

The ant-associations and diet of the ladybird *Coccinella magnifica* (Coleoptera: Coccinellidae)

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Abstract. The ladybird *Coccinella magnifica* is typically considered to be myrmecophilous, and primarily associated with the *Formica rufa* group of wood ants. It is regularly associated with ants of the *F. rufa* group in north-western Europe. The very limited data on the habitat preference of *C. magnifica* in the southern and eastern parts of its range indicate that its ant-associations change and that it may even be non-myrmecophilous in this region. *C. magnifica* might consist of geographically restricted species or semispecies, on the basis of its geographical variation in ant-association. Laboratory and field observations on north-western myrmecophilous populations *C. magnifica* appear to indicate it is a generalist predator of aphids. *Coccinella magnifica*'s potential dietary breadth is similar to that of its congener *Coccinella septempunctata*, which has been used as a model of *C. magnifica*'s non-myrmecophilous ancestor in evolutionary studies.

INTRODUCTION

The Palaearctic ladybird *Coccinella magnifica* Redtenbacher (= *C. distincta* Faldermann, *C. divaricata* Olivier, *C. labilis* Mulsant, *C. lama* Kapur) is considered myrmecophilous, occurring with the red wood ants, *Formica rufa* group (e.g. Donisthorpe, 1896, 1919–20; Wiśniewski, 1963; Majerus, 1989; Sloggett, 1998). The ladybird has been tacitly regarded as a generalist aphidophage, consuming a variety of aphids on different plants, most notably ant-tended species, within its habitat (e.g. Majerus, 1989, 1991, 1994; Sloggett & Majerus, 2000a). In this paper we reconsider the assumptions that have been made about *C. magnifica*'s ant-associations and dietary preferences, using published sources known to us and new observations we have made, as well as previously unpublished observations provided by Dr. John Muggleton (see acknowledgements).

COCCINELLA MAGNIFICA ANT - ASSOCIATIONS

Coccinella magnifica association with the *Formica rufa* group of ants

C. magnifica is typically associated with ants of the *F. rufa* group, throughout north-western Europe and into central Europe. Donisthorpe (1896) first recognised it as a regular associate of *Formica rufa*, and it has since been recorded associated with *Formica polyctena*, *Formica lugubris* and *Formica pratensis* (Table 1).

Most work on *C. magnifica*'s association with the *Formica rufa* group has been carried out in southern England, with *F. rufa*. Mating adults, eggs, larvae and pupae of *C. magnifica* are all found associated with this ant (Donisthorpe, 1919–20; JJS). Majerus (1989) suspected confusion with the generalist *Cocci-*

nella septempunctata L., which *C. magnifica* resembles, and checked the identities of 5971 seven-spotted ladybirds without consideration for the presence or absence of *F. rufa*. *Coccinella magnifica* was only found when *F. rufa* was present, thus the association with *F. rufa* is real. Numbers of *C. magnifica* also declined with distance from *F. rufa* nests (Majerus, 1989), and the ladybird is consistently associated with *F. rufa* throughout the year (Sloggett & Majerus, 2000a).

Published work supports the view that *C. magnifica* adults and larvae are less vigorously attacked by *F. rufa* than are other ladybirds, notably *C. septempunctata* (Donisthorpe, 1919–1920; Majerus, 1989; Sloggett et al., 1998). The adults also use physical defence on colonies of *F. rufa*-tended aphids, where the probability of ant attack is much greater (Sloggett et al., 1998). For similar reasons, *C. magnifica* larvae minimise the time spent on colonies of *F. rufa*-tended aphids and may also utilise limited chemical defence (J. J. Sloggett, unpub. data).

Associations of *C. magnifica* with non-*F. rufa* group *Formica* ants

Pontin (1959) recorded in England a *C. magnifica* larva associated with the slave-making ant *Formica sanguinea* Latreille, which is closely related to the *F. rufa* group, and shares many aspects of its biology with *F. rufa* group ants (Skinner, 1998). *Coccinella magnifica* has also been recorded with *Formica cinerea* Mayr in eastern Germany, at Königs Wusterhausen, near Berlin, although *F. rufa* was also present at this site (Schulze, 1919). In Luxembourg, Wasmann (1912) recorded *C. magnifica* with *Formica rufibarbis* F. enslaved by the ant *Polyergus rufescens* (Latreille).

Although many observations have been made on English aphid-tending *F. fusca* by one of us (JJS), only a single *C. mag-*

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TABLE 1. Members of the *Formica rufa* group of ants with which *Coccinella magnifica* is known by us to have been recorded. The list of published sources provided is not exhaustive, and for *F. rufa* is largely concentrated on significant contributions that summarise a number of records or provide additional details of the nature of the association (see text).

<i>Formica rufa</i> group host	Geographic areas where <i>C. magnifica</i> association has been observed	Source
<i>Formica rufa</i> L.	England, Luxembourg, Germany, Poland	Donisthorpe, 1896, 1919–20; Wasmann, 1912 (as <i>Formica truncicola</i> Nylander); Wiśniewski, 1963; Majerus, 1989; Sloggett & Majerus, 2000a; JHGvdS; WS; JJS; WV
<i>Formica polyctena</i> Förster	Germany, Poland	Wiśniewski, 1963; JHGvdS; WS; JJS; WV
<i>Formica lugubris</i> Zetterstedt	Scandinavia	R.S. Key in Hyman & Parsons, 1992
<i>Formica pratensis</i> Retzius	Germany	Wasmann, 1912; WS

nifica adult has been found with the ant *Formica fusca* L. in England, at Esher Common, Surrey, where *F. rufa* group ants occur in the immediate vicinity. However, in Central Europe adult *C. magnifica* and *F. fusca* have been recorded together in the absence of *F. rufa* group ants at two distant localities: near Tanowo in north west Poland (previously Falkenwald, Germany), at two sites (Schmidt, 1936), and at Seybothenreuth, near Bayreuth in south-eastern Germany, where single adults were found with *F. fusca* mixed with *Lasius niger* (L.) in both 1996 and 1997 (WV).

Formica rufa group and *F. fusca* pheromone trails possess a common component, mellein (Bestmann et al., 1992; Kern & Bestmann, 1994). If, like many other myrmecophiles, *C. magnifica* uses ant pheromone trails (see Bhatkar, 1982 on *Coccinella septempunctata*), then *C. magnifica* might accidentally become associated with *F. fusca* due to the shared chemical component of the two ants' trails. This seems a probable explanation for the English record particularly, since *F. rufa* group ants occurred very nearby. However, no *F. rufa* group ants were in the immediate vicinity of two of three sites given by Schmidt (1936), although they were present at a third site. Similarly, both observations at Seybothenreuth were on the same colony of *F. fusca*, some 400 metres distant from the nearest *F. rufa* group colonies. It thus appears that *C. magnifica* may more regularly associate with *F. fusca*, and perhaps with other non-*F. rufa* group *Formica* ants, in central Europe, and perhaps further east.

***Coccinella magnifica* associations with non-*Formica* ants**

Wasmann (1912) records *C. magnifica* in Luxembourg associated with several non-*Formica* species of ants, namely *Camponotus ligniperda* Latreille and *Myrmica rubra* (L.) (= *M. laevinodis* Nylander) as well as *Polyergus rufescens* and its *Formica rufibarbis* slaves. Adult and larval *C. magnifica* were also observed in England associated with aphid-tending *Myrmica ruginodis* Nylander, at Oxshott Heath, Surrey (JJS). However, these ladybirds were within a *F. rufa* territory, and *F. rufa* workers were also tending aphids on the same plant. A similar situation probably formed the basis for Wasmann's uncorroborated observations, since he also records *C. magnifica* associated with *F. rufa* group ants.

Thus, there is little convincing evidence that *C. magnifica* is ever associated with non-*Formica* ants, except by accident. *Coccinella magnifica*'s chemical counter to ant-aggression probably involves chemical repellence rather than chemical mimicry (Sloggett, 1998; Sloggett, unpub. data), and *C. magnifica* defence behaviour is, like its probable chemical adaptation, effective against most ant species (Arnold and others in Majerus, 1994, p.151; Sloggett et al., 1998). *Coccinella magnifica* may thus be potentially able to coexist with a wide variety of ant species, both typical and accidental associates, without suffering high ant aggression.

***Coccinella magnifica* recorded without clear ant associations**

Majerus (1989) notes that of over 1400 *C. magnifica* collected by him in south-eastern England, only one, netted in flight and probably dispersing, was found in the absence of ants. In southern France, at Entrechoux, near Vaison-la-Romaine, Vaucluse, two adult *C. magnifica* were recorded without obvious ant association. No *Formica* or other large ants were found nearby (J. Muggleton, pers. comm.). Although dispersal could be invoked to explain this record and *C. magnifica* have been recorded with *Formica* ants further west (J. Muggleton, pers. comm.), the occurrence of two individuals together make the *C. magnifica* at Entrechoux less likely to be accidental vagrants.

Published sources on *C. magnifica* from extreme eastern Europe and Asia exhibit some similarities to the French record. For example, Dyadechko (1954) records the occurrence of *C. magnifica* adults and larvae in Ukrainian cereal fields, where *F. rufa* group ants are unlikely to occur, although other ants would be present. Furthermore, one of us (MENM) collected numbers of *C. magnifica* from two sites near Lake Baikal in the Buratian Republic (Russia) in early September 1999: at one site, between Ulan Ude and Kyahta, *C. magnifica* were found with an unidentified non-*F. rufa* group ant; at the other, at Ulan Ude, no obvious ant associates were recorded.

In view of these observations, and those made of *C. magnifica* with *F. fusca* considered above, it seems possible that in southern and eastern parts of its range *C. magnifica* is non-myrmecophilous, or facultatively associated with a wider range of ant species, rather like *C. septempunctata* is in England (Sloggett & Majerus, 2000a). A similar geographic phenomenon is documented for *Coccinella quinquepunctata* L., which is specialised in river and lake shingle habitats in north-western Europe, but is a broader habitat generalist in the south and east of its range (Horion, 1961; Majerus & Fowles, 1989; Sloggett & Majerus, 2000b). Geographic variability in habitat preference could be correlated with underlying genetic divergence between populations (Sloggett & Majerus, 2000b). Further work is clearly needed to elucidate the exact associations of southern and eastern populations of *C. magnifica*, as well as their relationship to north-west European populations.

THE DIET OF NORTH WESTERN MYRMECOPHILOUS *C. MAGNIFICA*

Hodek (1973, 1996) points out that mere observation of association with or feeding on particular prey does not necessarily indicate that such prey constitutes a suitable diet. He argues that the essential prey of a ladybird species is that on which larval development, with low mortality, and high oviposition is obtained. However, not all diets fulfilling these criteria for particular ladybird species in the laboratory are encountered by these species in the field (Majerus, 1994; Hodek, 1996; Kal-

TABLE 2. Aphids with which *C. magnifica* has been recorded feeding on or associated with in the field.

Aphid species [Host plant]	Locality	Comments	Observer or source
<i>Anoecia</i> sp. [<i>Cornus sanguinea</i> L., dogwood]	Seybothenreuth, nr. Bayreuth, Germany	Two <i>C. magnifica</i> adults have been found associated with this aphid tended by <i>Formica fusca</i> in separate seasons (see section on non- <i>F. rufa</i> group <i>Formica</i> ant associates).	WV
<i>Aphis jacobaeae</i> Schrank [<i>Senecio jacobaea</i> L., ragwort]	East Dorset England	Larvae and adults observed feeding on this aphid, which may be ant-tended. Pupae were also present.	MENM (see Majerus, 1989)
<i>Aphis salicariae</i> Koch [<i>Chamerion augustifolium</i> (L.), rosebay willowherb]	Esher Common, Surrey England	<i>C. magnifica</i> larvae and adults have been observed associated with this aphid, sporadically tended by <i>Formica rufa</i> . Pupae were also present and an eclosing adult was observed.	JJS
<i>Aphis sarothamni</i> Transsen [<i>Cytisus scoparius</i> (L.), broom]	Wyre Forest, Worcestershire, England	A single larva observed feeding on this aphid tended by <i>Formica sanguinea</i> (see section on non- <i>F. rufa</i> group <i>Formica</i> ant associates).	Pontin, 1959
<i>Aphis ulicis</i> Walker [<i>Ulex europaeus</i> L., gorse]	Oxshott Heath, Surrey England	Both adult and larval <i>C. magnifica</i> have been found associated with this aphid, sporadically tended by <i>F. rufa</i> and <i>Myrmica ruginodis</i> (see section on non- <i>Formica</i> ant associates of <i>C. magnifica</i>).	JJS
<i>Cinara confinis</i> (Koch) (= <i>Todolachmus</i> sp.) [<i>Abies alba</i> Miller, silver fir]	Nr. Grafenau, Bavaria, Germany	A single <i>C. magnifica</i> adult has been observed with this occasionally tended aphid, and <i>F. rufa</i> .	WV
<i>Cinara piceicola</i> Cholo- dkovsky [<i>Picea</i> sp., spruce] [<i>Picea abies</i> , Norway spruce]	Esher Common, Surrey, England Bad Berneck, nr. Bayreuth, Germany	Large numbers of <i>C. magnifica</i> larvae, and adults, were observed at Esher Common in 1998 associated with this aphid tended by <i>F. rufa</i> . Predation by an adult has been observed. <i>Elatobium abietum</i> was also present (see below). At Bad Berneck, <i>C. magnifica</i> adults have been observed with this aphid tended by <i>Formica polyctena</i> , along with <i>Cinara pilicornis</i> (see next entry).	JJS, WV
<i>Cinara pilicornis</i> (Hartig) [<i>P. abies</i>]	Bad Berneck, nr. Bayreuth, Germany	Four adult <i>C. magnifica</i> have been observed associated with this aphid, tended by <i>Formica polyctena</i> , in visits in two successive seasons. <i>Cinara piceicola</i> was also present (see previous entry).	WV
<i>Cinara pilosa</i> (Zetterstedt) (= <i>C. pinea</i> (Mordwilko) of many British authors) [<i>Pinus sylvestris</i> L., Scots pine]	Esher Common and Oxshott Heath, Surrey, England	Adults and larvae of <i>C. magnifica</i> have been observed naturally feeding on untended individuals of this sporadically tended species, both on trees and on <i>F. rufa</i> foraging trails on the ground, where numbers of these aphids can often be found having fallen from vegetation.	JJS
<i>Cinara pini</i> (L.) [<i>P. sylvestris</i>]	Esher Common and Oxshott Heath, Surrey, England Bad Berneck, nr. Bayreuth, Germany	<i>C. magnifica</i> adults have been frequently found associated with this aphid, tended by <i>F. rufa</i> in England. An adult has also been found associated with this aphid tended by <i>F. polyctena</i> in Germany. In England adults have been observed naturally feeding on ant-tended colonies.	JJS, WV
<i>Elatobium abietum</i> (Walker) [<i>Picea</i> sp.]	Esher Common, Surrey, England	In addition to observations of this aphid occurring with <i>C. magnifica</i> on <i>Picea</i> sp., alongside <i>C. piceicola</i> (see above), adult <i>C. magnifica</i> have been found associated with this non-tended aphid alone early in the year. On this occasion, <i>F. rufa</i> were present feeding on the honeydew excreted by the aphid onto the plant surface.	JJS
<i>Schizolachnus pineti</i> (F.) [<i>P. sylvestris</i>]	Esher Common, Surrey, England	This non-tended aphid is often present along with <i>Cinara</i> spp. on <i>P. sylvestris</i> and it is thus often difficult to ascertain whether this aphid is also being predated. However a number of adult <i>C. magnifica</i> were observed associated with this aphid in the absence of <i>Cinara</i> spp. early in the season in 1996. <i>Formica rufa</i> were also present, feeding on the honeydew produced by the aphid on the surface of the needles.	JJS
<i>Sitobion fragariae</i> (Walker) [<i>Holcus lanatus</i> L.]	Oxshott Heath, Surrey, England	Six <i>C. magnifica</i> larvae were found on one occasion associated with this non-tended aphid.	JJS
<i>Symydobius oblongus</i> (von Heyden) [<i>Betula pendula</i> Roth, birch]	Esher Common and Oxshott Heath, Surrey, England	<i>C. magnifica</i> adults have been observed feeding on this aphid under attack from attendant <i>F. rufa</i> on several occasions in the summer.	JJS

ushkov & Hodek, 2001). A considerable degree of care is thus required when interpreting both field and laboratory observations on diet (Hodek, 1996).

Field observations

Observations on the natural diet of *C. magnifica* (Table 2) exclusively concern north-west European populations associated with *Formica* ants: most were made in southern England and near Bayreuth, in Germany. Although, in many cases, adults alone have been observed associated with or feeding on particular aphid species, in seven cases larvae are recorded. Hodek's criteria for essential prey are likely to be fulfilled by these aphid species, at least. The list as a whole, and particularly the occurrence of a number of larval records, suggests that *C. magnifica* is indeed a dietary generalist.

The high number of conifer-dwelling aphids on our list clearly reflects the common occurrence of conifers in habitats where *F. rufa* group ants often live: *C. magnifica* itself is not restricted to conifers. There is also a bias in the list towards ant-tended species, although *C. magnifica* readily feeds on untended colonies of tended species or non-tended aphids when they are available. Adults and larvae have been observed feeding on unidentified non-tended aphids on herbaceous plants in England (JJS). *Coccinella magnifica* also feed on *F. rufa* foraging trails, on *Cinara pilosa* that have fallen from pine trees (JJS). These aphids are ignored by *F. rufa* workers; the ants also rarely attack *C. magnifica* on foraging trails, in contrast to their defence of tended aphid colonies against the ladybird (Sloggett et al., 1998; J.J. Sloggett, unpub. data).

Availability of non-tended species may be limited, since *F. rufa* group ants often predate such aphids (Skinner, 1980). However, some non-tended species may occur in appreciable numbers, particularly earlier in the season. Additionally, certain ant-tended species may be present at such high levels earlier in the year that some colonies are only sporadically tended (Wellenstein, 1952; Way, 1963; Sloggett & Majerus, 2000a). Un- or non-tended aphids are undoubtedly less costly to obtain, perhaps even making them preferred prey. For example, *C. magnifica* larvae were observed associated with the non-tended *S. fragariae*, although, at this time, no larvae were found with tended *Aphis ulicis* nearby.

Laboratory observations

One of us (JJS) has successfully reared *C. magnifica*, adult to adult, on *Acyrtosiphon pisum* (Harris) (see also Majerus, 1989), *Aphis fabae fabae* Scopoli and *Microlophium carnosum* Buckton. Adult *C. magnifica* have additionally been maintained on *Aphis fabae cirsiacanthoidis* (Schränk) and *Aphis urticata* Gmelin, with no apparent ill effects (JJS). Very high mortality has been observed in *C. magnifica* larvae if they are fed *Aphis sambuci* L. or *Macrosiphum albifrons* Essig (JJS). *Coccinella magnifica* larvae will readily resort to cannibalism if provided with inadequate food, and under similar conditions *C. magnifica* adults will eat conspecific eggs (JJS). Kanervo (1940, 1946) records that *C. magnifica* will eat the immature stages of some chrysomelid beetles, although this seems an improbable natural diet for *C. magnifica*.

The laboratory observations on *C. magnifica* diet, in conjunction with field data, argue very strongly for north-west European *C. magnifica* being dietary generalists. Although naturally *C. magnifica* rarely encounters some of the aphids that it has been fed in the laboratory, its potential dietary breadth appears to be similar to that of its generalist congener *Coccinella septempunctata*. Like *C. magnifica*, *C. septempunctata* flourishes on *Acyrtosiphon pisum*, *Aphis fabae*, and *Microlophium carnosum*, and suffers high mortality when fed *Aphis sambuci* and

Macrosiphum albifrons (Hodek, 1956, 1957; Blackman, 1965, 1967; Gruppe & Roemer, 1988; Emrich, 1991). These similarities may arise through common descent, and other *Coccinella* species probably also possess these dietary traits. *Coccinella septempunctata* has been used as a phylogenetically close model for the ancestors of *C. magnifica* before myrmecophily evolved, in a number of comparative studies (Sloggett, 1998; Sloggett et al. 1998; Sloggett & Majerus, 2000). The shared effects of particular types of aphid food reinforce the suitability of *C. septempunctata* for comparison with myrmecophilous *C. magnifica*, in research on the latter and its origins.

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