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The habitat niches of aphidophagous ladybirds: Alois Honěk's 1985 paper*, its role in understanding ladybird habitat preferences and its messages for today

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Abstract. In 1985, after several years of work on coccinellid community composition, Alois Honěk published a paper called *Habitat Preferences of Aphidophagous Coccinellids*, on the niches of individual species and niche overlap between them. In it he showed that three factors, plant cover, aphid density and insolation, led to species having different and minimally overlapping habitat niches. In this paper, I discuss how studies of the three factors and their effect on habitat preference have developed over the subsequent thirty years. I consider how more recent studies have supported Honěk's view about niche overlap in coccinellids and the messages for researchers today. Researchers working on invasive ladybirds and their effects on native species particularly need to be aware that niche overlap is not only defined by plant species but by the other factors studied by Honěk as well.

Key words. Aphidophagous Coccinellidae, habitat preference, niche partitioning, principle component analysis.

INTRODUCTION

Aphidophagous coccinellids display a broad range of habitat specialisation. Species may be broad generalists, occurring on a wide variety of (aphid) host plants in a diversity of different biotopes, or they may be limited to individual types of plants, such as conifers, or particular habitats, such as river banks. We still do not fully understand what determines their habitat preferences, although it is clear that they are closely linked to their diet.

Prior to the 1980s much of the information available about coccinellid habitat preferences were descriptions of the species living in particular habitats and phenological observations (e.g. Banks 1955, Iperti 1965, Wheeler 1977). Other interesting information was scattered about the literature. For example, in respect of conifer-dwelling species, some interesting observations had been made on differences between coccinellid faunas living in older and younger tree stands (Gumoś & Wiśniewski 1960, Gagné & Martin 1968) and on the attraction of coccinellids to prey host plants (Kesten 1969). However, generally, the knowledge of both proximate and ultimate causes for why particular coccinellid species preferred particular habitats was much more limited than our understanding of what they ate.

In the late 1970s and early 1980s, Alois Honěk published a number of papers about the composition of coccinellid communities and the factors determining this composition (Honěk 1979, 1981, 1982, 1983, Honěk & Rejmánek 1982). Following on from this work, in 1985, he published a paper on the niches of individual species and niche overlap between them entitled *Habitat Preferences of Aphidophagous Coccinellids* (Honěk 1985a). This paper, which continues to be cited today, can arguably claim to have anticipated many of the subsequent developments that have occurred in

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*Honěk A. 1985: Habitat preferences of aphidophagous coccinellids (Coleoptera). *Entomophaga* **30**: 253–264.

Table 1. The ladybird species studied by Honěk and a summary of their preferences within the three principal environmental components he deduced. For more detail of the habitat preferences, see Honěk (1985a)

	plant cover (height of plants)	aphid density	insolation
Coccinella septempunctata	low herbs	high	sunny
Coccinella quinquepunctata	variable over season	low	sunny
Propylea quatuordecimpunctata	variable over season	all	broad range
Hippodamia (= *Adonia*) *variegata*	low herbs	high	sunny
Adalia bipunctata	herb-shrub height	high	sunny
Adalia decempunctata	trees	all	shaded
Calvia quatuordecimguttata	shrubs-trees	high	shaded

our understanding of coccinellid habitat preferences. In this article, I discuss Honěk's 1985 paper, its importance and the continuing messages it has for those studying coccinellids now.

THE PAPER

One reason for the value of Honěk's paper is the detailed and extensive field data which was used for the analyses. In 1982 and 1983, surveys were carried out in Czechoslovakia during the breeding season (May-July) on a variety of potential prey host plants for adult aphidophagous coccinellids of seven species (Table 1). Four environmental factors were recorded in nine different ways (quantitative variables: Table 2). The particular factors were chosen based on Honěk's earlier work on ladybird communities: in this respect this paper may be seen as a culmination of earlier findings about the factors responsible for species distributions. Principle component analysis was used to analyse coccinellid abundance data in respect of the variables. The method, the most widely used multivariate approach at the time, detects those components responsible for the widest variance in a dataset (James & McCulloch 1990, Janžekovič & Novak 2012). In this case it was used to reduce the collected variables to a smaller number of principle components responsible for variance in coccinellid abundance. The principle components were then used to study the habitat preferences of individual coccinellid species and niche overlap between them. For 1982 there were three principal components: aphid density, plant cover and insolation, while in 1983 they were date, plant cover and aphid density.

Ladybird species varied in response to the environmental principal components tested (aphid density, insolation and plant cover; Table 1). Only some ladybirds were able to tolerate low

Table 2. Table summarising the data recorded in each of the four categories of environmental variable studied by Honěk

environmental factors	quantitative variables
time	Julian date from 1 May physiological time (sum of temperatures from 1 May)
aphid density	number of aphids per cm^2 leaf area size of largest aphid colony observed in a plant stand
insolation	proportion of ground surface shaded from the sun (ordinal) plant density
type of plant cover	type of plant (herb or tree) maximum height of stand from ground type of plant stand (field; hedge/garden/forest margin; forest interior)

aphid densities, while most species exhibited marked preferences for sunny or shaded habitats or particular plant strata. Interestingly one species, *P. quatuordecimpunctata*, displayed broad "generalist" characteristics, tolerating a wide diversity of plant heights, insolation conditions and aphid densities without exhibiting clear preferences. However, plotted Euclidean distances for habitat breadth (calculated from the 25% of populations of species with the highest abundance) were similar for generalist and more specialised species alike. The overlap between species was generally low, typically less than 0.3.

The paper marked a significant step forward for two main reasons. First, it very clearly elucidated the important environmental variables differentiating the habitat preferences of aphidophagous coccinellid species. Although aphid density, insolation and plant cover had been previously considered by Honěk and others, here they were considered together. Honěk showed that these three factors alone could account for habitat differentiation observed. Second, Honěk's paper showed that there was very limited overall habitat overlap in aphidophagous coccinellids. This finding brought coccinellid studies of habitat in line with those of diet. It was already known that aphidophagous coccinellids varied in the prey they ate, and that while ladybird species might share an aphid prey species, different ladybirds ate different spectra of aphid prey (Hodek 1973). Honěk showed that although ladybird species might occur together in a habitat, the totality of their habitat preferences varied markedly between species.

SUBSEQUENT WORK AND MESSAGES FOR THOSE WORKING WITH LADYBIRDS TODAY

Honěk's paper has certainly enhanced our understanding of habitat selection in aphidophagous coccinellids. It continues to be cited today and its relevance for those working with aphidophagous ladybirds remains undimmed. Honěk identified three environmental components largely responsible for determining coccinellid habitat preference. Each of these has continued to receive attention and they are all deserving of more. Furthermore Honěk's conclusions about niche overlap between coccinellids are perhaps more important than ever in a world very different from 1985, where invasive species may be the commonest elements of the coccinellid fauna, and where much coccinellid research is focused exclusively on these species.

Plant cover and coccinellid habitat preferences

Before and certainly after Honěk's paper there was a tendency for researchers to divide coccinellids on the basis of the plants they were found on. Indeed some authors have referred to "host plants" for predatory coccinellids (e.g. Majerus 1991, Timms et al. 2008, Baker et al. 2012), even though more correctly the plant should be described as a habitat or an aphid host plant. This is unsurprising as the plant habitat is the most obvious manifestation of where a coccinellid lives. Plants are often easier to identify than the aphids they harbour, still more so than other biotic or abiotic factors that may be important for the ladybird. We therefore tend to take an anthropomorphic view of things and to describe the habitat in terms of what is important or obvious to us rather than the ladybird.

Since Honěk's paper, Nedvěd (1999) developed the plant habitat concept further analysing a wider variety of coccinellid species in the same geographic region as Honěk. He divided the species into eight groups on the basis of plant type. We also know rather more about what attracts coccinellids to particular plants. In addition to attraction to plant or aphid volatiles, which can clearly give a high level of specificity (e.g. Şengonca & Liu 1994, Heit et al. 2008, Glinwood et al. 2011, Auad et al. 2013), coccinellids may be able to discriminate vegetational height using visual cues (Kalil et al. 1985, Hattingh & Samways 1995, Lambin et al. 1996). Notably, Kalil et al. (1985), studying two species also studied by Honěk, found that the more strongly arboreal

A. bipunctata was attracted to taller objects whereas *C. septempunctata* was not. Plant colour could also contribute to habitat differentiation (Lorenzetti et al. 1997), although it is not yet clear whether this is the case within the Coccinellidae.

A challenge for the future is to explain why such preferences for particular vegetation types have evolved in the first place. Rather few studies have thus far addressed this issue. There is some evidence that coccinellids adapted for life in trees are less suited for life in the herbaceous layer or vice versa. *Adalia bipunctata* larvae are less prone to dropping from plants than *C. septempunctata*: unlike *C. septempunctata*, *A. bipunctata* tends to live in higher vegetation and the costs of dropping are greater. However, the reduced dropping behaviour makes *A. bipunctata* more vulnerable to predators, being less able to rapidly escape (Sato et al. 2005). In this case there is a clear trade-off related to the vegetational stratum in which the ladybird lives. Prey related trade-offs could also serve to tie ladybird species to one particular type of plant/stratum: these might be phenological (i.e. aphids on similar types of plants might exhibit similar population dynamics) or more directly related to the prey (e.g. many of the aphids on conifers are large and difficult to catch for smaller ladybirds; see below).

Aphid density

Honěk's finding that aphid density mediates species habitat preference provides a clear link between the habitat and the diet of aphidophagous coccinellids. Earlier work had also suggested this: for example, Gagné & Martin (1968) found that coccinellid specialists on red pine (*Pinus resinosa* Aiton) tended to inhabit older stands of trees than generalist ladybirds did. These older stands typically had lower aphid densities. Much subsequent work has focused on the relationship between aphid density and habitat or dietary specialisation (a lot of it the author's); this work is closely related to work on aphid density and ladybird phenology in individual habitats.

Starting with the latter, we begin with work carried out by Honěk before 1985. In two of his early papers, he observed that *C. septempunctata* required a particular threshold aphid density to colonise crop stands and oviposit there (Honěk 1978, 1980): the idea at the time was of particular interest as previously internal physiological state and temperature were considered to be of primary importance in moderating insect activity in spring (Tauber & Tauber 1976, Honěk 1978). Much later, Dixon (2007) argued that smaller ladybirds should begin to reproduce earlier on aphid colonies as being smaller they needed smaller threshold quantities of food for oviposition. This was supported by later work carried out by Honěk and Dixon together on *C. septempunctata* and *P. quatuordecimpunctata* (Honěk et al. 2008).

Smaller ladybirds cannot catch the bigger instars of large aphid species, however. For larger aphids, it is large ladybirds that would reproduce at the lower total aphid densities (Sloggett 2008a). An element of "size matching" would therefore occur between aphid species and ladybird species, with specialised ladybirds most closely matching their prey and feeding at the lowest densities, and thus potentially for longer in the same aphid patches and habitats. By contrast generalist ladybirds are medium sized (the most effective size for exploiting a range of species) but cannot exploit such low densities of aphid species as specialists (Sloggett 2008a).

These hypotheses can certainly explain why Honěk found habitat-related interspecific variation in the densities of aphids utilised by ladybird species. I have previously emphasised the specialist-generalist/aphid density difference in relation to the two sibling *Adalia* species studied by Honěk. The species with broader vegetational preferences, *A. bipunctata*, prefers higher aphid densities, while the more strictly arboreal *A. decempunctata* tolerates lower aphid densities (Sloggett 2005, 2008b). Interestingly, the broadest habitat generalist in Honěk's study (*P. quatuordecimpunctata*) also tolerated low aphid densities: this could be because it feeds on other food in addition to aphids (see Hodek & Evans 2012). Some evidence supporting this view comes from *C. septempunctata*, which in North America persists in alfalfa at lower aphid densities than native species, possibly because of it propensity to feed on non-aphid prey (Evans 2004). Future lines of enquiry could include how alternative food sources and other factors enhancing predation or capture efficiency (such as specialised searching behaviours) could influence tolerance of low aphid densities and interact with body size.

Insolation and the microclimate

Honěk's paper focuses specifically on insolation i.e. whether ladybirds prefer sun or shade. A number of his papers prior to this one were also concerned with microclimatic effects on ladybirds, in particular *C. septempunctata*. This species was found to prefer sparser cereal crop stands than *P. quatuordecimpunctata*, which Honěk interpreted as being indicative of its thermophilic nature (Honěk 1979). Later he studied the behaviour of this species in detail in relation to temperature and sunshine, showing that in the morning, when it is cool, this species basked in the sun (Honěk 1985b). Larvae showed similar tendencies to adults (Honěk 1983). Other studies of *C. septempunctata* in Japan are consistent with Honěk's observations (Sakuratani et al. 1991, Ohashi et al. 2005).

Subsequent work has also demonstrated that sympatric coccinellid species can differ in their preferred temperatures, although intraspecific variability may also be very great (Pekin 1993). Other potentially important microclimatic factors exist (Honěk 1979), but they have been rarely investigated. Pekin (1996) studied intraspecific variation in coccinellid preference and tolerance in relation to humidity. In general, relative humidity preferences were consistent with the habitats in which ladybirds lived, with species occurring near water, such as *Anisosticta novemdecimpunctata* (L.) and *Hippodamia tredecimpunctata* (L.), preferring a higher relative humidity to other species, and xeric species, such as *H. variegata*, preferring a low relative humidity. To a lesser extent species ability to withstand dessication also reflected their lifestyles.

As noted by Honěk much more recently (Honěk 2012), microclimate has received rather little attention in recent years and is certainly deserving of further work as a determinant of habitat preference. There are a number of ladybird species whose habitat preferences are apparently not primarily determined by plant or aphid prey species; trade-offs in the tolerance of different microclimates might explain why they live where they do and not elsewhere (Sloggett 2008b).

Coccinellid niches and niche overlap

Overlap between the habitat or microhabitat preferences of aphidophagous coccinellids has important implications both for the ability of coccinellids to suppress their prey and when thinking about the effects of exotic species on native communities (Snyder 2009). Broader interest in how biodiversity can affect ecosystem services (Dasgupta et al. 2013) is reflected in interest in how coccinellid or aphidophagous insect diversity can impact on aphid populations. There are two opposing possibilities: either that different species complement each other and enhance aphid control or alternatively that they interfere with each other (possibly by intraguild predation) and reduce overall effective aphid control. Honěk's observations suggest that the former rather than the latter is more likely to be the case: even in the same habitat, species occupy different niches, separated by aphid density or microclimate, or temporally, leading to complementarity in aphid biocontrol.

In a recent review, Snyder (2009) concluded that in most cases enhanced suppression was observed with enhanced biodiversity, at least in part due to niche separation. However, some of the studies he included did not involve aphid prey or involved only one coccinellid species. There are surprisingly few studies exclusively focused on coccinellids that do not involve invasive ladybirds, which may exhibit atypically large niche overlaps with native species (see below).

Evans (1991) tested *Hippodamia convergens* Guérin-Méneville pairwise with three other species on bean plants, *Vicia faba* L., infested with pea aphids, *Acyrthosiphon pisum* (Harris): he found no change in resulting aphid numbers in aphids consumed when compared to conspecific pairs of the individual species. More recently, Omkar et al. (2014) found antagonistic effects when testing different combinations of four aphidophagous Indian coccinellid species, but their experiments were conducted in Petri dishes and thus do not contain a habitat-related niche component. Certainly, more studies are necessary to gain a better understanding of the effects of biodiversity in natural, coevolved communities.

In recent years, coccinellid studies have undergone a radical change, as a consequence of the introduction of alien species to new geographic regions, which have then gone on to become invasive. Much work on coccinellids now focuses on these species and their (presumed) effects, particularly their interaction with and suppression of native species. Honěk's work provides a pattern for a coevolved, stable situation without invaders i.e. coccinellids possess limited niche overlap and thus the potential for competition is limited. This suggests that the introduction of additional species, which might have higher levels of overlap with some native species, could lead to some form of competitive displacement, due to similar exploitation of prey or contact leading to intraguild predation. This would provide a simple ecological rationale behind suspected declines in native species after the introduction of exotics, such as *C. septempunctata* in North America and *Harmonia axyridis* (Pallas) in both North America and Europe (e.g. Harmon et al. 2007, Roy et al. 2012).

However, although Honěk's work can help explain declines in native species, it also suggests that the current work arguing that this is what is occurring is insufficiently exact to support its claims. For example, studies have focused on plant type or species as an indicator of the threat posed to native ladybirds by the invasive species *H. axyridis* (e.g. Adriens et al. 2008, Kenis et al. 2010, Comont et al. 2014). It is clear that plant species are certainly useful when thinking about niche overlap and competitive effects; however, use of plant type alone, without supporting data on aphid density and microclimate, will lead to an overestimate of niche overlap and the threat posed by the invader. Risk assessments based on niche overlap need to be much more fine grained, using the sort of detailed field recording carried out by Honěk.

A few experimental studies have examined the effects of other factors on competition. The most noteworthy of these was by Evans (2004), investigating the invasive *C. septempunctata* in North America. He showed that a decline in native North American ladybird species coincided with a decline in pea aphids in alfalfa, *Medicago sativa* L., after the arrival of *C. septempunctata*. Alfalfa crops with experimentally elevated aphid densities attracted native species, suggesting that they had been displaced due to *C. septempunctata*'s ability to tolerate lower aphid densities. This study provides very good evidence for competitive displacement of native species by an invasive species based on aphid density. This may not always be the case however: overly gloomy predictions of the effects of invasive species on native species may be falsified. For example, the North American conifer specialist *Mulsantina picta* (Randall) remained reproducing on pine trees after *H. axyridis* dispersed; this appeared to be mediated by aphid density (Sloggett et al. 2008). Thus, dire predictions of the effects of generalist invaders on more efficient specialists living on the same plants are probably overstated.

CONCLUSIONS

At the time of my Ph.D., in the mid-1990s, I worked on habitat selection in an obscure specialised mymecophilous coccinellid, *Coccinella magnifica* (Redtenbacher). Initially I read a lot about myrmecophiles that lived with ants as a way of gaining clues to this ladybird's specialised behaviour. As time went on, I realised that the key to understanding *C. magnifica* lay not in it being a myrmecophile but in it being a ladybird. Later, I went on to study specialisation not in other myrmecophiles but in other ladybirds. At the time there was not a lot to read on the subject: Alois Honěk's paper was an important insight for me into understanding why ladybirds live where they do.

In the subsequent 20 years, interest in the habitat preferences of ladybirds has intensified, but there remain many areas where we incompletely understand their habitat preferences. This is in part because habitat and diet are so closely intertwined, meaning that much work on habitat preferences is more closely allied to diet. However, there are numerous species, which are in effect dietary generalists but still live in specialised habitats – from Honěk's study we might include *H. variegata* and *C. quinquepunctata*, at least in some parts of their ranges (see Sloggett & Majerus 2000). For these we need the insights provided by Honěk's paper as much as we ever did. Our overall knowledge of habitat preferences still lags behind our knowledge of dietary ones.

Furthermore, the study of ladybirds has undergone a massive upheaval due to interest in invasive species, which in its turn has led to an influx of new researchers into the study of ladybirds, in addition to the many who already study ladybirds for other academic or applied reasons. There is a temptation on the part of many of these researchers, like I did with *C. magnifica*, to look at their study species as invaders first and ladybirds second. Like me, they may find that looking at them as ladybirds, with the insight that that can ultimately provide, may prove more useful. Honěk's paper can certainly help them in doing so.

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