Ecological Entomology (2004) **29**, 123–127

SHORT COMMUNICATION

Low parasitoid success on a myrmecophilous host is maintained in the absence of ants

JOHN J. SLOGGETT, K. MARY WEBBERLEY and MICHAEL E. N. MAJERUS Department of Genetics, University of Cambridge, U.K.

Abstract. 1. Studies of *Dinocampus coccinellae*, a parasitoid of ladybird beetles, have generally shown congruence between field parasitism rates of different host species and parasitoid preference and/or host suitability in the laboratory, suggesting that host intrinsic factors rather than habitat-related extrinsic factors are of greatest importance in determining *D. coccinellae* occurrence.

2. The myrmecophilous *Coccinella magnifica* exhibits much lower *D. coccinellae* prevalence in the field than most other *Coccinella* species: it has been suggested that this is a manifestation of enemy-free space provided by the predatory *Formica rufa* group ants with which the *C. magnifica* occurs.

3. *Coccinella magnifica* collected at the same time and locality as parasitised *Coccinella septempunctata* were unparasitised by *D. coccinellae*. In the laboratory, in the absence of ants, although the parasitoid attacked *C. magnifica* as readily as *C. septempunctata*, *C. magnifica* was not parasitised successfully.

4. Such results are consistent with those from other ladybirds and *C. magnifica* does not now benefit directly from any putative *D. coccinellae*-free space provided by aggressive ants. Because its close relatives exhibit high levels of *D. coccinellae* parasitism, *C. magnifica* may be useful in determining some elements important in the evolution of host protection against parasitoid attack.

Key words. *Coccinella magnifica*, *Dinocampus coccinellae*, enemy-free space, host specificity, myrmecophily, prevalence.

Introduction

Dinocampus (*Perilitus*) *coccinellae* (Schrank), a cosmopolitan hymenopteran parasitoid, is a major cause of mortality in a number of taxa of ladybird beetle. This parthenogenetic braconid attacks ladybirds of the subfamily Coccinellinae, laying single eggs into mainly adult hosts. The larva that hatches from the egg develops inside its host until ready for pupation, at which point it emerges and spins a cocoon between the legs of the paralysed beetle. Most hosts die after a few days, ensnared in the cocoon (Ceryngier & Hodek, 1996; and references therein).

The prevalence of this parasitoid varies markedly across different ladybird taxa in the field (e.g. Richerson & DeLoach, 1973; Cartwright *et al.*, 1982; Majerus, 1997) and, in general, species that are parasitised less frequently in the field have also been found to be less preferred or less suitable hosts in laboratory studies of parasitism (e.g. Richerson & DeLoach, 1972; Obrycki, 1989; Orr *et al.*, 1992). This in its turn suggests that factors intrinsic to the host itself, such as host size, mobility, or chemical constitution, rather than extrinsic factors such host habitat choice, mediate *D. coccinellae* prevalence across different hosts (Sloggett & Majerus, 2000a), an assertion supported by the frequent occurrence of high prevalence, suitable hosts and low prevalence, unsuitable hosts together in the same habitat [e.g. the suitable *Coccinella septempunctata* (L.) and the unsuitable *Adalia bipunctata* (L.)].

A rare case in which extrinsic, habitat-related factors have been invoked to explain low parasitoid prevalence is that of the ladybird *Coccinella magnifica* Redtenbacher (*C. distincta* Faldermann, *C. divaricata* Olivier). In north-western Europe, this ladybird is invariably associated with

Correspondence: John J. Sloggett, Department of Animal Ecology I, University of Bayreuth, PO Box 101251, D-95440 Bayreuth, Germany. E-mail: john.sloggett@uni-bayreuth.de

ants of the *Formica rufa* group and allies, although further afield its habitat preferences are less clear (Donisthorpe, 1919; Majerus, 1989; Sloggett *et al.*, 2002). Although *D. coccinellae* parasitism of *C. magnifica* has been recorded (Lipa & Semyanov, 1967; Narayan *et al.*, 1967; Majerus, 1989, 1994, 1997), it appears to be extremely rare (well below 1%; Majerus, 1989, 1994, 1997). This is noteworthy, because the majority of other *Coccinella* species suffers relatively high levels of *D. coccinellae* parasitism (e.g. Lipa & Semyanov, 1967; Maeta, 1969; Cartwright *et al.*, 1982; Anderson *et al.*, 1986; Majerus, 1997), which may, on occasions, reach in excess of 50% in *Coccinella septempunctata* L. (Geoghegan *et al.*, 1997; Ceryngier, 2000). Majerus (1989, 1994, 1997) has therefore suggested that *C. magnifica* may be protected from *D. coccinellae* inadvertently because the wasp is eliminated by the aggressive and predatory *F. rufa* group ants with which it is associated; the ladybird in effect gains enemy-free space (Jeffries & Lawton, 1984; Berdegue *et al.*, 1996) through its myrmecophily. Ants have already been implicated as providers of enemy-free space for a number of other myrmecophilous taxa in both mutualistic and antagonistic associations (e.g. Way, 1963; Atsatt, 1981; Völkl, 1992; Letourneau *et al.*, 1993).

Two issues were addressed in the work reported here. (1) Whether *C. magnifica* exhibits lower *D. coccinellae* prevalence than its congener *C. septempunctata*, when temporal and site effects are controlled for: earlier *D. coccinellae* prevalence data had not been obtained for other *Coccinella* species at the same time or location as that for *C. magnifica*. (2) *Dinocampus coccinellae* parasitism of *C. magnifica* and *C. septempunctata* was compared in the laboratory, in the absence of ants, to examine whether host-intrinsic factors, rather than the ant-infested habitat in which *C. magnifica* lives, can explain the low prevalence of *D. coccinellae* in *C. magnifica* hosts. *Coccinella septempunctata* is a particularly suitable species for comparison, because in addition to its close relatedness to *C. magnifica* (Iablokoff-Khnzorian, 1982; G. D. D. Hurst, J. H. Graf von der Schulenburg and J. J. Sloggett, unpubl. data), it occurs at field sites alongside *C. magnifica*, although primarily in the absence of ants (see Sloggett & Majerus, 2000b; on *C. septempunctata–F. rufa* associations). Additionally the two species are of similar size: species size has been suggested as one cause of variation in the prevalence of *D. coccinellae* from different hosts (Richerson & DeLoach, 1972, 1973).

Materials and methods

Dinocampus coccinellae *field prevalence in* Coccinella magnifica *and* Coccinella septempunctata

To exclude any hitherto uncontrolled temporal and site effects, field collections of *C. magnifica* and *C. septempunctata* were made at the same locality at the same time, and *D. coccinellae* prevalence in these two ladybirds was compared. In 1995, two samples of adults of both species were collected from Brentmoor Heath, a heathland site in southern England (≈51°20′N, 0°39′W), where they, and the ant *Formica rufa* L., are common. The first sample was collected on 19 January, when both coccinellid species were overwintering. The second sample was collected on 7 August, and consisted of young adults.

The overwintering sample was kept cool (< 20 °C) and fed on an artificial diet (Henderson & Albrecht, 1988; Majerus & Kearns, 1989) for the first 3–4 days of captivity. Thereafter, all coccinellids were fed on excess aphids, mainly *Acyrthosiphon pisum* (Harris) with a few *Aphis fabae* Scopoli. Aphid food was reared on broad bean plants *Vicia faba* L. Ladybirds were housed in 9-cm diameter Petri dishes singly or in pairs in the laboratory. The August sample was transferred directly to the laboratory and fed on artificial food for 1 day before being transferred to aphid food. This sample was maintained at a density of approximately five ladybirds per 14-cm diameter Petri dish.

Both samples were retained in the laboratory for 40 days, this being sufficient time for the development of *D. coccinellae* to a cocoon at laboratory temperatures. *Dinocampus coccinellae* emerging from coccinellids were recorded, as were any ladybirds that died before the end of the 40 days.

Parasitism was compared between *C. magnifica* and *C. septempunctata* collected on the same date using chi-square tests (Siegel & Castellan, 1988). Individuals that died within the 40 days were excluded from the main analysis. A second chi-square test was used to compare mortality apparently unrelated to *D. coccinellae*, i.e. that which did not result from *D. coccinellae* emergence from a ladybird: individuals that had died within 40 days without parasitoid emergence were compared with those alive after 40 days and those from which *D. coccinellae* had emerged added together. It should be noted that chi-square tables contained low expected values (i.e. < 5); however, Siegel and Castellan (1988) advised that in such cases a chi-square test should still be used where the total sample size is greater than 50, which it was for both samples.

Relative acceptability and suitability of hosts for Dinocampus coccinellae

Experiments comparing *D. coccinellae* parasitism of *C. magnifica* and *C. septempunctata* in the absence of ants were carried out in the laboratory. *Coccinella magnifica* and *C. septempunctata* were bred from adults collected at Esher Common and Oxshott Heath (≈51°21′N, 0°22′W), a second Southern English heathland site with *F. rufa* ants (description by Sloggett *et al.*, 1998). Larvae were reared to adulthood on an aphid diet of *A. pisum* and *A. fabae*, again from broad bean. The resulting adults were either maintained on this diet or placed in a refrigerator until use. Coccinellids were fed on *A. pisum* to excess for a minimum of 5 days before testing.

Dinocampus coccinellae were reared from *C. septempunctata*, also collected from Esher Common and Oxshott Heath. This *C. septempunctata* stock was maintained on a mixed diet of *A. fabae* and *A. pisum*. Any resulting *D. coccinellae* cocoons were retained, in their Petri dishes of origin, when the other ladybirds were moved to fresh Petri dishes. After adult *D. coccinellae* emerged, they were transferred to a 9-cm diameter Petri dish and fed on ladybird artificial food for 1 day prior to testing.

In testing *D. coccinellae* host preference, paired no-choice tests were used within one trial: thus a single wasp was exposed first to one and then to the other potential host species. The order of presentation of the hosts was alternated over the course of the trials. Within trials, coccinellids were paired by sex. They were also paired by reproductive status, with individuals that had been kept cool in the refrigerator, which leads to sexual maturation (Majerus, 1989; Hodek & Hodková, 1996) or had been mated, in the case of females, being paired together. Such factors may play some role in *D. coccinellae* host choice (e.g. Cartwright *et al.*, 1982; Geoghegan *et al.*, 1997; Majerus *et al.*, 2000). *Coccinella magnifica* and *C. septempunctata* used in individual trials were unrelated to those used in other trials. Paired tests were conducted at a constant temperature, although the temperature varied across trials, between 20 and 28 °C.

Single coccinellids were placed in 9-cm diameter Petri dishes. *Dinocampus coccinellae* was added at the beginning of a test. Time from introduction of *D. coccinellae* to attack (*D. coccinellae* drilling or stinging a host with its ovipositor) was recorded. Each coccinellid and *D. coccinellae* individual remained together for 15 min. This typically provided sufficient time for hosts of both species to be attacked several times (see Results). The total sample size was 14. Data were analysed using a two-tailed sign test; thus, only the direction of the difference in time to attack was used, rather than the absolute time, this being due to the temperature differences between trials.

After testing, 10 random pairs of potential hosts were kept for 40 days singly in 9-cm Petri dishes, and fed excess *A. pisum*. Any *D. coccinellae* that emerged were recorded. Ladybirds, from these pairs, that died without obvious signs of parasitism or were still alive after 40 days, were preserved in 70% ethanol and dissected for signs of parasitism.

Parasitism in the pairs of potential hosts was compared using a two-tailed Fisher exact test (Siegel & Castellan, 1988).

Results and discussion

Dinocampus coccinellae *field prevalence in* Coccinella magnifica *and* Coccinella septempunctata

In both samples, *D. coccinellae* emerged only from *C. septempunctata*. No parasitoids emerged from *C. magnifica* (Fig. 1). This difference was significant, for both samples (January: $\chi^2 = 9.48$, 1 d.f., $P < 0.005$; August: $\chi^2 = 12.38$, 1 d.f., $P < 0.001$). There was no significant difference between species in mortality other than through *D. coccinellae* emergence, however there was a marked trend towards higher *C. magnifica* mortality in the January sample, when only *C. magnifica* died from causes presumed to be unrelated to *D. coccinellae* (January sample: $\chi^2 = 3.63$, 1 d.f., $0.10 > P > 0.05$; August sample: $\chi^2 = 0.025$, 1 d.f., NS). As a check that *D. coccinellae* really was not responsible for these *C. magnifica* deaths, for example through unsuccessful parasitism causing ladybirds to die, three of the six January-collected *C. magnifica* were dissected: none of them appeared to have been parasitised.

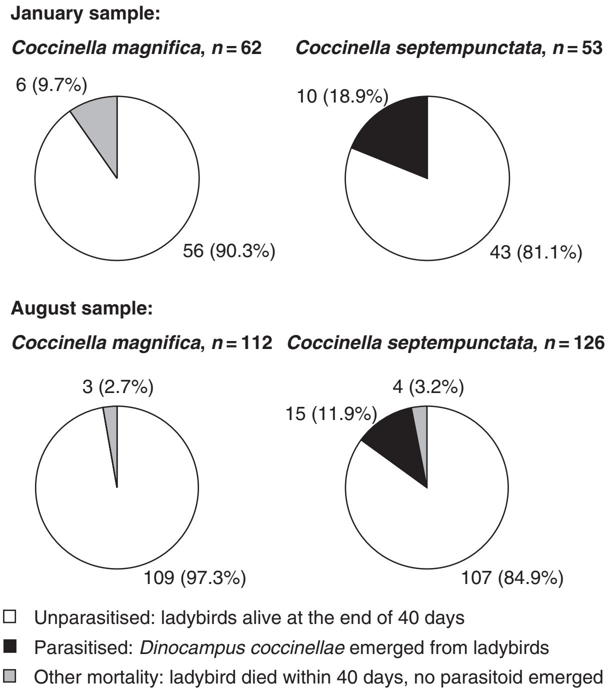

Fig. 1. *Dinocampus coccinellae* parasitism, and other mortality, in *Coccinella magnifica* and *Coccinella septempunctata* samples collected at Brentmoor Heath at the same time.

Thus, previous indications that *D. coccinellae* prevalence in *C. magnifica* is low relative to other *Coccinella* species are confirmed: the difference in *D. coccinellae* parasitism between *C. magnifica* and *C. septempunctata* hosts, at least, has not arisen due to temporal or locality differences in the collection of data for the two species, because it is maintained when these factors are controlled for.

Relative acceptability and suitability of hosts for Dinocampus coccinellae

Both ladybird species were attacked readily by *D. coccinellae*: 13 of the 14 *C. septempunctata* and all 14 *C. magnifica* were attacked. Neither species was attacked significantly more rapidly [mean ± SE: *C. magnifica* $= 48.4 \pm 8.0$ s, *C. septempunctata* $= 98.6 \pm 23.4$ s (excluding one in which *C. septempunctata* was not attacked). Sign test: 10 cases in which *C. magnifica* attacked faster (including one in which *C. septempunctata* was not attacked); four cases in which *C. septempunctata* was attacked faster, NS]. The

Table 1. *Dinocampus coccinellae* parasitism of *Coccinella magnifica* and *Coccinella septempunctata* after 40 days.

	C. magnifica	*C. septempunctata*
Coccinellids not attacked	0	1
Died within 40 days, unparasitised (from dissection)	2	0
Live after 40 days, unparasitised (from dissection)	8	0
Total unparasitised	**10**	**1**
Died within 40 days, parasitised (from dissection)	0	2
Dinocampus coccinellae emerged from ladybird	0	7
Total parasitised	**0**	**9**

overriding majority of potential hosts of both species was clearly attacked several times within the 15 min.

Successful parasitism in the 10 pairs of potential hosts maintained in laboratory for 40 days is shown in Table 1. *Dinocampus coccinellae* were recorded in all *C. septempunctata*, except the single unattacked individual. In contrast, no *D. coccinellae* emerged from *C. magnifica*, and no obvious signs of parasitism, such as first-instar head capsules and undeveloped larvae (Balduf, 1926), were found when the 10 *C. magnifica* were dissected. Larvae and head capsules were detected in both prematurely dead *C. septempunctata*. The difference in infection levels for the two species was highly significant [two-tailed Fisher exact test, $n = 10$ pairs (20 ladybirds), $P < 0.001$]. Mortality not due directly to *D. coccinellae* emergence was the same for both species (two of 10 individuals).

Thus, in the absence of ants *C. magnifica* were also not parasitised, even though the wasp readily attacked this species. An absence of obvious signs of parasitism suggests that the wasp fails to oviposit into the ladybird after inserting its ovipositor, as indicated for some potential ladybird hosts by Orr *et al.* (1992). It remains possible, however, that, in *C. magnifica*, the *D. coccinellae* egg typically fails to develop past its very earliest stages, which are small and unlikely to have been located in dissections after 40 days. Total developmental failure does seem less likely, particularly because occasional successful emergence of the larva or eclosion of the adult parasitoid has been observed (M. E. N. Majerus and J. J. Sloggett, pers. obs.).

Whatever the exact cause, it is clear that *C. magnifica* benefits little from any potential protection from *D. coccinellae* provided by ants. As in other ladybirds, there is agreement between field data on *D. coccinellae* prevalence and laboratory data on parasitism by *D. coccinellae*. Thus, low host acceptability or suitability can explain the low prevalence of *D. coccinellae* in field-collected *C. magnifica* and earlier suggestions that the low field prevalence of *D. coccinellae* from *C. magnifica* hosts is evidence that the ladybird benefits from ant-related enemy-free space is incorrect. While this study fatally weakens the earlier evidence for enemy-free space from *D. coccinellae* in *C. magnifica*, and sounds a warning note on the use of such observations as evidence for enemy-free space, however, it is worth noting that *F. rufa* group ants certainly do predate some braconids (Wichmann, 1953), and might eliminate *D. coccinellae* near their colonies in a similar manner, providing *C. magnifica* with largely redundant, additional protection against *D. coccinellae*. Furthermore, *D. coccinellae*-free space might still have been important in *C. magnifica*'s evolution of myrmecophily, if, at the point when myrmecophily evolved, the ladybird's ancestors were still susceptible to *D. coccinellae* attack in the absence of ants, as most other *Coccinella* species are today. There is no evidence for or against this view; clearer evidence links *C. magnifica* myrmecophily to availability of resources, in the form of ant-tended aphids (Sloggett & Majerus, 2000b), although this latter hypothesis does not exclude an additional role for enemy-free space.

Although they are probably not sibling species, *C. magnifica* and *C. septempunctata* are undoubtedly closely related, a view supported by both morphological and molecular genetic evidence (Iablokoff-Khnzorian, 1982: G. D. D. Hurst, J. H. Graf von der Schulenburg and J. J. Sloggett, unpubl. data). Their close relatedness makes the difference in their susceptibility to *D. coccinellae* parasitism striking. The factors that promote or deter *D. coccinellae* attack or development on different ladybird hosts are not yet fully clear (but see Richerson & Deloach, 1972; Orr *et al.*, 1992; Al Abassi *et al.*, 2001) and it is not possible to say which factors are important in this case. *Coccinella magnifica* and *C. septempunctata* are of similar size and coloration (e.g. see Majerus, 1989), however they differ, to some extent, in their movement (Sloggett *et al.*, 1998) and *C. magnifica*'s chemical defences differ from those of *C. septempunctata* and most other *Coccinella* species (Dixon, 2000; A. Beran, J. J. Sloggett & K. Dettner, unpubl. data). Further investigation of *D. coccinellae* parasitism of *C. magnifica* and *C. septempunctata* would be of help in determining the reasons why and mechanisms involved in the evolution of host protection against parasitoid attack.

Acknowledgements

We are extremely grateful to Surrey Wildlife Trust and Mary Adler for permission to work at Brentmoor Heath and assistance in our work there, and to Elmbridge Borough Council and the Elmbridge Commons Ranger, David Page, for permission to work at Esher Common and Oxshott Heath. We also wish to express our thanks to the Majerus family, for assistance in collecting ladybirds. John Sloggett and Mary Webberley were recipients of PhD studentships from the BBSRC.

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Accepted 26 September 2003