Habitat preferences and diet in the predatory Coccinellidae (Coleoptera): an evolutionary perspective

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Coccinellids (ladybird beetles) exhibit considerable diversity in habitat and dietary preference and specificity. This is evident even when comparing species within some coccinellid genera. Resource limitation and competition are suggested as of greatest importance in the evolution of coccinellid habitat preferences. Dietary and habitat specialization has probably occurred in some lineages within broader preferences possessed by generalist ancestors, to avoid the costs associated with migration between habitats and prey switching. Feeding in atypical habitats, on alternative food, when optimal prey are scarce, is likely to have been of great importance in facilitating evolutionary shifts to novel diets and habitats. The broad host ranges of many coccinellid parasitoids and observed interspecific differences in parasitoid prevalence resulting from physiological differences between coccinellid species argue that enemy free space has been of limited importance in habitat and prey shifts in this group. Rapid change may occur in coccinellid foraging patterns, perhaps due to conditioning, and coccinellids may swiftly adapt to new habitats through selection acting on the expression pre-existing traits. Diet, as a determinant of coccinellid migration and gene flow, is likely to affect probable modes of speciation in different coccinellid groups. Parapatric speciation and possibly sympatric speciation are suggested as of possible importance in the genesis of new coccinellid species through prey and habitat shifts.

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ADDITIONAL KEYWORDS:—exploitation competition – prey scarcity – feeding preference – habitat shift – aphidophagy – coccidophagy – specialization – enemy free space – migration – speciation.

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INTRODUCTION

The causes and consequences of habitat shifts have received considerable attention over the last forty years. Different workers have emphasized either resources and exploitation competition or apparent competition and enemy free space as factors responsible for moulding the ecological niches which organisms occupy (MacArthur & Levins, 1967; MacArthur, 1972; May & MacArthur, 1972; Holt, 1977; Jeffries & Lawton, 1984). Similarly, there has been much debate over the importance of geographic isolation for speciation arising as a consequence of host or habitat shifts (Mayr, 1963; Futuyma & Mayer, 1980; Tauber & Tauber, 1989; Bush & Smith, 1997).

A large amount of research on evolutionary changes of habitat and diet has been carried out on insects. Insects often occupy habitats which are relatively easily described, and they are highly abundant. Their importance in natural ecosystems cannot be underestimated. Work on phytophagous insects has suggested that in this group enemy free space is of most importance in mediating habitat and dietary preference (Lawton & Strong, 1981; Strong, Lawton & Southwood, 1984; Bernays & Graham, 1988; Holt & Lawton, 1993 but see Berdegue *et al.*, 1996). Phytophagous insects have also emerged as a paradigm for proponents of sympatric speciation (Tauber & Tauber, 1989; Bush & Smith, 1997). Factors influencing the distribution of parasitoids have also been extensively considered (May & Hassell, 1981; Völkl, 1992; Janssen *et al.*, 1995; Klopfer & Ives, 1997). The causes and consequences of evolutionary habitat shifts in predatory insect groups have, however, been less consistently researched (but see, for example, Tauber & Tauber, 1989; Tauber *et al.*, 1993; Gotelli, 1997; Mizuno *et al.*, 1997).

The biology of predatory Coccinellidae (ladybird beetles) has generally been well studied, in part due to their potential as biological control agents (Majerus, 1994; Hodek & Honěk, 1996; Obrycki & Kring, 1998). Despite numerous studies of habitat use in this group (Honěk & Hodek, 1996), the causative factors of habitat shifts within the group remain largely unexplored (Majerus, 1994; Honěk & Hodek, 1996). Furthermore, speciation in the Coccinellidae has rarely been considered, except in the case of phytophagous species (Katakura, 1997), and coccidophagous *Chilocorus* species, which exhibit karyotypic variation (Smith, 1959, 1966; Zaslavskii, 1963, 1996). In this paper it is suggested that resource limitation is of greatest importance in the evolution of habitat preference in predatory coccinellids. Homopteran prey scarcity occurring late or early in the active season of these beetles is suggested as a major driving factor in the evolution of novel dietary and consequent habitat preferences. Possible patterns of speciation in the group are also considered.

Dietary and habitat evolution within phytophagous coccinellid groups is not considered here, although the evolution of phytophagy in ancestrally predatory groups is discussed. The voluminous literature on plant-eating insects includes some

work on the evolution of diet and habitat preference in phytophagous coccinellids (Ohgushi & Sawada, 1985a, b; Katakura, 1997; Kobayashi *et al.*, 1998). The consideration of predatory coccinellids here reflects the author's experience, primarily of aphidophagous members of the tribe Coccinellini with temperate distributions. The Coccinellini have been the most intensively studied coccinellid group and there is a dearth of information on some groupings, particularly in the case of smaller and less conspicuous coccinellids such as occur in the subfamilies Coccidulinae and Scymninae. It should be emphasized from the outset that the conclusions of this paper may not necessarily hold true for all predatory coccinellids, although many are likely to. Wherever possible, predatory coccinellids which are not members of the Coccinellini have been discussed. This paper is intended to stimulate further research in this area: as such many of the ideas contained in it are speculative, and more work is required to confirm or refute their validity.

HABITAT PREFERENCE AND DIET IN PREDATORY COCCINELLIDS

There are in excess of 5000 named coccinellid species (Kuznetsov, 1997), exhibiting considerable variability and specificity in both habitat preference and diet (Hodek, 1993, 1996a; Honěk & Hodek, 1996). Whilst individual tribes within the Coccinellidae tend to predominantly feed on one category of food, either coccids, aphids or plant material, there are very numerous exceptions to the extent that discussion of the dietary specializations of entire tribes may be pointless (Hodek, 1996a).

The relationship between diet and habitat preference in coccinellids is clearly a close one. The prey of coccinellids are usually themselves phytophagous and restricted to one or a few species of plants. Coccinellids which are restricted to particular prey are thus restricted to particular kinds of plant. This is most clearly illustrated by the species *Myzia* (= *Sospita*) *oblongoguttata* (L.), an extreme dietary specialist on conifer aphids, mainly of the genus *Cinara* (Iablokoff-Khnzorian, 1982; Majerus, 1993, 1994). This species is almost exclusively restricted to conifer trees (Majerus, 1994). Within the habitat, there are well-studied behavioural mechanisms which maintain association between coccinellid species and their prey (reviewed in Hodek, 1996a). The habitats in which coccinellid larvae occur are clearly determined by adult oviposition preferences (Honěk & Hodek, 1996).

The association between 'essential' prey, on which a coccinellid species may successfully breed and complete its development (Hodek, 1973, 1996a), and habitat cannot be considered a perfect correlation. In the laboratory, 23 of 25 predatory British coccinellids will feed and breed on the pea aphid, *Acyrthosiphon pisum* (Harris). Only seven of these species have been found feeding *A. pisum* in the wild, and some coccinellids which can be reared it, for example conifer specialists, would be most unlikely to ever encounter it naturally (Majerus, 1994). This ability to deal with unusual prey might result from a need to effectively convert atypical food to energy when the more typical prey resource is scarce (see below). Alternatively, such cases may represent examples of evolutionary lag, whereby species which now live in one habitat for most of the year, retain the ability of more generalist ancestors to reproduce on a more catholic diet.

Some coccinellids are more restricted in their habitat preferences than their prey. For example *Myrrha octodecimguttata* (L.) is largely restricted to the crowns of older

pine trees (Klausnitzer, 1968; Majerus, 1988) although its aphid prey most certainly occurs elsewhere, on lower branches and on younger trees. In such cases prey density is a significant distributional factor (Gagné & Martin, 1968; Honěk, 1985). Microclimatic suitability is also of probable importance (Rosen & Gerson, 1965; Ewert & Chiang, 1966).

Dietary and habitat specificity varies markedly within the Coccinellidae. For example, amongst the primarily aphidophagous members of the tribe Coccinellini, *Adalia bipunctata* (L.) and *Coccinella septempunctata* L. can feed upon many species of aphid and occur in a variety of habitats (Majerus, 1994; Hodek, 1996a; Honěk & Hodek, 1996). At the other end of the spectrum of prey and habitat specificity is *M. oblongoguttata*, which is highly restricted in both diet and habitat (see above). Through much, or perhaps even the entirety of its range, all life-history stages of *Coccinella magnifica* Redtenbacher (= *C. distincta* Faldermann, *C. divaricata* Olivier) are restricted to the vicinity of *Formica* ants, primarily wood ants, *Formica rufa* group (Donisthorpe, 1896, 1919–1920; Pontin, 1959; Wiśniewski, 1963; Majerus, 1989; Sloggett, 1998): *Coccinella magnifica* is thus highly habitat specific, although it is a generalist aphidophage (Sloggett, 1998; J. Muggleton pers. comm.; J. J. Sloggett unpub. data).

Some members of the Coccinellini have abandoned aphidophagy partially or even completely. *Aiolocaria hexaspilota* (Hope) (= *A. mirabilis* (Motschulsky), *Coccinella heiroglyphica* L. and *Coleomegilla maculata* (Degeer) all eat immature Coleoptera (Iwata, 1932, 1965; Hippa, Koponen & Neuvonen, 1977; Hippa, Koponen & Laine, 1978; Hippa, Koponen & Roine, 1982, 1984; Iablokoff-Khnzorian, 1982; Groden *et al.*, 1990). *Coleomegilla maculata* is noteworthy as highly polyphagous, readily consuming both aphids and pollen, as well as non-homopteran invertebrates (Britton, 1914; Conrad, 1959; Putman, 1957, 1964; Benton & Crump, 1981). Some groups closely allied to the Coccinellini have adopted pollenivory and mycophagy: both are major constituents of the diet of *Tytthaspis* (= *Micraspis*) *sedecimpunctata* (L.) (Ricci, 1986a), and *Bulaea lichatshovi* (Hummel) apparently includes leaves in its diet, in addition to pollen (Capra, 1947; Dyadechko, 1954; Savoïskaya, 1970, cited by Hodek, 1973). The mycophagous Psylloborini and the leaf-eating Epilachninae, also closely allied to the Coccinellini, have undergone considerable diversification after evolving non-animal diets (Hodek, 1996a).

Dietary and habitat preferences can vary within genera. For example, within the Coccinellini, the large genus *Coccinella* not only contains dietary and habitat generalists, such as *C. septempunctata* and *Coccinella transversalis* F. (Debaraj & Singh, 1995) but some dietary and habitat specialists, such as the myrmecophilous *C. magnifica* and the chrysomelid-eating *C. heiroglyphica*, which is restricted to bog or heathland habitats (Majerus, 1994; Honěk & Hodek, 1996). Genera in other coccinellid tribes exhibit similar interspecific variability in dietary and habitat specificity and preference, for example *Rhyzobius*, in the Coccindulini, (Pope, 1981; Richards, 1981; Ricci, 1986b, c), *Hyperaspis*, in the Hyperaspidini, (Silvestri, 1903; Philips, 1963; Sullivan, Castillo & Belotti, 1991; de Almeida & Vitorino, 1997) and *Chilocorus*, in the Chilocorini, (Samways, 1984; Hattingh, 1991; Hattingh & Samways, 1991). Not all genera exhibit similar variability. In the aphidophagous Coccinellini, members of the genus *Myzia* are largely restricted to feeding on conifers and the genus *Anisosticta* is primarily restricted to reed beds and other humid places (Belicek, 1976; Iablokoff-Khnzorian, 1982; Kuznetsov, 1997).

Habitat preferences sometimes vary geographically within currently defined species. In Europe a number of species are apparently specialists in the north and west of their ranges, but are more generalist in the south and east (Table 1). In several cases, in different tribes, coccinellids originally considered to be single species have transpired to be two related species with differing dietary and habitat preferences (Sasaji, 1980; Pope, 1981; Richards, 1981; Hattingh, 1991).

SEASONAL VARIATION IN COCCINELLID HABITAT AND DIET

Many coccinellids do not remain in a single habitat, or feed on a single type of prey throughout the year. Aphids particularly constitute an ephemeral resource, and colonies of prey in a particular habitat may rapidly dwindle due to aphid dispersal and in some cases predation and parasitism (Kindlmann & Dixon, 1996; Holst & Ruggle, 1997; Rosenheim et al., 1997; Dixon, 1998), forcing coccinellids to move to new patches and habitats (see Hemptinne, Dixon & Coffin, [1992] on the patch dynamics of Adalia bipunctata). Aphidophagous coccinellids are known to be highly mobile, indeed more so than coccinellids feeding upon other types of prey, such as coccids or vegetable matter (Hagen, 1962; Savoïskaya, 1966; Honěk & Hodek, 1996; Majerus & Majerus, 1996).

The movements of some aphidophagous species between different habitats have been well documented (Honěk & Hodek, 1996). Adalia bipunctata, for example, moves between a number of different tree species, shrubs and herbaceous plants through the year, the exact sequence depending upon geographic location (Lusis, 1961; Iperti, 1965; Brakefield, 1984; Hemptinne & Naisse, 1988; Honěk & Hodek, 1996 and incl. refs.). Iperti (1965) documents the varied movements of seven species of aphidophagous coccinellid, including A. bipunctata, between different aphid-infested plants in southern France. Although coccidophagous coccinellids are apparently less mobile than aphidophagous species, there is evidence that some species do prey switch (Kato, 1968) and move between habitats (Samways, 1984; Hattingh & Samways, 1991).

In, usually later, parts of the active season of predatory coccinellids, optimal coccinellid prey types, in many habitats, are scarce due to dispersal, predation or parasitism. This has been well documented for aphid prey (e.g. Ibrahim, 1955; Iperti, 1965; Sloggett & Majerus, 2000). Although coccinellids cease to breed at this time, they often need to obtain enough food to survive a period of dormancy before the next active season and many coccinellids, particularly poorly resourced individuals, continue to forage (Barron & Wilson, 1998). At the beginning of the coccinellid active season, typical prey may not have reached exploitable densities before coccinellids emerge from dormancy and they may also encounter a similar problem of prey scarcity at this time (e.g. Hemptinne & Desprets, 1986). Coccinellids adopt a variety of foraging strategies, not utilized when prey are abundant, in order to acquire sufficient resources for survival during prey scarcity. They frequently feed on high risk or lower quality food (Forbes 1880, 1883; Clausen, 1940; Hagen, 1962; Table 2), often in atypical habitats (Iperti, 1965; Majerus, 1994; Sloggett & Majerus. 2000; Table 2). Coccinellid species which do not enter a period of dormancy can persist in this way for many weeks (Bishara, 1934; Ibrahim, 1955).

TABLE 1. European ladybird species believed to exhibit geographic variability in habitat preference. Only in the case of *C. undecimpunctata*, where morphological differences are recognized have the differing ecotypes been divided taxonomically, into subspecies. *Coccinella undecimpunctata* undoubtedly represents a more advanced stage of evolutionary divergence between ecotypes than do the other examples

Species	Northern and western habitat preference	Southern and eastern habitat preference	Sources
Coccinella undecimpunctata L.	Restricted to high latitude northern beaches, probably living on aphids occurring in coastal environments (subsp. *boreolitoralis* Donisthorpe).	Widespread generalist subspecies occurring throughout Europe and Asia (subsp. *undecimpunctata* L.). Two other subspecies occur in south-eastern Europe (subsp. *tripunctata* L.) and the Middle East (subsp. *arabica* Mader). Their habitat preferences are incompletely characterized.	Donisthorpe, 1918; Benham & Muggleton, 1970; Iablokoff-Khnzorian, 1982; Entwhistle & Moran, 1997
Coccinella quinquepunctata L.	Restricted to shingle habitats near lakes and rivers.	Widespread in numerous habitats including orchards, conifers and crop fields.	Rye & Sharp, 1863; Rye, 1866; Horion, 1961; Honěk, 1985; Majerus & Fowles, 1989; Mann *et al.*, 1993; Honěk & Hodek, 1996 and incl. refs.; Nedved, 1999
Coccinella magnifica Redtenbacher	An obligate myrmecophile, living with ants of the *Formica rufa* group and closely allied species.	Unclear, but possibly dissimilar from those in the north-west. A limited number of observations suggest it might associate with different ant species or even be facultatively- or non-myrmecophilous.	Donisthorpe, 1896, 1919–1920; Wasmann, 1912; Schmidt, 1936; Dyadechko, 1954; Pontin, 1959; Wisniewski, 1963; Majerus, 1989; Sloggett, 1998; Sloggett & Majerus, in press; J. Muggleton pers. comm.; W. Völkl pers. comm.
Adonia variegata (Goeze)	Well-drained habitats, mainly heathland.	Widespread generalist.	Majerus, 1994; Honěk, 1985; Honěk & Hodek, 1996 and incl. refs.; J. J. Sloggett & K. M. Webberley unpub. data
Hippodamia tredecimpunctata (L.)	Restricted to marshy habitats.	In crop and other herbaceous habitats, as well as near water.	Joy, 1932; Majerus, 1994; Honěk & Hodek, 1996 and incl. refs.; Nedved, 1999; J. J. Sloggett & K. M. Webberley unpub. data

TABLE 2. Foraging strategies adopted by ladybirds when their typical prey is scarce

Foraging strategy	Benefits and costs	Examples	References
Movement to less suitable, atypical habitats.	Aphids or other prey present in less suitable habitat when aphids absent in optimal habitat. Possible costs related to prey or microclimatic suitability.	*Adalia bipunctata* (L.), *Adalia* (= *Coccinella*) *decempunctata* (L.) and *Synharmonia* (= *Harmonia*) *conglobata* (L.) move from trees and shrubs to cultivated maize, *Zea mays* L., in late summer in southern France.	Iperti, 1965
		The conifer specialists *Anatis ocellata* (L.) and *Harmonia quadripunctata* (Pontopiddan) move to deciduous trees in late summer in England.	Majerus, 1994; J. J. Sloggett unpub. data
Feeding on unsuitable, unpalatable or semi-toxic homopteran prey	Less suitable prey may persist when more palatable aphids are scarce, possibly because of reduced predation pressure on these species. Feeding on such prey may allow a coccinellid to survive, although typically the prey would be unsuitable for reproduction.	In central Europe, *Coccinella septempunctata* L. predate *Aphis sambuci* L. directly after overwintering, although this aphid is an inadequate food for *C. septempunctata*.	Hodek, 1956, 1957
		Propylea quatordecimpunctata (L.) feeds on the aphid *Aphis nerii* Fonscolombe in late summer in southern France, despite its toxicity to the coccinellid.	Iperti, 1965, 1966
Feeding on ant-tended Homoptera	Tended Homoptera tend to persist later in the season than colonies of untended aphids (Bristow, 1984; Mahdi & Whittaker, 1993) but are defended by aggressive ants (Way, 1963). There is thus a risk of injury or even death associated with feeding on them.	*Myzia oblongoguttata* (L.) and *C. septempunctata* association with aphid-tending ants of the *Formica rufa* group.	Bhatkar, 1982; Sloggett & Majerus, in press
Feeding on galling Homoptera	Galling Homoptera may perhaps persist later into the season. However most coccinellids are limited in the rate at which they can feed as they cannot enter the gall and can only eat aphids which appear at the gall entrance. Some aphid galls are defended by a soldier caste (Foster & Rhoden, 1998).	*A. bipunctata* association with galls of the aphid *Pemphigus spirothecae* Passerini (= *P. spirothecae* Passerini).	Cooke, 1987; P. K. Rhoden pers.comm.

TABLE 2. *continued*

Foraging strategy	Benefits and costs	Examples	References
Feeding on non-homopteran invertebrate prey	Other invertebrates will be present whilst typical homopteran prey is scarce. Cost possibly in terms of prey suitability.	*Coccinella undecimpunctata* L. and *Cheilomenes propinqua* (Mulsant) (= *Chilomenes vicina* Mulsant) feed on eggs and larvae of *Prodenia litura* F. (Lepidoptera) in Egypt during aphid scarcity. *Prodenia litura* is an inadequate diet for *C. undecimpunctata*.	Bishara, 1934; Ibrahim, 1955
		In Ontario, a higher proportion of remains of the red mite *Panonychus ulmi* (Koch) found in the guts of peach orchard-dwelling coccinellids later in the season, when the aphid *Myzus persicae* (Sulzer) was scarcer.	Putman, 1964
		Cheilomenes sexmaculatus (F.) (= *Menochilus sexmaculata* (F.)) predates *Chilo zonellus* (Swinhoe) (Lepidoptera) during aphid scarcity on *Sorgum* in India.	Jotwani & Verma, 1969
Pollenivory and nectar-feeding	Food available when Homoptera are scarce, especially during early season prey scarcity, before coccinellid reproduction. There is probably little cost, although in most cases such food is insufficient alone for reproduction.	In Belgium, *A. bipunctata* eat spring pollen before aphids become abundant.	Hemptinne & Desprets, 1986
		In North Carolina, the introduced coccidophage *Chilocorus kuwanae* (Silvestri) feeds on the pollen and nectar of *Euonymous* sp., a host of one of its diaspidid prey, when prey are absent.	Nalepa, Bambara & Burroughs, 1992
		Records of extra floral nectary feeding by coccinellids have been reviewed. The habit has been recorded in five of the six coccinellid subfamilies, usually in the absence of other prey.	Pemberton & Vandenberg, 1993
Mycophagy	Some mildews perhaps available when homoptera are scarce. Fungal spores associated with honeydew may be frequently consumed by homopteran-eating coccinellids.	Over half *C. septempunctata* dissected contained *Alternaria* sp. and *Puccina* sp. fungal spores in their guts during ladybird reproduction and prehibernation in Germany, although the proportion with aphids in their guts fell over the same period. Although consumption of fungal spores appears typical of *C. septempunctata*, the benefit gained by consumption may be greater during the prehibernation phase.	Triltsch, 1997

RESOURCES AND EVOLUTIONARY CHANGES OF COCCINELLID DIET AND HABITAT

There have been very few studies directly addressing those factors which are important in coccinellid habitat and dietary shifts. However the wealth of information available on coccinellid ecology perhaps allows the deduction of which factors are the most important. It is argued here that resources are of more importance than enemy free space in moulding coccinellid habitat preferences.

In the field it has been observed that there is limited niche overlap between sympatric predatory coccinellids. Ewert & Chiang (1966) pointed out that *Hippodamia convergens* Guerin, *Hippodamia tredecimpunctata* (L.) and *Coleomegilla maculata* differed in their vertical distribution in crop stands. Honěk (1985), in an examination of niche overlap between seven Czech aphidophagous coccinellid species, found that habitat overlap was generally low and could be explained by differing preferences for aphid density, insolation and plant type (which relates to aphid prey type). This study provides some evidence that resource competition is important in determining coccinellid habitat preferences. Thus, coccinellid habitat shifts are probable when a diet in a particular habitat is 'underexploited' by coccinellids or other predatory taxa.

Increased specialization within the preferred dietary range of a generalist ancestor

There is some evidence that specialization can occur within the board preferences of an ancestral generalist, perhaps by individuals remaining in one habitat, rather than changing habitat through the season. Thus, whereas the generalist ancestor bred in a wide variety of habitats, the specialist only breeds in one or a few of these habitats. Comparisons of the habitat preferences of *Adalia decempunctata* (L.) with those of *A. bipunctata*, its sibling species, and the more distantly related *Adalia tetraspilota* (Hope) (Lusis, 1973; Iablokoff-Khnzorian, 1982; Fig. 1), suggest that such a narrowing of habitat preference may have occurred in the *A. decempunctata* lineage. *Adalia bipunctata* feeds and breeds in a wide variety of habitats, encompassing trees, shrubs and herbaceous plants (Banks, 1955; Brakefield, 1984; Honěk, 1985; Majerus, 1994; see above). *Adalia tetraspilota* occurs in similar habitats where it is sympatric with *A. bipunctata* (Lusis, 1973). *Adalia decempunctata*, on the other hand, is primarily restricted to trees and shrubs, being much rarer in herbaceous habitats (Redenz-Rüsch, 1959; Honěk, 1985; Majerus, 1994). It is parsimonious to assume that the common ancestor of *A. bipunctata* and *A. decempunctata* was a habitat generalist, like *A. tetraspilota* and *A. bipunctata*. It is thus likely that the *A. decempunctata* lineage increased its dietary and habitat specialization within the preferences which its ancestors already exhibited (Fig. 1).

What can be gained through such specialization? A specialist can avoid some of the costs which a generalist will incur. These costs are associated with migration between different habitats or with prey switching. For example, in coccidophagous generalist *Chilocorus* species, prey switching from one coccid diet to another often temporarily reduces fecundity (Hattingh & Samways, 1992). Decreasing dietary breadth, through a narrowing of habitat preference, reduces such a cost. Specialist aphidophagous coccinellids are frequently able to utilize lower aphid densities than generalists (Gagné & Martin, 1968; Honěk, 1985). Within the *Adalia* genus, the specialist *A. decempunctata* often occurs associated with lower aphid densities than the
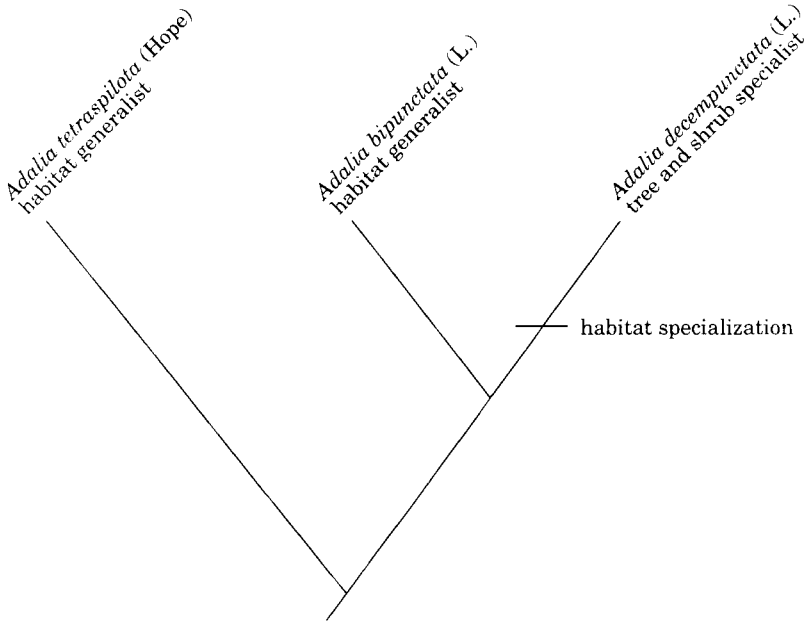
Figure 1. Phylogenetic relationships and habitat preferences of *Adalia tetraspilota, A. bipunctata* and *A. decempunctata*. The *A. decempunctata* lineage has specialized in living in one of the habitat types in which the other two generalist species occur.

generalist *A. bipunctata* (Honěk, 1985). Thus, there is likely trade-off between the costs of remaining in the same habitat and exploiting lower aphid densities (*A. decempunctata*) and the costs of moving to new herbaceous habitats and associated prey switching (*A. bipunctata*).

Prey scarcity and its role in the evolution of dietary and habitat preferences

In many cases, shifts to novel habitats and diets have occurred. The incorporation of a new homopteran prey into the diet of a ladybird lineage, must have occurred many times, since different ladybird species, even those considered generalists, vary in which homopteran species they can most effectively utilize (Hodek, 1996a). However individual examples of dietary shifts are difficult to detect: they not only require detailed phylogenetic information about the group being studied, but comprehensive lists of the essential prey (*sensu* Hodek, 1973) of all group members. The most easily detected, and easily studied, novel shifts are those which involve the adoption of highly unusual and noteworthy diets or habitats, which are clearly different from those of close relatives. In this category may be included *Coccinella magnifica* myrmecophily, a unique habit within the tribe Coccinellini, the consumption of non-homopteran insect prey by species such as *Aiolocaria hexaspilota, Coccinella hieroglyphica* and *Coleomegilla maculata*, and the consumption of pollen or other vegetable matter by *C. maculata* and other coccinellid groups, such as the Tytthaspidini, Psylloborini and the Epilachninae.

The adoption of unusual novel habitats and prey by coccinellids, as well as many

less spectacular novel dietary and habitat shifts, probably arise as a consequence of ancestors feeding on atypical diets in uncharacteristic habitats when prey is scarce (see Table 2). Ancestral individuals are forced into a novel habitat where they do not typically breed, due to prey scarcity in their characteristic habitat. Over evolutionary time, some individuals remain in this 'alternative' habitat to mate and breed. Such an evolutionary pathway could lead to specialization in novel habitats and on novel preys, or even produce increased generalization with the incorporation of the novel element into the ancestral dietary and habitat breadth.

For example, feeding on alternative prey during prey scarcity provides the most likely starting point for the evolution of specialized myrmecophily in *C. magnifica*. *Coccinella magnifica*'s non-myrmecophilous congener, *C. septempunctata*, and other non-myrmecophilous *Coccinella* species, feed on ant-tended aphids during scarcity of untended aphid prey, although other coccinellid species adopt different survival strategies at this time. It is probable that *C. magnifica*'s non-myrmecophilous ancestor also consumed ant-tended aphids during prey scarcity, facilitating a habitat shift and an obligate association with ants, even during the breeding season (Sloggett & Majerus, 2000).

Coleomegilla maculata, on the other hand, exhibits broad dietary preferences perhaps due to ancestral feeding habits during prey scarcity. In addition to aphids, the *C. maculata* diet regularly includes items taken by most other aphidophagous ladybirds primarily during prey scarcity, such as some types of pollen (Forbes, 1883; Britton, 1914; Smith, 1960; Benton & Crump, 1981) and non-homopteran invertebrates (Putman, 1957; Conrad, 1959; Whitcomb & Bell, 1964; Groden et al., 1990). *Coleomegilla maculata* habitat preferences have been linked to its pollenivory (Ewert & Chiang, 1966; Andow & Risch, 1985) and to its predation of non-Homopteran invertebrates (Groden et al., 1990) as well as to its aphidophagy (Wright & Laing, 1980; Andow & Risch, 1985). That pollen is a more recent inclusion in the diet of *C. maculata* is suggested by a decreased rate of larval development, longer preovipositional period and reduced fecundity of *C. maculata* fed exclusively on this diet relative to one of aphids, although many pollen types are sufficient for development and oviposition (Smith, 1960, 1961; Hodek, Ružička & Hodková, 1978; Hazzard & Ferro, 1991). It is possible that the ancestors of this species utilized pollen and non-aphid invertebrates as food when aphid prey was scarce and that *C. maculata*'s broad diet has arisen from this ancestral habit. More data on *C. maculata*'s phylogenetic relationships would be of use in evaluating such a hypothesis: this species is placed close to or even within the typically pollenivorous Tytthaspidini, rather than the aphidophagous Coccinellini by some taxonomists, although its closest relatives are thought to be aphidophagous (Iablokoff-Khnzorian, 1982; Gordon, 1985; Kovár, 1996).

Both the examples given above involve unusual coccinellid dietary and habitat preferences. However, there is no reason to doubt that similar evolutionary pressures also result in less spectacular evolutionary innovations in diet or habitat preferences, although these are more difficult to detect (see above). Simple shifts in the preferred homopteran diet or habitat of a predatory coccinellid lineage could easily result from changes in the homopteran species eaten or habitats visited which occur in coccinellids during scarcity of their own typical prey (Hodek, 1956, 1957; Iperti, 1965; Table 2). Movements related to prey scarcity, at the end of a season would provide a mechanism whereby predatory coccinellids would begin to colonize those

habitats in which there are, overall, fewest competitors, where prey would persist longest.

In some cases coccinellids remain in the same habitat, feeding on alternative food sources during prey scarcity (Bishara, 1934; Pemberton & Vandenberg, 1993). In a such species, adaptation to one particular type of prey during prey scarcity can facilitate greater habitat and dietary specialization than would otherwise be the case. This indirect effect of prey scarcity on dietary and habitat specialization is evident in *Myzia oblongoguttata*. This species is an extremely effective predator of ant-tended *Cinara* aphids, unlike other conifer specialists, such as *Anatis ocellata* (L.) and *Harmonia quadripunctata* (Pontoppidan) (Sloggett, 1998). During prey scarcity, *M. oblongoguttata* remains on conifers, feeding on ant-tended aphids (Sloggett & Majerus, 2000), whilst many *A. ocellata* and most *H. quadripunctata* migrate to deciduous trees (Majerus, 1994; see Table 2). Of the three species *M. oblongoguttata* is by far the most specialized: unlike the other two species, *M. oblongoguttata* adult fail to breed in the laboratory and larvae of this species suffer high mortality if fed on non-conifer aphids (Majerus & Kearns, 1989; Majerus, 1993, 1994).

Some habitats of particular importance during prey scarcity are also utilized for breeding by coccinellids at other times of year. Specialization into these habitats often does not truly constitute an evolutionary innovation, as has been described for *C. magnifica* and *C. maculata*: the evolution of this specialization is more akin to narrowing of dietary and habitat breadth within the preferences of an ancestral generalist, described in the previous section. For example, aphidophagous ladybirds, such as *C. septempunctata* often move to damper places, such as wetlands, or the banks of rivers and ponds when aphids are scarce (Hodek *et al.*, 1966, cited by Honěk & Hodek, 1996). In such areas, especially if conditions are hot and dry, aphids remain more abundant than on water-stressed foliage elsewhere (J. J. Sloggett & K. M. Webberley, pers. observ.). Specialists have evolved to exploit such humid habitats, such as northern *C. quinquepunctata* populations, which exhibit a preference for shingle habitats near lakes and rivers (Table 1) and *Anisosticta* species, which live in reed beds (Iablokoff-Khnzorian, 1982; Kuznetsov, 1997). However, such humid habitats are also exploited as breeding areas by generalist species (J. J. Sloggett & K. M. Webberley, pers. observ.). It is likely that the more generalist ancestors of specialized humid-habitat species, not only utilized damp habitats during prey scarcity but also sometimes bred at these sites. Thus, specialization into humid habitats can be seen as specialization within a broader ancestral habitat range rather than an evolutionary innovation.

Specialists living in habitats where they benefit from reduced exposure to prey scarcity, are less able to colonize and exploit patches of more ephemeral prey outside their preferred habitat than generalist species. The specialist *C. quinquepunctata* and *C. magnifica* both lay larger eggs relative to their body size than the generalist *C. septempunctata* (J. J. Sloggett, pers. observ.; J.-L. Hemptinne, pers. comm.). They thus appear be more *k*-selected, suffering high levels of intraspecific competition: a trade off exists between the costs and benefits of habitat specialization. This could explain why many coccinellids have not evolved habitat specialization as a means of avoiding prey scarcity.

ENEMY FREE SPACE AND THE EVOLUTION OF COCCINELLID HABITAT PREFERENCES

Because of their chemical defences (Daloze, Braekman & Pasteels, 1995; Glisan King & Meinwald, 1996), coccinellids are primarily attacked by specialized parasitoids

and parasites than by more generalist predators (Ceryngier & Hodek. 1996). some parasitoids and parasites can reach extremely high levels in coccinellid populations (Iperti, 1964; Iperti & van Waerebeke, 1969; Disney, Majerus & Walpole, 1994; Geoghegan, Thomas & Majerus, 1997; Majerus *et al.*, 1998). It therefore might be expected that these groups might exert some influence on ladybird habitat preferences, particularly parasitoids as occurs in phytophagous insects.

The evidence relating to the role of enemy free space in moulding coccinellid habitat preferences is limited: the parasitoids and parasites of many coccinellid species are incompletely known and in many known cases prevalence is very poorly characterized. However, the evidence available does not support enemy free space being of overriding importance in the evolution of habitat preference in the predatory Coccinellidae. For example a similar array of parasitoids attack *Adalia bipunctata* and *A. decempunctata*, which differ in habitat preference (Table 3; see Fig. 1 on the species habitat preferences). The evidence for other sibling species is fragmentary, as complete lists of parasitoids and parasites are unavailable. In cases where geographic variability is found in the habitat preferences of a species, the comparison is confounded by geographic variation in the parasitoids and parasites present, or in their prevalence.

Many coccinellid parasitoids are not highly host specific and occur in a diverse array of habitats, parasitizing those coccinellid species which occur there (Klausnitzer, 1976; Kuznetsov, 1987; Ceryngier & Hodek, 1996; Majerus, 1997). Thus, habitats in which coccinellid parasitoids are absent or scarce will be of rare occurrence reducing any possible role for enemy free space in moulding coccinellid habitat preferences. Work on *Dinocampus* (= *Perilitus*) *coccinellae* (Schrank) suggests that interspecific differences in prevalence observed in the field are attributable to differences in the physiological susceptibility of the hosts and to parasitoid host preferences (e.g. Richerson & DeLoach, 1972; Orr, Obrycki & Flanders, 1992; Sloggett, 1998).

One study has directly addressed a role for enemy free space in the evolution of coccinellid habitat preference. The myrmecophilous *C. magnifica* is exhibits very low levels of *D. coccinellae* parasitism relative to most other *Coccinella* species (Majerus, 1997; Sloggett 1998). Majerus, (1989, 1997) suggested that *C. magnifica* might be freed from parasitism by *D. coccinellae* because aggressive ants eliminated the parasitoid from the vicinity of their nests, thus providing a rationale for the evolution of *C. magnifica* myrmecophily. However, Sloggett (1998) found that *C. magnifica* was not successfully parasitized by *D. coccinellae* in the laboratory. *Coccinella magnifica* is believed to be extremely chemically repellent, in order to deter the ants with which it is associated from attacking it. Sloggett concluded that this chemical adaptation was pleiotropically responsible for the lack of *D. coccinellae* parasitism of this coccinellid. Thus Sloggett's findings support a view of physiological factors being more important than habitat in determining coccinellid parasitism levels.

In rare cases coccinellid larvae live in well-protected environments, for example inside ants' nests or aphid galls, but the adults act as a dispersive phase and only visit these habitats to oviposit (e.g. Silvestri, 1903; Wheeler, 1911; Sasaji, cited by Honěk, 1996a). There is a probable role for enemy free space in the evolution of this mode of life. Such habitats undoubtedly provide a refuge against many natural enemies of coccinellid larvae. Furthermore, larvae are less frequently subject to prey scarcity than coccinellid adults (but see Takahashi, 1989). This makes explanations for such larval habitats based on food availability less tenable, although an adult ovipositional preference might potentially have arisen as a result feeding in such

TABLE 3. Parasitoids of the sibling species *Adalia bipunctata* and *A. decempunctata*. The two species appear to possess a common array of parasitoid enemies. Most important are the pupal parasitoids *O. scaposus* and *Phalacrotophora* spp., with other parasitoids being rare, even *D. coccinellae*, which is generally widespread and attacks a diverse array of Coccinellini. It should be noted that *A. bipunctata* is the more frequently studied species and has a geographic range covering both the Palaearctic and the Nearctic, whereas *A. decempunctata* is restricted to the western Palaearctic (Iablokoff-Khnzorian, 1982). There is thus a bias towards the recording of parasitoids from *A. bipunctata*. General sources: Richerson, 1970; Klausnitzer, 1976; Ceryngier & Hodek, 1996. Specific studies: Bryden & Bishop, 1945; Iperti, 1964, unpub. data (cited in Hodek, 1973); Klausnitzer, 1969; Richerson & DeLoach, 1972; Filatova, 1974; Cartwright, Eikenbary & Angalet, 1982; Dean, 1983; Grigorov, 1983; Belshaw, 1993; Disney, Majerus & Walpole, 1994; Majerus, 1997; J. J. Sloggett pers. obser.

Parasitoid	Coccinellid life-history stage attacked	*Adalia bipunctata*	*Adalia decempunctata*
HYMENOPTERA			
Dinocampus (= *Perilitus*) *coccinellae* (Schrank)	Adult	Very low prevalence	Very low prevalence
Oomyzus scaposus (= *Tetrastichus coccinellae*) (Thomson)	Pupa	Yes	Yes
Aprostocetus (= *Tetrastichus*) *neglectus* (Domenichini)	Pupa	? – see Klausnitzer, 1969. Probably misidentified *Oomyzus scaposus*: *A. neglectus* attacks members of the tribe Chilocorini, not the Coccinellini to which *Adalia* belongs (e.g. Kuznetsov, 1987).	Not recorded
Homalotylus spp.	Larva	Rarely recorded	Not recorded
DIPTERA			
Medina spp. [probably all *Medina separata* (Meigen)]	Adult	Very low prevalence	Low prevalence
Phalacrotophora fasciata Fallén	Pupa	Yes	Yes
Phalacrotophora berolinensis Schmitz	Pupa	Yes	Yes

habitats during prey scarcity (see Table 2). In his study of *Platynaspis luteorubra* (Goeze), a primarily larval myrmecophile, Völkl (1995) found evidence of both a resource advantage, possibly mediated by prey density, and protection against a host-specific parasitoid, provided by its association with ants.

The fragmentary evidence available argues that enemy free space is much less important than resources in moulding coccinellid habitat preferences. However, much more research into the phenomenon is needed. Some of this research is very basic, such as comparing parasitoid or parasite prevalences in closely related coccinellids with different habitat preferences. The possibility that habitat and dietary shifts might affect coccinellid susceptibility to parasites, through changes in sequestered chemical defence, is worthy of investigation (see Rothschild, von Euw & Reichstein, 1973; Witte, Ehmke & Hartmann, 1990; Eisner *et al.*, 1994 on sequestered chemical defence). Similarly, that Müllerian or Batesian mimicry of specific coccinellid species or other insects characteristic of particular habitats (Brakefield, 1985) has affected some species' habitat preferences should also be considered.

ADAPTATION TO NEW HABITATS

Although coccinellids are believed to respond to microclimatic, visual and olfactory cues in locating habitats (Ewert & Chiang, 1966; Kesten, 1969; Hattingh & Samways, 1995), work on mechanisms of habitat location in coccinellids is limited and currently it is difficult to assess which factors are most important and the nature of sensory changes which occur during habitat shifts.

Rapid inclusion of novel prey types into the diet of coccinellid species does appear to occur. In the field, in Kenya, Kirkpatrick (1927) noted that the primarily aphidophagous *Cheilomenes* (= *Chilomenes*) *lunata* F. underwent rapid dietary change, to include the coffee mealybug, *Planococcus* (= *Pseudococcus*) *lilacinus* (Cockerell) amongst its prey. It is probable that conditioning to particular prey types plays a role in such rapid dietary shifts, although evidence of conditioning in coccinellids is limited. Although Houck (1986) found that after the acarophagous *Stethorus punctum* (LeConte) had been fed on the mite *Tetranychus urticae* Koch, it preferred this prey, similar effects were not observed when this *S. punctum* was fed *Panonychus ulmi* (Koch). No effects of feeding history on the prey choice of *Chilocorus nigritus* (F.) were found by Hattingh & Samways (1992).

Intraspecific variability in the foraging behaviour of coccinellids could also allow them to rapidly adapt to new prey. In *Semiadalia* (= *Adonia*) *undecimnotata* (Schneider) larvae, considerable intraspecific variability has been characterized in intensive searching behaviour. Variation was recorded in the occurrence of intensive search before and after prey capture. Variability was also recorded in how quickly intensive search is adopted, the number of periods of intensive search undertaken and their duration after prey capture (Ferran *et al.*, 1994). A period of conditioning to aphid prey is required by newly moulted larvae and recently enclosed adults, before intensive search is adopted in this species (Ettifouri & Ferran, 1992). In *Harmonia axyridis* (Pallas), rearing for several years on an artificial diet of lepidopteran eggs, produced larvae without the typical intensive search response after feeding on the aphid *A. pisum*. After eating an aphid, larval movements were intermediate between

those of intensive and extensive search. Similar observations were made on larvae from a *H. axyridis* culture maintained on *A. pisum*, which were given lepidopteran eggs. There were some differences between the foraging behaviours of larvae from the two cultures when fed on their own prey (Ettifouri & Ferran, 1993). Since the *H. axyridis* larvae used in experiments were obtained directly from the cultures it is impossible to say whether the differences in foraging behaviour on the two prey types were due to selection within the cultures, or due to conditioning, as asserted by the authors. However it seems clear from these experiments, and those on *S. undecimnotata*, that coccinellids may rapidly acquire suitable behaviour to forage successfully on novel prey types. It is perhaps worth noting that *S. undecimnotata* and *H. axyridis* are dietary generalists (see Iperti, 1965; Hodek, 1996a) and are thus more likely to exhibit phenotypic plasticity related to diet than specialist species.

Other adaptations to new habitats also arise rapidly through selection on pre-existing traits, probably controlled by polygenic systems. The behavioural adaptations of adult *Coccinella magnifica* for circumventing ant aggression are also present but poorly developed in the non-myrmecophilous congeneric *C. septempunctata*. Selection probably acted on the expression of behaviours already present in *C. magnifica*'s non-myrmecophilous ancestors, rather than *C. magnifica* adaptation occurring through the, more difficult, acquisition of novel traits (Sloggett, Wood & Majerus, 1998). Such a pattern in the evolution of traits adapting coccinellids to new environments is consistent with that observed in predatory chrysopids (Tauber *et al.*, 1993).

SPECIATION AND HABITAT SHIFTS IN THE COCCINELLIDAE

Classical allopatric speciation has clearly played a role in the differentiation of broad faunal provinces, such as between the Palaearctic and Nearctic. However, it has been suggested as less important within such areas. In his study of the zoogeography of the coccinellid fauna of north west Canada and Alaska, Belicek (1976) argues that the Rocky Mountains have not been important as a barrier to the dispersal of coccinellids, although the genesis of this mountain range provided an important new source of habitats for coccinellids. Whilst this generalization may be true, it appears probable that the relative importance of geographic isolation may vary between coccinellid taxa. In highly mobile, migratory groups speciation mechanisms requiring geographic isolation or low vagility are less likely to have been of importance, whereas in more sendentary taxa allopatric or peripatric (founder effect) speciation is likely to be more important.

Food availability is a major determinant of migration in predatory coccinellids. On a broad scale, non-aphidophages are less prone to prey scarcity induced migration than aphidophagous species (Hagen, 1962; Savoïskaya, 1996; Honěk & Hodek, 1996; Majerus & Majerus, 1996). Thus, members of the aphidophagous tribe Coccinellini probably have higher levels of gene flow than coccidophagous groups such as the Chilocorini. Within the Coccinellini, habitat and dietary generalists suffer prey scarcity more frequently than specialists (Majerus & Majerus, 1996): this probably arises, at least in part, because avoidance of prey scarcity frequently provides the selective pressure for specialization (see above). The wildly fluctuating population numbers and consequent starvation-induced migration of generalist aphidophages, suggests that these are least likely to undergo speciation as a result

of geographic isolation. Because generalists and specialists can be closely related, mode of speciation could thus vary markedly, even within genera.

In the coccidophagous genus *Chilocorus* in America and Russia, speciation is associated with changes in chromosome configuration. It has been suggested that in this group speciation has occurred in parapatry or in part through founder effects (peripatric speciation) (Smith, 1959, 1966; Zaslavaskii, 1963, 1996). Any habitat changes in these species are not well documented. There is no evidence of habitat changes in the Russian *Chilocorus* species (Zaslavskii, 1963), but in north America chromosomal fusions have occurred in two independent lineages during their parallel spread northwards, suggesting they may be of selective value in colonizing northern habitats (Smith, 1959, 1962). In this coccidophagous and thus relatively sedentary group, parapatric or peripatric hypotheses are fully tenable. However, for the aphidophagous Coccinellini, peripatric speciation, at least, seems unlikely: marginal populations would be periodically overwhelmed by new immigrants, seeking food.

Even in the Coccinellini, migration does not render species genetically homogeneous over the entirety of their range. Species within this tribe can exhibit consistent geographic variation in colour pattern (Dobzhansky, 1933; Honěk, 1996b; Majerus, 1998), the ability to continuously breed, which has a genetic basis (Hodek, 1996b), and habitat preference. The geographic segregation of ecotypes in some European Coccinellini (Table 1) might arise as a result of differences in ladybird voltinism or length of period for reproduction, related to climate. North-western ladybird populations are typically univoltine whereas south-eastern populations are probably bivoltine or multivoltine. In north-western populations, it may be possible for species to reproduce in one habitat over the whole season, leading to specialization, whereas south-eastern populations may move between different habitats each generation, selecting for generalist tendencies.

The observations on geographic variability in the habitat preferences of European Coccinellini, which are highly mobile, suggest that parapatric speciation through habitat shifts could occur throughout much of the Coccinellidae. Environmental factors in a part of an ancestral species' range could cause a geographically restricted habitat shift, ultimately leading to speciation. In the area where populations with differing habitat preferences contact, gene flow could be restricted as a result of the differing habitats occupied by the two ecotypes. This appears to be the case in areas where the two *C. undecimpunctata* subspecies, *C. u. undecimpunctata* and *C. u. boreolitoralis* occur together (Cruttwell, cited by Donisthorpe, 1902; Donisthorpe, 1918). Mating preferences could also play a role in reproductive isolation. Sasaji, Yahara & Saito (1975) found some evidence for such prezygotic reproductive isolation between the Japanese sibling species *Propylea quatuordecimpunctata* (L.) and *Propylea japonica* (Thunberg), at least between females of the former and males of the latter. These two species exhibit broad-scale habitat segregation, with *P. quatuordecimpunctata* generally preferring higher altitudes to *P. japonica*, although areas of contact between the two species do occur.

Similar arguments to those supporting parapatric speciation can be used to support sympatric speciation occurring in the predatory Coccinellidae. However, there is no evidence clearly supporting sympatric speciation occurring in the predatory Coccinellidae, unlike parapatric speciation. For sympatric speciation to occur, marked novel habitat shifts are required. These are most likely to be those associated with prey scarcity, which could cause diversification into completely new habitats and consequent restriction of gene flow. Since coccinellids typically mate in their

characteristic habitats, a considerable degree of reproductive isolation might be obtained in a relatively short period of evolutionary time. It is possible that interbreeding between two incipient sympatric species might occur at shared dormancy sites: mating at dormancy sites is known to occur in a number of species (Hodek & Landa, 1971; Hemptinne & Naisse, 1987; Ceryngier *et al.*, 1992). However, coccinellids mate a number of times during adulthood (e.g. Fisher, 1959; Kesten, 1969; Brakefield, 1984; Ueno, 1996) and later matings occurring within sub-populations in their typical habitats would limit the number of progeny produced from pre- or post-dormancy matings.

The predatory Coccinellidae without doubt exhibit a diversity of modes of speciation. Only parapatric speciation and possibly sympatric speciation are integrally linked to shifts in habitat and diet. However, diet, as a determinant of migratory activity, is also an arbiter of gene flow and thus mode of speciation. Further research is required in a number of areas important to studies of speciation, such as the importance of previous experience on dietary and habitat preferences (Corbet, 1985; Jaenike, 1988; see above), species recognition and mating preferences (Hemptinne, Dixon & Lognay, 1996; Hemptinne, Lognay & Dixon, 1998) and natural population genetic structure (Lusis, 1947; Coll, Demendoza & Roderick, 1994; Johnstone & Hurst, 1996). More importantly, studies using specific coccinellid models are needed, to elucidate how evolutionary changes of diet and habitat may lead to speciation in this group.

CONCLUSIONS

In this paper, it is suggested that resource acquisition is of more importance in moulding coccinellid habitat preferences than enemy free space. Prey scarcity appears to be particularly important in the production of novel habitat preferences through the evolution of novel diets. Habitat shifts and consequent adaptation may occur rapidly, through changes in conditioning of coccinellids or selection acting upon pre-existing traits. Speciation of predatory coccinellids remains relatively poorly investigated, although parapatric speciation related to habitat shifts is of probable occurrence in the group.

Most of the discussion here has centred on coccinellids which belong to the aphidophagous tribe Coccinellini. Work comparing coccid-eaters with aphidophagous coccinellids suggests that they may differ in some key biological parameters (Dixon, Hemptinne & Kindlmann, 1997). Although where possible non-aphid predators have been considered here, there has been much less work carried out on such species, particularly in a non-agricultural context. Thus, whilst the view of coccinellid habitat preferences given here is probably applicable to coccidophagous and other non-aphidophagous predatory coccinellids, more data is required on these groups to confirm or refute this assertion.

Molecular phylogenetic work on predatory coccinellids has lagged behind that on many other insect groups, although morphology-based taxonomic work on coccinellids is extensive (e.g. Iablokoff-Khnzorian, 1982; Gordon, 1985). Species phylogenies, coupled with detailed data on the habitat and dietary preferences would undoubtedly be of value in understanding the nature of coccinellid habitat preference evolution. Further studies of closely related coccinellids which differ in habitat

preference would be of immense value in elucidating how and why evolutionary changes of habitat occur. As already indicated, there are some very suitable systems for this work, in which habitat preferences vary intraspecifically, or between sibling species. Studies of such groups may also throw much needed light on the nature of coccinellid speciation. Of equal importance is a fuller understanding of the cues used by coccinellids in finding their preferred habitat. This area has until relatively recently been remarkably poorly worked.

This paper provides a starting point with which to address some questions about habitat and dietary evolution in predatory insects. Coccinellids make fine models for this work, because our understanding of their biology is, in many areas, extremely good. Suitable coccinellid systems for further study are already known. In further studying these systems, it should be possible to advance from merely observing and describing particular coccinellid habitat and dietary preferences, to determining why and how they occur.

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