OS	OA	PI	OS	OA
2nd inst. vs adult						
total	51	13	0	173	114	74
mean	2.55	0.65		8.65	5.70	3.7
median	2	0		7.5	5	3
range	0–8	0–3	0	1–17	0–12	0–9
3rd inst. vs adult						
total	39	15	1	155	93	61
mean	1.950	0.75	0.05	7.75	4.65	3.05
median	1.5	0	0	7	4	2
range	0–6	0–3	0–1	1–19	1–14	0–10
4th inst. vs adult						
total	64	26	7	175	108	76
mean	3.2	1.3	0.35	8.75	5.4	3.8
median	2	1	0	8	5	3
range	0–9	0–5	0–2	1–23	0–18	0–13
Pupa vs adult						
total	23	3	0	182	116	83
mean	1.15	0.15		9.10	5.80	4.15
median	0.5	0		8.5	5.5	4
range	0–5	0–1	0	2–18	0–13	0–11

TABLE 2. Number of adult coccinellids found to be infected by *D. coccinellae* when offered in choice tests with pre-imaginal *C. septempunctata*. (N.B. no pre-imaginal coccinellids were infected in these tests.)

Test	Number of imagines infected	Total number of eggs found
2nd instar vs adult	13	45
3nd instar vs adult	13	45
4nd instar vs adult	15	48
Pupa vs adult	14	48

The frequency of interaction between wasps and pre-imaginal stages was significantly lower than that with adults for all pre-imaginal stages and all types of interaction (Table 3). Total number of interactions of wasps with coccinellid larvae in general increased with instar, but differences were not significant. Interactions between the wasp and pupae were less frequent, in some instances significantly so, than with any of the larval instars tested for both PI and OS (Mann-Whitney tests: PI – 2nd instar, W = 485.5, p = 0.036; 3rd instar W = 455.0, p = 0.208; 4th instar W = 502.0, p = 0.011; OS – 2nd instar W = 466.0, p = 0.055; 3rd instar W = 466.0, p = 0.055; 4th instar W = 510.5, p = 0.002). No oviposition attacks on pupae were observed in any of the replicates.

The frequency of interaction between wasps and adult coccinellids was not significantly affected by the pre-imaginal stage offered as an alternative in tests (PI – $\chi^2 = 2.317$, df = 3,

$p > 0.05$; OS – $\chi^2 = 3.015$, df = 3, $p > 0.05$; OA – $\chi^2 = 3.442$, df = 3, $p > 0.05$; number of beetles infected – $\chi^2 = 0.191$, df = 3, $p > 0.05$; number of eggs – $\chi^2 = 0.194$, df = 3, $p > 0.05$).

TABLE 3. Mann-Whitney test values and probabilities for comparisons between the interactions (PI - pursuance/investigate; OS – oviposition stance; OA – oviposition attack) of *D. coccinellae* to pre-imaginal and adult *C. septempunctata* in choice tests (summary data in Table 1).

	PI	OS	OA
2nd instar vs adult	267.5, $p < 0.0001$	247.5, $p < 0.0001$	253.5, $p < 0.0001$
3nd instar vs adult	259.5, $p < 0.0001$	257.0, $p < 0.0001$	244.0, $p < 0.0001$
4nd instar vs adult	282.5, $p < 0.001$	273.5, $p < 0.001$	257.5, $p < 0.0001$
Pupa vs adult	221.5, $p < 0.0001$	223.0, $p < 0.0001$	242.5, $p < 0.0001$

Reactions of young and old wasps to pre-imaginal and adult host stages

The total number of interactions of each type across all replicates for each life history stage tested, for tests with both young and old wasps, are given in Table 4.

TABLE 4. The number of interactions (PI – pursuance/investigate; OS – oviposition stance; OA – oviposition attack), in 1 hour, between young (1–2 day old) or old (7–8 day old) *D. coccinellae* and different life history stages of *C. septempunctata*, and the number of parasitoid eggs found on dissection of the coccinellids, after 24 h exposure (No. eggs). Numbers given are combined totals for all replicates of a particular test.

	2nd instar	3rd instar	4th instar	Pupa	Adult
Young wasps					
PI	25	53	75	16	137
OS	10	24	35	2	93
OA	0	1	6	0	61
No. eggs	0	0	1	0	109
Old wasps					
PI	44	78	96	35	165
OS	36	45	67	18	110
OA	4	19	35	0	71
No. eggs	0	4	14	0	157
χ^2 values comparing young and old wasp data and assuming equal expectation (df = 1 in all cases; significance levels are indicated by: ns – $p > 0.05$, * – $p = 0.01$–0.05, ** – $p = 0.001$–0.01, *** – $p < 0.001$)					
PI	5.23*	4.77*	2.57ns	7.08**	2.60ns
OS	14.70***	6.39**	10.04***	12.8***	1.42ns
OA	–	16.2***	20.51***	–	0.76ns
No. eggs	–	–	11.27***	–	8.66***

Dinocampus coccinellae interacts much more frequently with adult coccinellids than with any other life history stage tested. The number of PI interactions shown by young wasps with adult coccinellids was almost twice that observed with 4th instar larvae which gained the next highest score. Differences in levels of OS and OA interaction with adults compared to 4th instar larvae were even greater, the difference for OA being an order of magnitude. Furthermore, while 109 eggs were discovered in the 25 adult beetles used in these tests, only a single egg was found in any other stage.

A similar pattern is seen in the tests using old wasps, with adults again eliciting much higher levels of interaction from the parasitoids than any other stage, although the differences are somewhat reduced when compared to tests involving young wasps. For example, the number of ovipositional attacks on adults was only twice that on 4th instar larvae.

The results for larvae show that interactions of both young and old wasps increase with larval instar. Young wasps both investigate and take-up the ovipositional stance significantly more in response to 3rd instar than 2nd instar larvae (PI – $\chi^2 = 10.051$, df = 1, $p < 0.001$; OS – $\chi^2 = 5.529$, df = 1, $p < 0.05$). They show further increases in interaction to 4th instar larvae, but the increase over 3rd instar larvae is not significant (PI – $\chi^2 = 3.781$, df = 1, $p > 0.05$; OS – $\chi^2 = 2.051$, df = 1, $p > 0.05$). A similar pattern of increasing frequency of interaction with larval instar is seen in the tests with old wasps, although the increase for OS is not significant between 2nd and 3rd instars ($\chi^2 = 1$, df = 1, $p > 0.05$), while the increase for OS between 3rd and 4th instars is significant ($\chi^2 = 4.321$, df = 1, $p < 0.05$).

Interactions of all monitored types occur less with pupae than with any other stage. As in the choice tests, no parasitoid eggs were found in any of the pupae.

Direct comparison of the results from tests using young and old wasps shows that old wasps interacted more with coccinellids of all stages, most of the differences in respect of pre-imaginal stages being statistically significant (see Table 4).

Suitability of pre-imaginal and adult hosts

The number of adults and 4th instar larvae parasitised or not parasitised, the number from which wasp larvae emerged and the number of infected individuals that died before wasp larvae emerged are given in Table 5. Adult *C. septempunctata* were more often parasitised than 4th instar larvae ($\chi^2 = 7.025$, df = 1, $p < 0.01$). Furthermore, the proportion of infected larvae that died before parasitoid larvae emerged was significantly higher than for adult hosts (χ^2 with Yates' correction = 4.177, df = 1, $p < 0.05$).

TABLE 5. Assessment of developmental success of *D. coccinellae* in 4th instar larval and adult hosts.

Stage	Number parasitised	Number not parasitised	Number giving wasp cocoon	Number of infected hosts that died
Larva	12	8	7	5
Adult	19	1	18	1

DISCUSSION

These results show that British *D. coccinellae* are reluctant to oviposit in pre-imaginal stages of *C. septempunctata*. Although oviposition attacks on 3rd and 4th instar larvae were observed, no oviposition into a pre-imaginal individual was recorded when adult coccinellids were available. In no-choice tests using young, recently eclosed wasps, a single 4th instar larva contained one parasitoid egg, while many of the adults were parasitised, indicating that even when more suitable adult hosts are not available, *D. coccinellae* females are initially reluctant to oviposit in pre-imaginal coccinellids.

The rate of parasitisation of pre-imaginal stages by week old wasps that have previously been prevented from ovipositing in coccinellids, was considerably higher than that by young wasps, but still much lower than the rate of parasitisation of adult coccinellids by both young and old wasps. This suggests that the reluctance of *D. coccinellae* to oviposit into pre-imaginal coccinellids is reduced with time if wasps are kept isolated from potential hosts and if more favoured hosts are not offered as alternatives.

We deduce that, in Britain, the rarity of records of *D. coccinellae* from pre-imaginal coccinellids is not a consequence of under-recording, nor is it primarily a direct result of reported low suitability of larvae and pupae as hosts (David & Wilde, 1973; Obrycki et al., 1985), although this will undoubtedly have some effect. Rather, British *D. coccinellae* will not oviposit into pre-imaginal coccinellids if adults are present and even when adult coccinellids are unavailable, *D. coccinellae* is reluctant to oviposit in pre-imaginal coccinellids.

We believe the reluctance of British *D. coccinellae* to oviposit in pre-imaginal coccinellids, particularly when adult coccinellids are available, to be adaptive. Selection has favoured the assessment of the suitability of potential hosts for larval development by ovipositing females, as previously reported by Luck et al. (1982) for an aphelinid wasp. In Britain, *C. septempunctata* is univoltine. The majority (about 90%) of British *C. septempunctata* will not reproduce continuously, requiring a dormant period following eclosion before mating (Majerus & Kearns, 1989). Furthermore, the protracted spring, and variable weather through March, April and May, generally mean that the oviposition period for populations of *C. septempunctata*, is longer than in more continental climates. The consequence of this is that, in most years, the first adults of a new generation have eclosed several weeks before the last adults of the over-wintered generation have died. It will thus be rare that adult hosts are not available to ovipositing *D. coccinellae*. Given this, it is possible that *D. coccinellae* females will face a choice between young and old *C. septempunctata* for oviposition. In such a situation, a preference to oviposit in young rather than senescent adults would be favoured. Such a preference has recently been demonstrated (Majerus et al., in prep.).

The adaptive explanation is given additional weight by the lower proportion of wasps that successfully developed in hosts parasitised as 4th instar larvae, compared with those parasitised as adults. It must also be noted that there would be additional risks to *D. coccinellae* which oviposited in pre-imaginal stages in the field. In Britain, rates of pupal mortality may be very high. Rates of parasitisation of *C. septempunctata* pupae by the phorids *Phalacrotophora fasciata* (Fallén) and *P. berolinensis* Schmitz may be as high as 80% (Disney et al., 1994), while predation by predatory Hemiptera, such as *Deraeocoris ruber* (L.) may also be significant (Majerus, 1994).

Comparison of our results with records of *D. coccinellae* parasitising pre-imaginal coccinellids, including *C. septempunctata*, in America and Japan, raise the possibility that British populations of *D. coccinellae* differ from those in other parts of the world. Field data suggests that *D. coccinellae* has two, or perhaps occasionally three, generations per year in southern Britain, but may be univoltine in Scotland (Geoghegan and M. Majerus, pers. obs.). Eclosion of overwintered *D. coccinellae* occurs at a time when the new generation of *C. septempunctata* are emerging. Second generation *D. coccinellae* will also have young (non-overwintered) *C. septempunctata* available to them. It is thus probable that situations in which female *D. coccinellae* only have pre-imaginal stages of *C. septempunctata* available to them will be rare.

It is difficult to comment on the high prevalence of *D. coccinellae*, recorded by Sunderland (1978) in larval and pupal *C. septempunctata*, in England, in 1978. One possible cause is that uninfected overwintering adult coccinellids all died before new generation adults eclosed, leaving a significant period when only pre-imaginal coccinellids were available. Another possibility is that abnormal conditions in respect of the population densities of *D. coccinellae* and *C. septempunctata* pertained as a hang-over from the *C. septempunctata* population explosion of the summer of 1976, and the ensuing crash in numbers in the late summer of the same year (Majerus & Majerus, 1996). This may have had an effect on parasitoid prevalence and behaviour. However, given that parasitisation rate and coccinellid abundance are reported to be positively correlated (Ceryngier & Hodek, 1996), the nature of such an effect is unclear.

One other point in respect of Sunderland's data is worth considering in the light of our findings. In none of our tests did *D. coccinellae* oviposit into pupae. Yet Sunderland found 92% of pupae infected (n = 48), but only 29% of "old" larvae infected (n = 294). If *D. coccinellae* does not oviposit in pupae, which is likely, given that it appears to detect potential hosts by movement (Balduf, 1926), it is difficult to account for the huge increase in prevalence between "old" larvae (presumed to be 4th instar) and pupae.

ACKNOWLEDGEMENTS. We are grateful to D. Harkins for help in collecting samples in Scotland, and D. Bertrand for culturing aphids in Cambridge. We thank two anonymous referees for useful comments on an earlier version of the manuscript. We acknowledge the assistance of the British Council Granting Authority and Scottish Office Agriculture, Environment and Fisheries Department for supporting this research in part. The work in Cambridge took place in a laboratory funded by the Wolfson Foundation to whom we are grateful.

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Received September 2, 1997; accepted September 19, 1998