Habitat and dietary specificity in aphidophagous ladybirds (Coleoptera: Coccinellidae): Explaining specialization

John J. Sloggett
Tussen Beide Markten 45, 9712 CC Groningen, The Netherlands, E-mail: johnsloggett@yahoo.co.uk

In this paper I review the factors responsible for the evolution of dietary and habitat specialization in the aphidophagous Coccinellidae. Trade-offs related to foraging and capture efficiency, particularly body size, are probably more important in determining diet breadth than trade-offs related to aphid chemistry/nutritional suitability. Habitat specialization occurs when a species is able to persist on aphids in a particular habitat type for a long period of time: this is more important than aphid abundance. The trade-offs underlying habitat specialization remain a matter for speculation. The underlying factors responsible for ecological specialization in ladybirds may differ from those in other aphidophagous insects, due to adult feeding on aphids, which occurs to a much greater extent in ladybirds than in many other aphidophages.

Keywords: Coccinellidae, aphids, specialization, trade-offs

In one sense all aphidophagous ladybirds are specialized because their primary food consists of one particular group of homopteran insects. Aphids considered as a group are ubiquitous and it is unsurprising that ladybirds and members of other insect groups, such as lacewings and syrphids, have become specialized to feed on them. Much work on ladybirds has addressed how aphidophagy affects the life histories, ecology and behaviour of ladybirds and the adaptations that ladybirds use to effectively exploit aphid prey (e.g. Dixon 2000).

However, even within this already specialized mode of life there is also a further diversity of specialization. The ladybird Myzia oblongoguttata feeds on aphids on pine trees and other conifers and is rarely found elsewhere (Majerus 1994, Klausnitzer & Klausnitzer 1997). By contrast Adalia bipunctata feeds on aphids on a diversity of trees, shrubs and herbaceous plants and consumes a wide diversity of aphid species (e.g. Banks 1955, Mills 1981, Majerus 1994). Coccinella magnifica, on the other hand, feeds on a diversity of aphid species, but its habitat, in western Europe at least, is limited to the immediate vicinity of colonies of wood ants (Formica rufa group) (Sloggett et al. 2002).

We may divide this specialization into two types, diet-related and habitat-
related. Dietary breadth is the easier of the two to describe, and may be defined as the number of different aphid species that a ladybird species consumes and, more particularly, breeds on in the wild. It is not feasible to accurately quantify this for most species, particularly generalists, which may feed on tens or even hundreds of different prey species, and this simple definition glosses over some of the complexities of ladybird diet (see Hodek 1996, Michaud 2005 for reviews); however, within this framework it is generally possible on the basis of known data to establish how specialized the dietary breadths of individual species are in relation to each other.

A clear definition of habitat specialization is yet more elusive. The problem arises because there are many different ways of describing the habitat (Honek 1986, Honek & Hodek 1996): we might, for example, use microclimate, plant type or some other feature of the biotic or abiotic environment. Generally the habitat is described as we perceive it ourselves, based on host plant or some other important feature, for example the presence of ants for myrmecophiles (e.g. Majerus 1994), and this approach is used here. Even more than dietary breadth, it is not possible to provide a quantifiable measure of habitat specialization; however, again it is possible to say how specialized different species are in relative terms.

It is the dispersive adult ladybird that determines the diet and habitat of its larvae through oviposition preferences. Although the relationship between dietary and habitat specialization is close, it is not simple. The assumption that all aphids within the chosen habitat are suitable prey [i.e. (habitat) preference and (dietary) performance are linked] may be impossible to test rigorously: even within habitats as perceived by the researcher, both aphid and ladybird microclimatic and microhabitat preferences may be operating, thus aphids which appear to co-occur with certain ladybird species may not actually do so. However the evidence available does not support an invariable association between preference and performance. Although in England A. bipunctata feed and breed on the black bean aphid, Aphis fabae (e.g. Banks 1955), the aphid is a poor quality prey for this species (e.g. Blackman 1965, 1967a, El-Hariri 1966); this is also the case for some A. bipunctata prey on trees and shrubs (Hodek 1996). Conversely, many aphids which ladybird species do not encounter naturally seem to be suitable prey for breeding and larval growth in the laboratory (e.g. Majerus & Kearns 1989, Kalushkov & Hodek 2001). Although in many cases, dietary specialization is correlated with habitat specialization, such as in M. oblongoguttata and A. bipunctata mentioned above, there are a number of cases where species that consume a wide variety of prey exhibit restricted habitat preferences, such as C. magnifica and Coccinella quinquepunctata, which despite a catholic diet is limited to shingle habitats near water in Britain and nearby areas (Majerus & Fowles 1989, Sloggett & Majerus 2000a). It is noteworthy that the reverse is never the case: habitat generalists do not appear to exhibit dietary specialization.
In this paper I attempt to some extent to tease apart dietary and habitat specialization and to provide an overview of what we do and do not yet understand about what factors are responsible for ecological specialization (i.e. both types of specialization together) in aphidophagous ladybirds. The division I make between diet and habitat is to some extent artificial as an understanding of both is necessary to fully understand either. In some cases the reader may feel that some things which I assign to one section could be equally assigned to the other (for example foraging behaviour which is not only related directly to the prey but also the host plant habitat). This is certainly true: however, I here adopt a utilitarian approach, to hopefully provide a clear progression of the narrative. This is also not a comprehensive review of all aspects of ladybird specialization, merely its underlying causes. For further information the reader is referred to several older reviews and books (Majerus 1994, Hodek & Honek 1996, Sloggett & Majerus 2000a).

DIET BREADTH

Work on dietary breadth in ladybirds, like other insects, is centred around trade-offs: that is, a specialized ladybird that performs very well on aphid A will, as a consequence, perform badly on aphid B and vice versa. A generalist will perform moderately well on both aphids, but will not perform as well as a specialist on its preferred aphids. Trade-offs are a central tenet of evolutionary biology and underlie many important biological processes (e.g. Stearns 1992); their role in dietary specialization in ladybirds is unquestionable. However the nature of these trade-offs, i.e. what exactly is being traded off, has been a matter of debate.

Prey suitability trade-offs

A large proportion of the interest in dietary specialization in ladybirds and other aphidophagous insects has been focused on trade-offs related to diet suitability for growth or reproduction, as a consequence of nutritional differences or aphid chemistry (e.g. Albuquerque et al. 1997, Sadeghi & Gilbert 1999, Rana et al. 2002). There are two underlying reasons pertinent to ladybirds for this. Most work on dietary trade-offs has been concentrated on phytophagous insects, where diet suitability, especially the effects of plant chemistry, appears to be very important (Jaenike 1990, Schoonhoven et al. 1998); researchers on predatory insects have thus tended to wish to draw parallels between their own studies and those on phytophages. Additionally in aphidophagous ladybirds diet suitability has been extensively studied from the 1950s on, partly due to the ease of testing different aphid diets in the laboratory, and this approach has and continues to form the basis for the majority of discussion and debate about ladybird diet (Hodek 1996, Dixon 2000, Michaud 2005).

Apart from indirect evidence from other aphidophagous groups (Albuquerque et al. 1997, Sadeghi & Gilbert 1999), evidence for suitability-relat-
ed trade-offs operating in ladybirds has relied on a single study that claimed that trade-offs in performance related to aphid chemistry were of primary importance in determining dietary breadth (Rana et al. 2002). In this study, two groups of *Adalia bipunctata*, a generalist, exhibited increased fitness on one of two aphids, *Acyrthosiphon pisum* and *Aphis fabae*, after selection for enhanced performance on that aphid as might occur when dietary specialization evolves. They were also found to perform better on their own prey than ladybirds from the other group. However, this result only demonstrates that performance on the two prey is not positively correlated; performance on the two prey species might be uncorrelated (*i.e.* there is no trade-off), in which case it is hardly surprising that lines selected for enhanced performance on one prey type perform better on it than ladybirds from the other group. Some evidence that this may actually be the case can be seen when the final fitness parameters for the selected lines on the alternative prey are compared to those of the other selection group from early in the selection process. Here differences in fitness are small or non-existent rather than being lower in the selected lines, as would be expected were the trade-off necessary for dietary specialization to be operating.

Even were Rana *et al.*'s method to be modified to include unselected lines, which would act as a better comparator for the selected ones, these are difficult to sustain in the laboratory. Ladybirds provided with both types of prey might feed more or less on one of them and inadvertent selection might occur, ultimately giving misleading results. A different and arguably more reliable approach has been used by Ueno (2003) and Fukunaga & Akimoto (2007) both using the generalist *Harmonia axyridis*. In both cases they used a large number of genetic lines to examine how performances on two different prey types were correlated across these lines. Both Ueno, using *Acyrthosiphon pisum* and *Aphis craccivora*, and Fukunaga & Akimoto, using *Aulacorthum magnoliae* from two different host plants differing in their dietary suitability for *H. axyridis*, found positive correlations between performance on their two aphids. However in both cases, only larval characters (development time, growth rate, pupal size) were examined. Because different life history components may respond differently to dietary treatments (*e.g.* Sadeghi & Gilbert 1999, Michaud 2005), additional measures of prey suitability, such as adult fecundity, are desirable: only with these measures can the overall fitness on the different prey be calculated.

Circumstantial data arguing against an important role for prey-suitability related trade-offs in determining diet breadth may also be found in more basic studies of feeding and natural history in ladybirds. In contrast to phytophagous insects, there are no ladybirds that are known to be specialized on particularly toxic prey, as might be expected were prey chemistry to be a significant factor in determining specialization. Furthermore, as discussed above, ladybirds may perform poorly on aphids that they feed on naturally and well on aphids that they do not. While other explanations such as evolutionary lag (Sloggett &
Majerus 2000a) may be tenable to explain this pattern and some more supportive feeding data can also be found in the literature (Kesten 1969, Majerus 1993), overall the evidence acquired thus far does not support a major role for prey suitability related trade offs playing in dietary specialization. However, because of the limitations of studies thus far conducted on prey suitability trade-offs in aphidophagous ladybirds (Rana et al. 2002, Ueno 2003, Fukunaga & Akimoto 2007), additional work is required to verify that this is indeed the case.

**Prey switching**

It has been suggested that switching between different prey might in itself impose a cost and that specialists trade-off a lowered fecundity consequent on remaining with resources for longer with a cost to generalists of regularly changing prey species (Sloggett & Majerus 2000a). It is known from coccidophagous ladybirds that such switching can lead to a temporary decrease in fecundity (Hattingh & Samways 1992), although no such experiments have been carried out with aphidophagous species.

Specialist aphidophages are known to be found associated with lower densities of aphids than generalists (Sloggett & Majerus 2000a, b). However, more recent work on body size and on foraging adaptations in specialist ladybirds (see next sections) suggests that there is no intrinsic cost to this association, but that it arises due to increased efficiency; thus one side of this putative trade-off does not appear to be supported. Additionally, while it remains possible or even probable that generalists do suffer some cost of frequent prey switching, it is questionable whether within their lives individuals of even generalist ladybirds switch prey sufficiently often that a major cost would be incurred: although generalist species may feed on many types of aphids, not all individuals feed on all prey types during their lives. Thus, while prey switching is certainly of interest in the context of prey specialization, it seems unlikely that in itself it can explain the evolution of specialized feeding in aphidophagous ladybirds.

**Finding and catching prey: foraging adaptations**

In spite of the wealth of data in the literature describing how ladybirds locate and catch aphid prey (reviews in Hodek 1996, Dixon 2000), this aspect of ladybird feeding ecology has received relatively little attention as a potential factor determining specialization until relatively recently. This is perhaps surprising: almost thirty years ago, Mills (1979) argued that the suitability of an aphid species as ladybird prey was most influenced by capture efficiency. Although this work is sometimes cited, the historical adherence to prey suitability and the greater difficulty of designing and carrying out realistic experiments on prey foraging and capture compared to prey suitability have arguably meant that Mills' conclusions have not been carried through to their logical endpoint.

Our knowledge of the foraging behaviour of dietary specialists has also lagged a long way behind that of generalists. Most research on aphidophagous
ladybirds, including on feeding, has in fact been carried out on a rather narrow range of generalist ‘model’ species, primarily due to their perceived importance in aphid biological control (Sloggett 2005). However, in a recent paper Bethiaume et al. (2007) compared *Anatis mali*, which feeds predominantly on conifer aphids, with the generalist *Harmonia axyridis*, which also sometimes feeds on conifers, on the aphid *Mindarus abietinus* in Christmas tree plantations. Both adults and larvae of *A. mali* were more active in foraging for *M. abietinus*, which generally occurs at rather low densities, and adult *A. mali* exhibited a characteristic behaviour of using its head to open up compact conifer needles and penetrate bursting buds in order to feed on concealed aphids there. In consequence *A. mali* was able to feed earlier on developing aphid colonies than *H. axyridis*, exhibited greater reproductive synchrony with aphid populations and had an adult-to-adult reproductive rate three times that of *H. axyridis*. Both the distribution of *A. mali* on the trees and microhabitat ovipositional preferences also differed from those of *H. axyridis*.

Although Berthiaume et al. emphasize the specialist-generalist difference, they also conclude that these differences may be a consequence of a long period of coevolution between the North American *A. mali* and *M. abietinus* compared to that for *H. axyridis*, which has only been established in North America for about 20 years. However, in its native range *H. axyridis* also predates aphids on conifers (e.g. Sasaji 1980), thus the difference seems more likely to be a case of a dietary specialist evolving specific behaviour to more effectively forage within its more limited prey spectrum. Neither, has a trade-off specifically been identified: to do this it would be necessary to show that on non-conifer aphids, *A. mali*’s foraging behaviour was less efficient than that of *H. axyridis*. Nonetheless it is easy to envisage that *A. mali*’s needle loosening behaviour, for example, might result in a lower foraging efficiency on other types of plants, if aphids were not concealed in buds.

In addition to Berthiaume et al.’s study, work on myrmecophilous ladybirds has followed that on chrysopids (Eisner et al. 1978, Milbrath et al. 1993) in identifying a number of behavioural and chemical adaptations to potentially aggressive aphid-tending ants that will consequently increase foraging efficiency on ant-tended aphids (reviewed in Majerus et al. 2007), but again the underlying trade-offs have not been fully investigated. It is clear that unlike prey suitability and body size (discussed below) no one single trade-off is involved in such cases as a diverse collection of differing adaptations in behaviour and physiology are involved; in consequence their evaluation must proceed on a specific case-by-case basis.
Catching prey: body size

The role that body size plays in ladybird specialization has been overlooked for a long period of time, although recent work suggests it may be a key trade-off. For a long time it was considered that there was no relationship between the body size of aphidophagous ladybird species and the size of the prey that they consumed (Dixon & Stewart 1991, Stewart et al. 1991, Dixon 2007). Predator size was considered to be exclusively related to prey density, with smaller species feeding and reproducing on lower aphid densities (Dixon 2007). Recently, it has been shown that the relationship between predator size, prey size and prey density is more complex than was previously assumed (Sloggett 2008). Small ladybird species can feed on low densities of small aphid species, which they can easily catch. However, large ladybird species cannot because there is insufficient aphid biomass to sustain high levels of reproduction for a large ladybird that will consume more prey; large ladybirds thus require high densities of small aphids. However, large ladybirds can feed on low densities of large aphid species because they can easily capture even the biggest aphids, which are much greater energy sources than small ones, by virtue of their size. Small ladybirds cannot catch the larger instars of big aphid species and require high densities of large aphid species, where there will be sufficient numbers of small instars that they can easily capture.

This means that while small ladybirds can generally exploit small aphid species, they can only sometimes exploit large ones, and that the reverse is true for large ladybirds. Some degree of size matching between predator and prey is expected. Specialists that exploit a narrower prey spectrum should more closely match the size of their prey than generalists, which will adopt a ‘one-size-fits-all’ medium-sized strategy to exploit a large range of prey sizes. Because a specialist’s body size will be optimized for exploiting its particular prey, specialists can thus exploit lower densities of their prey than generalists, allowing them to remain associated with fewer prey for longer periods of time (Sloggett 2008). Since body size is known to be heritable in ladybirds (Ueno 1994), it would thus comprise a clear trade-off influencing specialization.

Because specialists are expected to more closely match the size of their prey, they should exhibit a greater diversity of body sizes than medium sized generalists. This has been tested for native British aphidophagous Coccinellini, which are all ecologically well-characterized (e.g. Majerus 1994). After they were dichotomized into dietary specialists and generalists this prediction was confirmed: the specialist group showed a greater size range with some specialist species being bigger and smaller than generalists (Sloggett 2008). Some specialists do occur within the size range of generalists: however, as dietary breadth observed today is also a consequence of evolutionary history and phylogeny this is unsurprising and in no way invalidates the contention that body size trade-offs are significant in determining dietary breadth and specialization (Sloggett 2008).
Indirect evidence, related to aphid density, also supports the assertion that body size and dietary breadth are related. It has been known that specialized ladybirds tend to exploit lower densities of aphids than generalists for some time (Sloggett & Majerus 2000a, b). Gagné & Martin (1968) showed that the conifer aphid specialists Anatis mali and Mulsantina picta both tend to exploit aphids on older pine trees where densities are lower, whereas more generalist Coccinella species utilize younger trees with higher aphid densities. Although the data is more scattered, the same is also true for European conifer aphid specialists (Sloggett & Majerus 2000b and incl. refs). Differences in foraging behaviour (Berthiaume et al. 2007; see above) certainly also contribute to this pattern; however, it is notable that some conifer aphid specialists (Anatis, Myzia) are extremely large as are a number of common conifer aphids, notably the members of the genus Cinara. A more phylogenetically controlled example of the relationship between specialization and aphid density comes from Adalia bipunctata, which is a broad aphidophagous generalist and its sibling species Adalia decempunctata, which is more specialized, feeding and breeding almost entirely on tree and shrub aphids (e.g. Hemptinne & Naisse 1988, Majerus 1994). In the course of characterizing the habitat preferences and niche overlap of a number of Czech ladybird species, Honek (1985), showed that the more specialized A. decempunctata is associated with lower aphid densities than A. bipunctata.

It is also noteworthy that body size and capture efficiency provide an automatic link between preference and performance (Sloggett 2008). Ladybirds that are not satiated are likely to disperse elsewhere to find food. If body size is a major determinant of capture efficiency then ladybirds of the ‘wrong’ size in a patch of aphids of a particular size and density will not catch a sufficient number of aphids, will lay few or no eggs there and will disperse from the patch: thus a preference could be a passive satiation-mediated process. Additional means of locating the ‘right’ aphid colonies would be likely to evolve over evolutionary time to reduce patch searching time: for example Anatis ocellata use of pine volatiles to locate conifer aphids (Kesten 1969). However such additional mechanisms are not initially necessary in the evolution of a ladybird-aphid association to provide a means for a ladybird to find suitable (in terms of capture efficiency) prey. By contrast, it is unlikely that such a mechanism would work if prey were dietarily unsuitable as satiation remains possible even if what has been consumed is of poor quality or even toxic.

The broad scale evidence obtained thus far clearly supports body size being a significant trade-off influencing diet. Future studies need to be directed at specific systems to further test the role that body size plays in the evolution of specialization. It is also necessary to look at other life history stages, which thus far have received little attention: immature size appears to play a role in prey specialization in chrysopids (Tauber et al. 1995, Albuquerque et al. 1997).
The relative importance of different trade-offs in determining diet breadth

The studies conducted thus far are more supportive of trade-offs related to foraging and capture of prey being important in determining dietary breadth, rather than trade-offs related to prey suitability and (if any) prey switching. Body size and its relationship with capture efficiency seems to be a particularly important unifying factor across a broad range of species, given the ability of such arguments to explain the size distributions of dietary specialists and generalists. As discussed above, behavioural and other foraging adaptations comprise a diverse collection of trade-offs and generalities are difficult to make: while they are likely to be of considerable significance in certain cases, such as in cases of myrmecophily (e.g. Sloggett et al. 1998, Sloggett & Majerus 2003) they may not be of universal importance. However, it may require many differing studies to establish whether this is indeed so.

Although further work is required to verify this, the evidence for dietary suitability playing a significant role in specialization is exceedingly weak and prey suitability does not appear to be primary importance, although it may be a secondary factor. Reasons for this may be sought in the feeding ecology of ladybirds. Unlike many other aphidophagous insects, including syrphids (Gilbert 1993) and to a lesser extent chrysopids (Principi & Canard 1984, Canard 2001), adult ladybirds, like the larvae, rely predominantly on aphids as food (Hodek 1996). Ladybird fecundity and consequent fitness are strongly influenced by the amount of aphid prey that they consume (e.g. Dixon & Guo 1993) and thus the capture efficiency of adults. By contrast in syrphids, for example, in which the adults do not feed on aphids, adult fecundity and fitness will be more strongly influenced by larval fitness parameters and thus larval aphid prey suitability. The adult requirement for aphids means that throughout much of the year, ladybirds must continuously feed on aphids if they are available. As aphids are an ephemeral and sometimes unpredictable food source, the majority ladybirds must on occasions also exploit atypical prey, notably late in the season when their own prey are scarce and they are not breeding (Sloggett & Majerus 2000a). Because of this necessity to utilize unusual food sources, the underlying digestive physiology of ladybirds might have evolved in a way that strong negative prey suitability-related trade-offs do not operate. Ultimately ladybird dependence on aphid prey as adults probably explains why prey suitability related trade-offs might play a significant role in some other aphidophagous groups (e.g. Sadeghi & Gilbert 1999) but do not appear to do so in ladybirds.

Habitat utilization and specialization

Habitat specialization and prey specialization are closely intertwined, though not perfectly correlated, and it is difficult to delineate a fixed border between the two. In aphidophagous ladybirds, the primary factor responsible for habitat pref-
ence appears to be resource-based. Although natural enemies or competitors may exert an effect on, for example, microhabitat ovipositional preferences or patch choice (e.g. Rå icka 1997, Schellhorn & Andow 1999), there is little evidence that they exert any strong role in broad species habitat preferences: that is, enemy free space (Jeffries & Lawton 1984) is not a primary concern.

Two examples serve to support this view. A comparison of Adalia bipunctata, which occurs in trees, shrubs and herbaceous habitats, and Adalia decempunctata, which is largely restricted to trees and shrubs, showed that their natural enemy spectrum was largely the same and thus that natural enemies were unlikely to have played a role in their habitat preferences (Sloggett & Majerus 2000a). Similarly although the myrmecophile Coccinella magnifica exhibits exceedingly low parasitization rates by the coccinellid parasitoid Dinocampus coccinellae, unlike the generalist Coccinella septempunctata (Majerus 1989, 1997), this is because the ladybird is an unsuitable host for the parasitoid, rather than because of enemy free space provided by the ants with which it lives (Sloggett et al. 2004). This is unsurprising: the majority of ladybirds are chemically defended (Daloze et al. 1995, King & Meinwald 1996) and current evidence suggests that chemical defence evolves to provide the primary protection for ladybirds against the natural enemies occurring in the habitat in which they have evolved to live (Sloggett 2005).

It is therefore necessary to return to ladybird relationships with their aphid prey. Trade-offs determining dietary breadth can explain why specialized ladybirds do not eat other types of prey, but do not fully explain why specialists specialize to eat the aphids they do and thus why they live where they do. To understand this it is necessary to know what features of certain types of aphids and their environments make them suitable for specialization. Two schools of thought exist on this subject, one centred on aphid abundance and the other concentrated on longevity of the aphid resource.

**Aphid abundance**

Rana et al. (2002) have argued that aphid abundance is important in determining specialization. They point out, correctly, that a high abundance renders an aphid source of high value for oviposition and larval development. Their argument is consistent with their assertion that prey suitability trade-offs are responsible for dietary specialization; if aphids of a particular type are extremely abundant then many ladybirds will feed there and the fittest of these will be the least well adapted to feed other prey sources. However their arguments are less consistent with body-size related dietary trade-offs. With an abundant food source, capture efficiency related selection is likely to be relaxed and the largest individuals are likely to be invariably the fittest. This does not match the observed pattern of body size in dietary specialists, which may also be very small. Similarly the evidence that many specialists feed on low aphid densities is also inconsistent with their arguments.
Furthermore, as conceded by them, an aphid source which is abundant but short-lived will not alone lead to enhanced fitness if the ladybirds feeding on it cannot exploit an alternative resource before or afterwards. One possibility is that the breeding seasons of specialists are shorter than generalists and synchronized with abundant prey. This is known in chrysopids, in which the myrmecophilous *Chrysopa slossonae* is primarily univoltine whereas its generalist sibling species *Chrysopa quadripunctata* is often multivoltine (Tauber & Tauber 1987, Tauber et al. 1993); however, there is little evidence that this is true in ladybirds. Both *Adalia bipunctata* and *Adalia decempunctata* undergo a single generation in Britain and sometimes produce a partial second generation (Majerus 1994) and in Bayreuth (Bavaria, Germany) both species are bivoltine (J.J. Sloggett pers. obs.). Nor is there any evidence that the length of specialist ladybird breeding seasons is shorter. Both *A. bipunctata* and *A. decempunctata* reproduce in Britain between about mid-April and early July and in Bayreuth between about mid April and early August (J.J. Sloggett pers. obs.). The breeding season of the myrmecophile *Coccinella magnifica* is considerably longer than that of its generalist congener *Coccinella septempunctata* in Britain: while *C. septempunctata* generally breeds from mid-April to late June, *C. magnifica* regularly breeds until late July (J.J. Sloggett unpublished data).

Thus attempts to relate ladybird specialization to aphid abundance are inconsistent with a number of other factors associated with specialization in ladybirds. It therefore does not seem that habitat specialization is closely linked to prey abundance.

### Aphid resource longevity

The original arguments in favour of habitat preferences being linked to aphid resource longevity sprang from the observation that certain types of habitat specialization were associated with particularly long-lived aphid resources: examples include ant-tended aphids, which tend to persist in substantial numbers later in the year than untended ones, and aphids in wetland areas, which also appear to persist for longer than ones in drier biotopes (Sloggett & Majerus 2000a, b). A long-lived resource permits continued reproduction in the same habitat over a long period of time; such a resource may not consist of one type of aphid but a number of aphid species occurring together in the same habitat. This can explain why some dietary generalists, such as the myrmecophile *Coccinella magnifica* exhibit a habitat specialization: *C. magnifica* may be found breeding around the same ant colonies, although on different aphid species, throughout their entire breeding season (J.J. Sloggett pers. obs.). The mechanism for the evolution of such habitat preferences is probably very simple. Ancestral ladybirds exploit a long-lived resource when aphids in their more typical habitats are scarce and ultimately specialize to use this resource all the time: this appears to be the case for *C. magnifica*’s myrmecophily (Sloggett & Majerus 2000b).
Additional support for this argument comes from a handful of European species that appear to change their habitat preferences across their range. In all cases these ladybirds exhibit greater habitat specificity in north western Europe and decreased habitat specificity towards the south and east (Sloggett & Majerus 2000a). Two particularly well researched cases are those of *Coccinella quinquepunctata* and *Coccinella magnifica*. In Britain and northern France *C. quinquepunctata* is restricted to shingle habitats near water (e.g. Rye & Sharp 1865, Majerus & Fowles 1989, Mann et al. 1993) whereas further west in, for example, Germany and the Czech republic *C. quinquepunctata* is found in a diversity of non shingle habitats, that are also not necessarily associated with water (e.g. Honek 1985, Klausnitzer & Klausnitzer 1997, Nedved 1999). Similarly although *C. magnifica* is an obligate myrmecophile associated with *Formica rufa* group ants in north-west- and central Europe, in the south and east it seems probable that it is only facultatively myrmecophilous (Sloggett et al. 2002). Interestingly, as one moves south and east aphids generally remain abundant for longer leading to longer breeding seasons for ladybirds and a greater number of ladybird generations per year. As noted above, *A. bipunctata* are primarily univoltine and breed from mid April to early July in Britain, but are fully bivoltine and breed from mid April to early August in Bayreuth. Under the latter circumstances the benefits to a specialist of remaining in their particular habitat for the entire breeding season are decreased, as aphids remain to be exploited outside of this habitat for longer. Thus in southern and eastern areas, when the benefit of resource longevity in the specialist habitat compared to other habitats is lost, so is the habitat preference.

Thus far only resources that are intrinsically long-lived have been discussed. In other cases adaptation in the specialist facilitates longer exploitation of resources that are not intrinsically long-lived (e.g. *Adalia decempunctata* on deciduous trees). This is strongly linked to dietary specialization and to body size trade-offs and foraging adaptations: both facilitate more efficient location and capture of prey and thus exploitation of lower aphid densities; in its turn the exploitation of lower aphid densities means that aphid resources can be exploited earlier and for longer.

A hypothetical example serves to show how such specialization could evolve: a medium sized generalist feeds on several aphids of different sizes. When feeding on a small aphid species, the largest individuals of this ladybird require the highest aphid densities to sustain egg laying and thus are associated with this aphid for the shortest period of time, while the smallest can continue to reproduce at lower aphid densities and remain associated with this aphid for longer. Over time these smaller ladybirds evolve a habitat preference that maintains the association with the smaller aphids and become a separate species specialized on the small aphids. The new specialist species is smaller than the ancestral generalist and can utilize the same resource for longer. Such a scenario could explain
the evolution of the habitat preferences of *Adalia decempunctata* for trees and shrubs, from an ancestor with broader *A. bipunctata*-like habitat preferences.

Aphid resource longevity can explain the evolution of habitat specialization: specialists specialize on long lived resources, or adapt to exploit the same resources for longer. The importance of resource longevity again probably reflects the fact that ladybird adults eat aphids: because adult ladybirds are foraging for aphids for much of the year, exploiting these aphids for breeding is favoured. Again in this respect, ladybirds differ from some other aphidophagous insects that feed primarily on aphids as larvae or use a resting stage to limit the length of the breeding season to allow specialization on particularly abundant prey.

**Habitat-related trade-offs: why don’t habitat specialists occur elsewhere**

It is apparent in many cases of closely related dietary and habitat specialization that specialists may not move to other habitats because the aphids in these habitats would be difficult to exploit. However, in the cases of many dietary generalist habitat specialists the question of why they are not found elsewhere for at least part of the season is a problematic one. It is easy to envisage why *Coccinella magnifica* is found with ant-tended aphids when aphids elsewhere are scarce, but less so when other prey are common, particularly as untended or non-tended aphids form a substantial part of its diet even in the presence of ants (Sloggett et al. 2002, Sloggett & Majerus 2003). Furthermore it is of a similar size to the generalist *Coccinella septempunctata*, so is unlikely to have problems exploiting other aphid prey: why therefore does it remain where it does?

We do not yet have any clear answers to such a problem, although some ideas are promising. One possibility is that adaptation to other factors such as microclimate may make such species less fit elsewhere. For example *Anisosticta novemdecimpunctata* and *Hippodamia tredecimpunctata* which both live near water use evaporative cooling to reduce body temperature under warm conditions (Pekin 1996). In less humid habitats, such a mechanism might prove costly. Different ladybird species do appear to possess characteristic microclimatic preferences (Honek 1985): thus microclimatic trade-offs seem of likely considerable importance in maintaining habitat associations.

It has been suggested that dispersal might in itself be costly and that specialist ladybirds remain in the same habitat to avoid such costs (Sloggett & Majerus 2000a). This was suggested for *C. magnifica*, which is an extremely sedentary species, with ladybirds breeding round the same ant colonies all season and across multiple seasons (Sloggett & Majerus 2000b). It does seem likely that in cases such as this, relocating suitable habitat when aphids become scarce might prove problematic if ladybirds have strayed a long way from their vicinity. However, an assessment of the full costs of dispersal is likely to prove difficult to achieve and currently such a hypothesis remains open.
Another possibility, related to neural processing and information, is that generalists are less efficient than specialists in locating suitable habitats as a consequence of the habitat diversity they face. This idea, that animals may be constrained in their habitat preferences by the amount of information from the environment that they are able to process, has been most frequently discussed in the context of phytophagous insects choosing host plants (Levins & MacArthur 1969, Fox & Lalonde 1993, Bernays 2001) but may be equally applicable to predaceous insects (e.g. see Vet & Dicke 1992, Steidle & van Loon 2003). Further work is needed to examine the relative efficiencies of specialist and generalist ladybirds in detecting aphids. However, it is worth noting in this context that habitat specialists appear to use rather simple chemical habitat cues: for example, the conifer specialist *Anatis mali* uses pine volatiles (Kesten 1969) and the myrmecophile *Coccinella magnifica* uses ant trail pheromones (Godeau *et al.* 2003). By contrast the cues used by generalists appear to be much more variable (e.g. Blackman 1967b, Sengonca & Liu 1994, Mondor & Warren 2000, Pettersson *et al.* 2005).

Thus, a number of potentially fruitful lines of enquiry exist for the future, but at the moment it is impossible to assess their relative importance. In all the examples given here, even fundamental knowledge is limited: for example, although our understanding of how ladybirds locate habitats and prey has improved in recent years it is still far from complete. Thus we are still some considerable way from understanding fully the trade-offs involved in habitat (as opposed to prey) specialization.

**CONCLUSIONS**

Since the last review of specialization in ladybirds was published (Sloggett & Majerus 2000a), a considerable amount of relevant work has been carried out, which has done much to clarify thinking on the matter. Nonetheless, as indicated in many of the sections above, firm conclusions in many areas remain difficult to make and additional work on most aspects of ladybird specialization is required. As is also apparent, much of the work that has been carried out has been concentrated on a rather narrow range of systems, and the basis of our knowledge of ladybird specialization needs to be expanded: there remain some exceedingly suitable, but under-researched systems in this respect (e.g. Sasaji 1980).

An underlying theme of this paper has been the differences between ladybirds and other aphidophagous insects, which may affect the evolution of specialization. The comments on the limitations of currently available work on specialization in ladybirds also apply to other aphidophages and a fuller understanding of the differences between these groups is likely to be informative. In general aphidophagous insects provide good systems with which to study predator specialization due to the simplified prey range involved and the large body of
existing research, in part linked to the capacity of these groups for aphid biocon-
trol.

Such research may not just expand our knowledge base, but may have value in an applied context. Most ladybirds used in aphid biocontrol are generalist species: their success has been patchy at best (Dixon 2000) and has had undesirable side-effects (e.g. Koch 2003, Harmon et al. 2007). Specialized ladybirds may be more useful and effective as biocontrol agents in agroecosystems where they occur (Sloggett 2005): current evidence indicates that this is indeed the case (e.g. Goidanich 1943, Cecilio & Ilharco 1997, Leather & Kidd 1998, Berthiaume et al. 2007). Thus ultimately further work on specialized ladybirds and other aphidophagous insects may be of value beyond that to the interested naturalist or academic.

REFERENCES


Blackman, R.L. 1967b. Selection of aphid prey by Adalia bipunctata L. and Coccinella 7-


Dixon, A.F.G. & Guo, Y.Q. 1993. Egg and cluster size in ladybird beetles (Coleoptera:


Redtenbacher, a myrmecophilous coccinellid, to aggression by wood ants (Formica rufa group). I. Adult behavioral adaptation, its ecological context and evolution. J. Insect Behav. 11: 889-904.


