EUROPEAN JOURNAL OF ENTOMOLOGY

ISSN (online): 1802-8829
http://www.eje.cz

*Eur. J. Entomol.* **116**: 93–103, 2019
doi: 10.14411/eje.2019.011

ORIGINAL ARTICLE

# Factors determining local and seasonal variation in abundance of *Harmonia axyridis* (Coleoptera: Coccinellidae) in Central Europe

**Alois HONĚK[1], Marek BRABEC[2], Zdenka MARTINKOVÁ[1], Anthony F.G. DIXON[3], Stano PEKÁR[4] and Jiří SKUHROVEC[1,*]**

[1] Crop Research Institute, Drnovská 507, 16106 Prague 6 – Ruzyně, Czech Republic; e-mails: honek@vurv.cz, martinkova@vurv.cz, jirislavskuhrovec@gmail.com

[2] Department of Nonlinear Modeling, Institute of Computer Sciences AS CR, Prague, Czech Republic; e-mail: mbrabec@cs.cas.cz

[3] School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK; e-mail: a.f.dixon@uea.ac.uk

[4] Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic; e-mail: pekar@sci.muni.cz

**Key words.** Coleoptera, Coccinellidae, Sternorrhyncha, Aphididae, *Harmonia axyridis*, *Eucallipterus tiliae*, adult, larva, seasonal dynamics, abundance, annual variation, Central Europe

**Abstract.** To determine the causes of the variation in the seasonal dynamics of *Harmonia axyridis* (Pallas) in Central Europe, numbers of adults and larvae of this invasive species were recorded on trees (*Acer*, *Betula*, *Tilia*) throughout the growing seasons from 2011 to 2016. Each year beetles were collected every two weeks, using a standardized sweeping method. The seasonal dynamics was expressed as plots of abundance (number of individuals per 100 sweeps) against time (Julian day) and these plots (seasonal profiles) were compared in terms of their size (area under the seasonal profile curve), range, timing and height of the mode (maximum abundance). Timing and size of seasonal profiles varied among hostplants, years and sites. Abundance of larvae paralleled aphid occurrence and peak abundance of adults followed that of larvae 10 to 20 days later. Population dynamics before and after the peak were determined by dispersal. Adults arrived at sites before the start of aphid population growth and persisted there long after aphid populations collapsed. The abundance of *H. axyridis* decreased from 2011 to 2013 and then increased, achieving the previous levels recorded in 2015 and 2016. The variation in seasonal profiles revealed that *H. axyridis,* in terms of its response to environmental conditions, is a plastic species and this flexibility is an important factor in its invasive success.

## INTRODUCTION

*Harmonia axyridis* (Pallas) is an invasive ladybeetle (Coleoptera: Coccinellidae) that arrived in the Czech Republic in 2006 (Sprynar, 2008). In three years, between 2007 and 2009, *H. axyridis* became a dominant species (Nedved, 2014), at times making up more than 90% of the adult ladybird species in coccinellid communities (Honek et al., 2015). The massive occurrence of *H. axyridis* decreased the diversity of coccinellid communities, not only by virtue of numerical dominance (Kindlmann et al., 2017), but also because of its likely detrimental effect on the abundance of some native species (Honek et al., 2016). Due to competition for prey and/or intraguild predation (Gagnon & Brodeur, 2014), this non-native species may negatively influence not only coccinellids but also other aphidophagous taxa (Brown et al., 2015). Since well-founded worries exist about *H. axyridis* devastating natural coccinellid assemblages (Roy et al., 2016; Brown & Roy, 2018) it deserves further attention.

Within Europe, *H. axyridis* dominates coccinellid communities on trees (Honek et al., 2015) and at times also in stands of wild herbaceous plants and maize, while it is rare in other crops (Vandereycken et al., 2013; Honek et al., 2014). Adult *Harmonia axyridis* leaves hibernacula in April, reproduces from early May until mid-September and during this period produces up to three generations (Honek et al., 2018a). Although females lay their eggs from mid-May until mid-September, not all of the females exploiting abundant prey populations are capable of laying eggs (Honek et al., 2018a). Scattering eggs among many plants (Osawa, 2011), laying small batches of eggs (Honek et al., 2018a), high dispersal capacity (Osawa, 2000) and weak tendency to enter dormancy (Reznik & Vaghina, 2013; Reznik et al., 2017) are characteristics that support suc-

---

[*] Corresponding author; e-mail: jirislavskuhrovec@gmail.com

cessful propagation of *H. axyridis* in recently invaded areas.

The factors that shape the timing and extent of the seasonal variation in abundance of *H. axyridis* are likely to be similar in both its native and invaded areas (Osawa, 2011). Aphids are essential for *H. axyridis*. Due to *H. axyridis*'s great ability to locate prey (With et al., 2002) and quickly start reproducing, this species is able to establish sub-populations in temporary habitats, patches of hostplants populated by aphids and persist there for a long time (Osawa, 2005). In urban and suburban areas there are trees, which are populated by abundant populations of aphids (Flückiger & Braun, 1999; Mackos-Iwaszko et al., 2015). Adult *H. axyridis* prefer to stay within sub-populations on such trees although the beetles that move away may have a good chance of reaching a patch with a higher aphid density (Osawa, 2000). This habitat fidelity is supported by readiness to accept, besides essential aphid prey (Hodek & Evans, 2012), a wide range of alternative animal and plant food such as Sternorrhyncha (McClure, 1987; Michaud & Olsen, 2004), Heteroptera (Tillman, 2013), Thysanoptera (Zhang et al., 2014), Coleoptera (Stuart et al., 2002), Lepidoptera (Koch et al., 2003), immatures of other predators (Pell et al., 2008), mites (Lucas et al., 1997), pollen, nectar and fruit (Koch et al., 2004; Lundgren et al., 2004; Mathews et al., 2016).

Although many aspects of the life history of *H. axyridis* in Central Europe are well known, the seasonal dynamics of local populations in Central Europe need further study. Particularly unexplored are the variations in local and annual abundance of sub-populations (populations on groups of trees at particular sites) within a metapopulation (a group of partially isolated sub-populations) of *H. axyridis* (Lincoln et al., 1998). This study summarizes six years of records of the abundance of larvae and adults of *H. axyridis* on different species of trees in a suburban area. We address the seasonal variation in abundance of larvae and adults of *H. axyridis* on particular trees and analyze the relationship of this species with site, hostplant and aphid abundance. We tested the hypothesis that the timing and the size of the peak in adult abundance are determined by the size of larval populations that develop at a site rather than the number of adults that arrive at and/or leave the site.

## MATERIAL AND METHODS

### Sampling *H. axyridis*

*Harmonia axyridis* were sampled in the western part of the Czech Republic, at 8 sites situated within a 5.0 × 1.5 km area, centred at 50.0860N, 14.2954E. The sites with groups of lime (*Tilia cordata* Mill., 7 sites), maple (*Acer platanoides* L., 2 sites) and birch trees (*Betula pendula* Roth., 2 sites) were at least 200 m apart from each other (Table 1).

**Table 1.** Characteristics of the sites sampled: Site number (used throughout this study), coordinates of the sites, tree species growing at each site (Species: A – *Acer platanoides* L., B – *Betula pendula* Roth., T – *Tilia cordata* Mill.), number of trees growing at each site (n), their trunk diameter at 1 m height (Diam.) and height (Height). In the text, localities are indicated by a combination of tree species and site number, such as T1 = *Tilia* stand at site 1.

| Site | Coordinates | | Tree | | | |
|---|---|---|---|---|---|---|
| | N | E | Species | n | Diam (cm) | Height (m) |
| 1 | 50.08079 | 14.26303 | T | 16 | 15–60 | 15 |
| 2 | 50.08399 | 14.26806 | T | 26 | 30 | 7 |
| 3 | 50.08566 | 14.30273 | A | 14 | 20–40 | 4–8 |
| | 50.08566 | 14.30273 | B | 6 | 12 | 3 |
| 4 | 50.08677 | 14.30494 | T | 6 | 20 | 6 |
| | 50.08677 | 14.30494 | A | 7 | 20 | 3–6 |
| 5 | 50.08429 | 14.31123 | T | 6 | 50 | 10 |
| 6 | 50.08150 | 14.31119 | T | 9 | 20–45 | 5–10 |
| | 50.08150 | 14.31119 | B | 6 | 30 | 7 |
| 7 | 50.09288 | 14.31325 | T | 4 | 25–40 | 5–7 |
| 8 | 50.09325 | 14.33056 | T | 14 | 20–45 | 7–10 |

Each year sampling started after budburst, in late April or early May, and terminated at leaf fall, in late October to mid-November. The coccinellids were sampled at intervals of two weeks, between the 5th to10th and 20th to 25th each month. The beetles were swept at particular sites from the lower canopy of the same trees and from heights up to 3 m (measured from the ground). Sampling was done by the same person (AH) using a standard sweep net (35 cm in diameter, 140 cm handle), on sunny and calm days, between 08:00 and 18:00 h. Each sampling session involved collecting coccinellids at a particular site from a particular species of tree and lasted 15–30 min depending on the number of trees. Successive sampling at the same site was done using the same number of sweeps. Adults and larvae (3rd and 4th instar, which can be quickly and correctly identified) of *H. axyridis* were counted and immediately released at the site. In total, there were 727 sessions with a mean 127 ± 2.3 sweeps per session (range 50–301 sweeps). To compensate for the differences in the intensity with which the adults and larvae were sampled on each sampling session, the numbers were recalculated to numbers per 100 sweeps (further "n/100"), which is referred to as "abundance".

### Sampling aphids

Tree stands in this study were populated by host specific and holocyclic species of aphids. *Tilia* stands were regularly populated by *Eucallipterus tiliae* (L.), which has a single peak of abundance, the timing and the size of which vary from year to year (Dixon & Barlow, 1979; Dahlsten et al., 1999). The dynamics of *E. tiliae* populations are determined by the size of the overwintering population, hostplant condition, predator activity (Dixon & Barlow, 1979) and aphid behaviour (Kidd, 1976). *Betula* stands were populated by *Euceraphis betulae* (Koch) whose winged females do not aggregate (Dixon & Thieme, 2007) and infest young as well as senescent foliage (Johnson et al., 2003), or by *Calaphis flava* Mordvilko which prefers young foliage (Dixon & Thieme, 2007). *Acer* stands were populated by *Drepanosiphum platanoidis* (Schrank), a holocyclic species whose winged females live dispersed on the undersides of leaves (Dixon & Thieme, 2007) and the seasonal dynamics of which is determined by hostplant quality and population density (Dixon et al., 1993). *Periphyllus* spp. (not identified to species) was also present on maple. The term "hostplant" thus includes plant species, its architecture and microclimate, and behaviour (distribution on hostplant, escape behaviour) of the aphid fauna. Aphid abundance on *Tilia* was classified on a scale of four degrees (hereafter referred to as 'degree of aphid abundance' [daa]). These degrees were based on the aphid counts on 50–500 leaves, with (1) indicating no aphids, (2) < 0.002 aphids per leaf (aphids in swept material but no individuals found on 500 leaves), (3) ≥ 0.002 to 1.0 aphid per leaf, and (4) > 1.0 aphid per leaf.

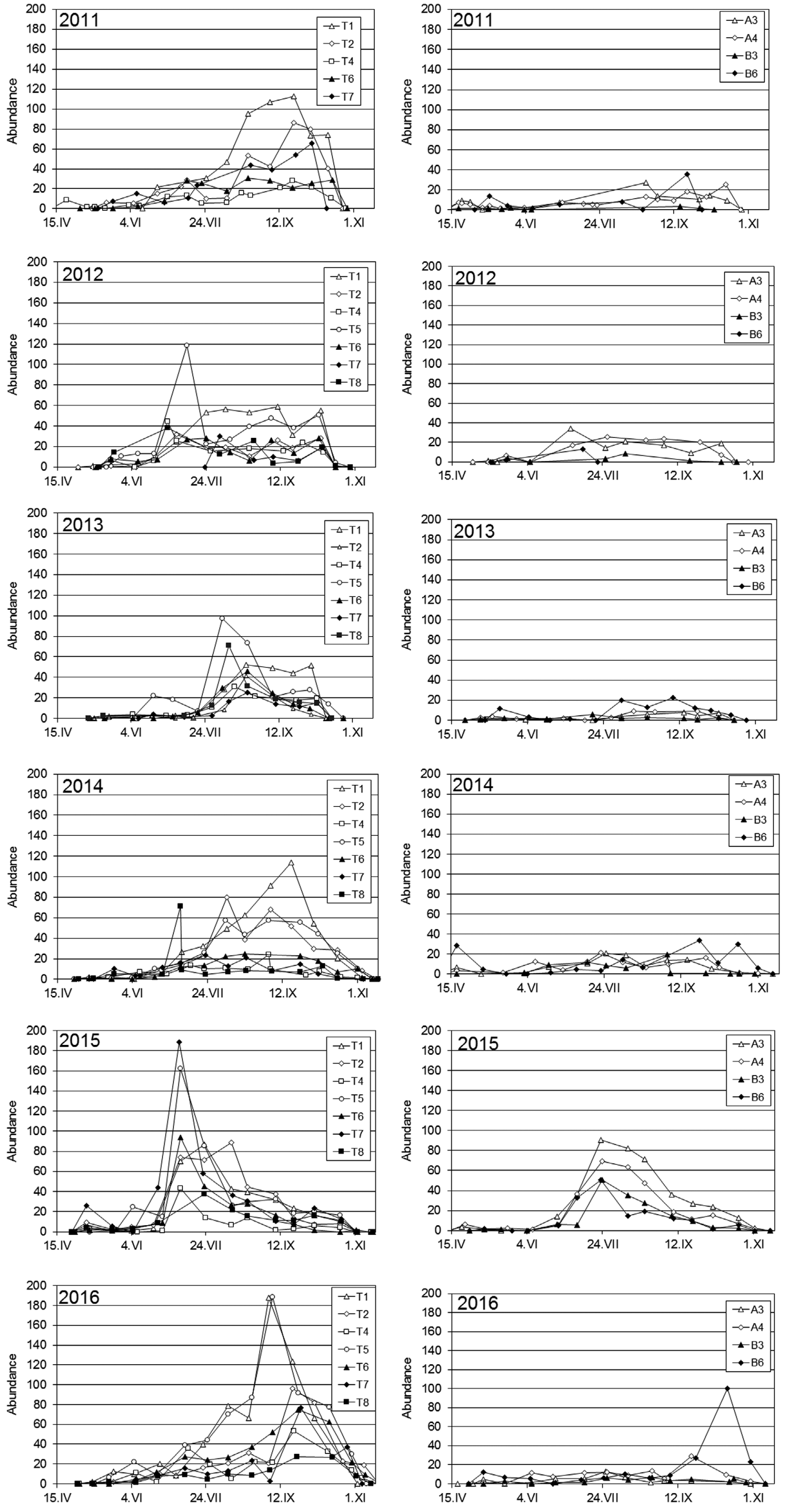

**Fig. 1.** Annual variation in seasonal profiles of the abundance (number of individuals per 100 sweeps) of *H. axyridis* adults on *Tilia* (figures on left-hand side, sites T1–T8), *Acer* (figures on right-hand side, sites A3 and A4) and *Betula* (figures on right-hand side, sites B3 and B6).

### Data analysis

For each hostplant, site and year, the abundance of *H. axyridis* established for particular sampling sessions was plotted against calendar time (Julian days) and the plots (further called "seasonal profiles") were described by four characteristics: (i) "Size" of the area below the profile of the seasonal curve i.e. a product of abundance and time given in "individual*days" units [IDU], (ii) "Range" equal to number of days that elapsed between the earliest and the latest date of species presence, (iii) "Mode position" corresponding to the Julian day when maximum abundance of a species was attained in a given year. (iv) "Mode height" equal to maximum abundance given as number of individuals per 100 sweeps (further n/100).

Analyses were carried out using the seasonal profiles of three hostplants, *Betula* (two sites), *Acer* (two sites) and *Tilia* (seven sites) (Table 1), and six (adults) or five (larvae) years. Variation in seasonal profiles was first investigated using ANOVA (anova), followed by Tukey's HSD (multiple-comparison-corrected) test (hsd) with the characteristics of each profile (profile size, range, mode position and mode height) as response variables and hostplant or year as factors.

To investigate the relationship between the seasonal profiles of adults and larvae two methods were used: (i) The coefficients of regression of the population characteristics (defined above) of adults on those of larvae. To compare the seasonal dynamics of abundances of larvae and adults a regression of maximum adult abundance on maximum abundance of larvae was calculated. To compensate for differences between adults and larvae and for annual variation in their abundances, the data for a particular developmental stage (larva or adult) and year were standardized within years using the formula xs = (xo – xa)/sx, where xs is the standardized value of abundance, xo is the original (observed) value of abundance, xa is average abundance and sx is the standard deviation of the abundance values. (ii) Plotting the seasonal course of adult abundance against time scaled according to the course of development of the larvae. For each site and year, the data were normalized as follows: On the abscissa (x-axis representing time) are the dates on which sampling occurred, the date of the peak (mode position) number of larvae was set to 0 and the dates on which sampling occurred were designated by the length of the period (number of days) prior to the population peak (negative values) or by length of period (number of days) after the population peak (positive values). On the ordinate (y-axis), the relative abundance of adults was expressed for each site as a percentage of the maximum (mode-value) attained in a particular year. The data were fitted using the Asymmetric Double Sigmoidal (ADS) function, which explained maximum variance in the data, using TableCurve 2D (Systat Software, 2002 ).

## RESULTS

Seasonal profiles and changes in the abundance of *H. axyridis* in calendar time were unimodal and their characteristics varied among hostplants, years and sites.

### Variation in the seasonal dynamics of adults of *H. axyridis*

For adult *H. axyridis* (Fig. 1), the size of the seasonal profiles was significantly ($p_{ANOVA}$ = 0.0007) affected by hostplant. Abundance on *Tilia* (N = 40, mean = 3982 ± 372.1 IDU) was significantly greater than that on *Acer* (N = 12, 2159 ± 461.9 IDU, $p_{HSD}$ = 0.0252) or *Betula* (N = 11, 1464 ± 323.4 IDU, $p_{HSD}$ = 0.0019). The range of the seasonal profiles varied significantly ($p_{ANOVA}$ = 0.0167, F = 4.388) and was broadest on *Acer* (192 ± 5.3 d), more narrow on *Betula* (180 ± 5.5 d) and narrowest on *Tilia* (170 ± 4.6 d). Out of the three possible pairwise comparisons, only *Acer* – *Tilia* was significant ($p_{HSD}$ = 0.0140). The timing of the mode of the seasonal profile (date when maximum abun-

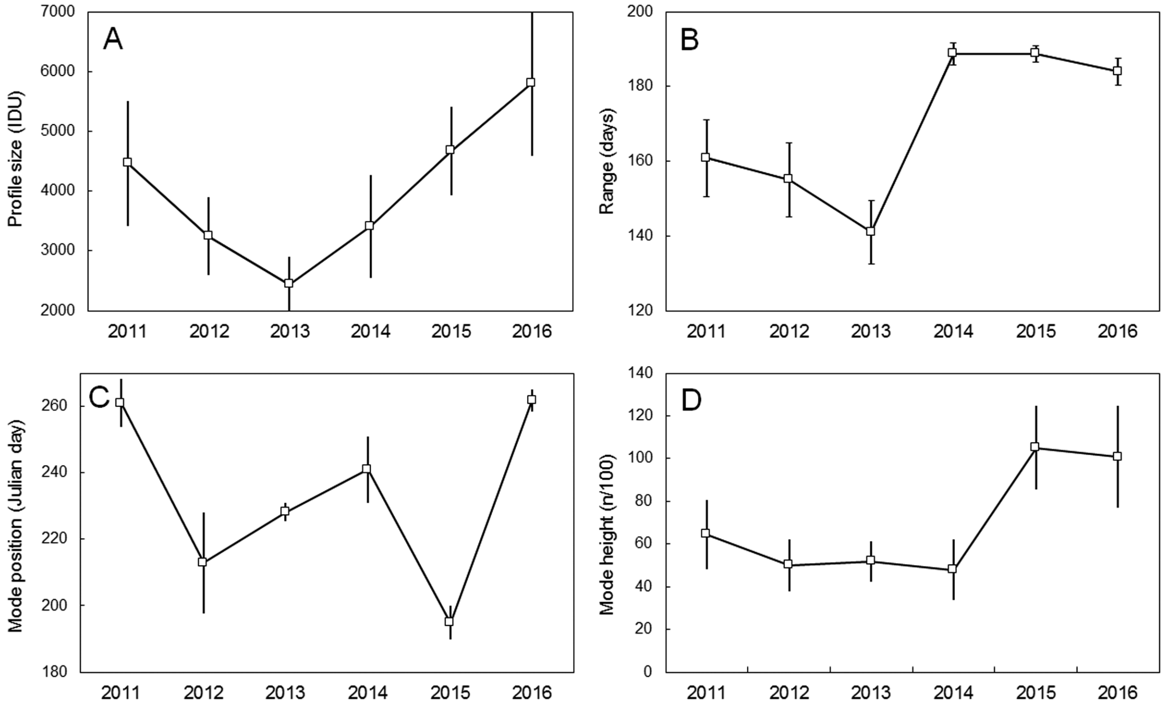

**Fig. 2.** Annual variation in mean (± SE) values of characteristics of the seasonal profiles of *H. axyridis* adults on *Tilia*. A – size of the area below the seasonal profile curve (individual*days units IDU), B – range of the seasonal profile curve (days that elapsed between the earliest and the latest date of species occurence), C – mode position (Julian day when maximum abundance of adults was attained), D – mode height (maximum abundance, number of adults per 100 sweeps).

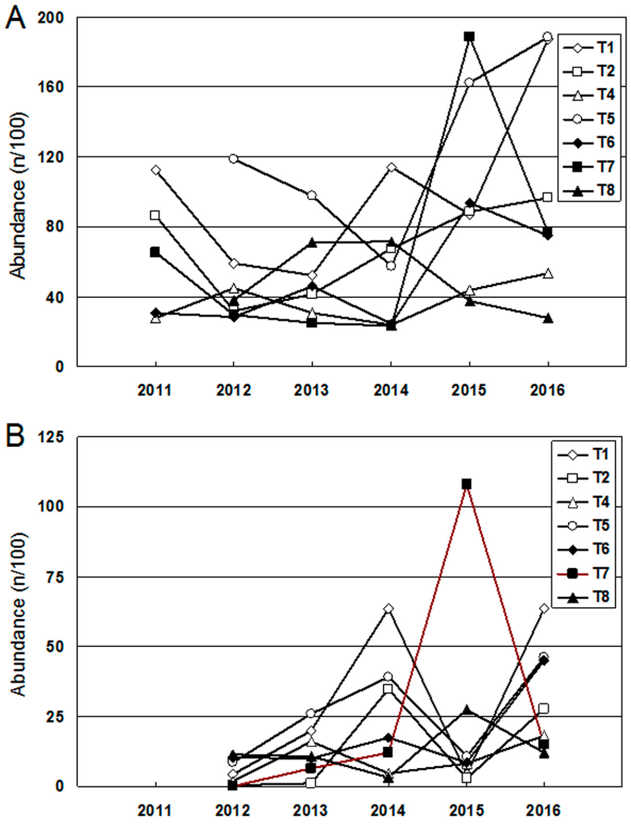

**Fig. 3.** Annual variation in maximum abundance (number of individuals per 100 sweeps) of *Harmonia axyridis* at 7 sites on *Tilia* (T1–T8, Table 1). A – adults, B – larvae.

dance was attained) was not significantly affected by hostplant ($p_{ANOVA} = 0.493$, $F = 0.716$) because it varied greatly between years. The height of the mode (maximum abundance) differed among hostplants significantly ($p_{ANOVA} = 0.0025$, $F = 6.646$). It was significantly higher on *Tilia* (70 ± 7.5 n/100) than on *Acer* (31 ± 7.1 n/100, $p_{HSD} = 0.0148$) or *Betula* (31 ± 8.7 n/100, $p_{HSD} = 0.0177$).

Annual variation in the seasonal profiles of adults was as important as variation among hostplants. There were significant annual differences (Fig. 2) in the area of the seasonal profiles ($p_{ANOVA} = 0.0204$, $F = 2.932$) and their ranges ($p_{ANOVA} < 0.0001$, $F = 14.156$), which were narrowest in 2013 and broadest in 2016. There was significant variation ($p_{ANOVA} < 0.0001$, $F = 12.849$) in the position of the mode (timing of maximum abundance), which was early in 2012 and 2015 and 40–60 d later in 2011 and 2016. Mode height (maximum abundance) varied significantly ($p_{ANOVA} = 0.0024$, $F = 4.255$) and was highest in 2015 and 2016. There was no interaction between hostplant and annual effects for any of these characteristics.

Local (among sites) variation in the size of the seasonal profile ($p_{ANOVA} < 0.0001$, $F = 10.259$) and maximum abundance (mode height) ($p_{ANOVA}$ 0.0012, $F = 5.090$) was important on *Tilia*. The ranking of sites based on mode height was different in particular years (Fig. 3A). At some sites, the values of these characteristics were consistently low as e.g. at site T4 where mean size of the seasonal profile was 2140 ± 355.7 IDUs (range 1326–3721 IDUs) and mean mode height (maximum abundance) was 37 ± 4.7 n/100 (range 24–53 n/100). In contrast, at site T5 mean profile size was 6658 ± 1036.4 IDUs (range 4780–10638 IDUs) and mean mode height (maximum abundance) was 125 ± 23.3 n/100 (range 57–188 n/100).

### Variation in the seasonal dynamics of larvae of *H. axyridis*

For larvae, the effect of hostplant was less conspicuous than for adults (Fig. 4). Comparison of the sizes of the seasonal profiles was on the borderline of formal significance ($p_{ANOVA} = 0.0643$, $F = 2.911$). Size of the seasonal profile was greatest on *Tilia* (638 ± 34.0 IDUs) and smallest on *Acer* (308 ± 8.0 IDUs) and *Betula* (133 ± 8.0 IDUs). The ranges in the seasonal profiles (90 ± 6.4 d for *Tilia*, 85 ± 10.5 d for *Acer* and 69 ± 20.5 d for *Betula*) did not differ significantly ($p_{ANOVA} = 0.4210$, $F = 0.882$). Mode height (maximum abundance) (21 ± 3.9 n/100 for *Tilia*, 11.0 ± 4.0 n/100 for *Acer* and 4.3 ± 1.2 n/100 for *Betula*) was not significantly affected by hostplant ($p_{ANOVA} = 0.0863$, $F = 2.583$). But the position of the mode (date of maximum abundance) was significantly different among tree species ($p_{ANOVA} = 0.0046$, $F = 6.047$). The population mode occurred later on *Tilia* (Julian day 215 ± 6.1 d, which is 2nd August) than on the other two tree species, *Acer* (Julian day 175 ± 13.7 d, which is 23rd June, $p_{HSD} = 0.0277$) and *Betula* (Julian day 174 ± 18.5 d, which is 22nd June, $p_{HSD} = 0.0256$).

There was a significant hostplant x year interaction for range characteristics ($p_{ANOVA} = 0.0027$, $F = 3.793$) and position of the mode ($p_{ANOVA} < 0.0001$, $F = 10.130$). In 2014 and 2016 the ranges of the seasonal profiles were broad and the mode (maximum abundance) was attained later, while the reverse was true in 2012, 2013 and 2015 (Fig. 5). In contrast, sizes (area) of the seasonal profiles ($p_{ANOVA} = 0.0582$, $F = 2.478$) and mode height (maximum abundance) ($p_{ANOVA} = 0.1641$, $F = 1.715$) did not vary significantly among years.

On *Tilia,* there was no significant variation among sites in the size (area) of the seasonal profiles ($p_{ANOVA} = 0.2557$, $F = 1.404$) and mode height (maximum abundance) ($p_{ANOVA} = 0.5990$, $F = 0.773$), (Fig. 3B). As in adults, at some sites, the values were consistently low or high. Thus at site T4 mean size of seasonal profile was 2140 ± 355.7 IDUs (range 1326–3721) and mean mode height (abundance) was 37 ± 4.7 n/100 (range 24–53), while at site T5 mean size of seasonal profile was 6658 ± 1036.4 IDUs (range 4780–10638) and mean mode height was 125 ± 23.3 n/100 (range 57–188).

### Factors determining population dynamics

Adult peaks (total n = 50) coincided or immediately (on the next sampling date) followed larval peaks in 28 (56%) cases (combinations of year x site). In 19 cases (38%) adult peaks followed larval peaks 1 to 3.5 months later and in only 3 cases (6%) did the adult population peak precede the larval peak, by 1 to 2 months. The extreme asynchrony was recorded in cases when adults assembled before (*Betula*) or

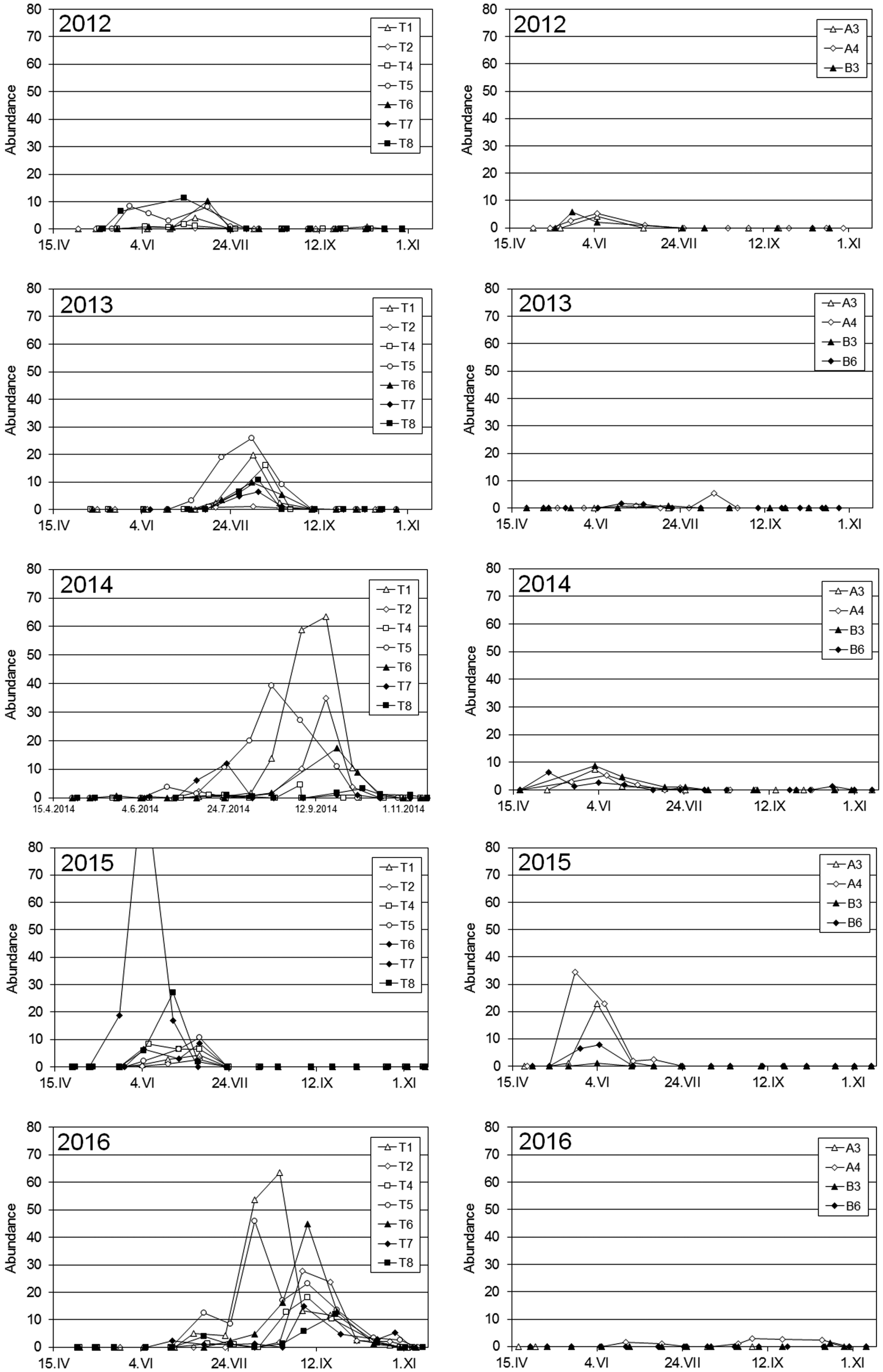

**Fig. 4.** Annual variation in seasonal profiles of the abundance (number of individuals per 100 sweeps) of *H. axyridis* larvae on *Tilia* (figures on left-hand side, sites T1–T8), *Acer* (figures on right-hand side, sites A3 and A4) and *Betula* (figures on right-hand side, sites B3 and B6).

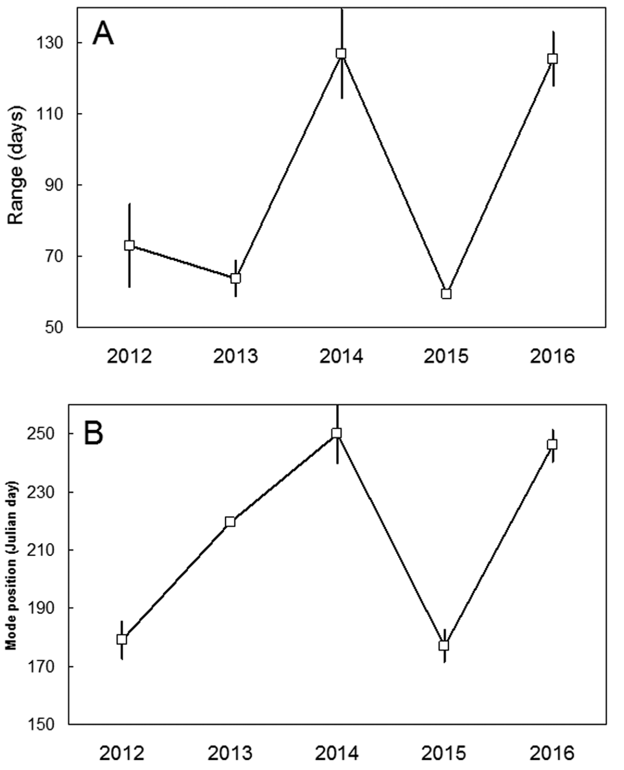

**Fig. 5.** Annual variation in mean (± SE) values of characteristics of the seasonal profiles of *H. axyridis* larvae on *Tilia*. A – range of the seasonal profile curve (days that elapsed between the earliest and the latest date of species occurrence), B – mode position (Julian day when maximum abundance of adults was attained).

after (*Acer*) hibernation, without any relation to breeding at the site.

Despite the rare asynchrony in occurrence, abundance of larval populations and abundance of adult populations, there were significant correlations between the seasonal profiles of adults and larvae, the sizes ($p < 0.0001$, $r = 0.7474$), range ($p = 0.0159$, $r = 0.3394$), mode position ($p < 0.0001$, $r = 0.5788$) and height of mode ($p < 0.0001$, $r = 0.7127$) (Fig. 6). The match of larval and adult seasonal dynamics was best on *Tilia* (Fig. 7) where the larval peaks occurred when aphid abundance was highest and adult peaks followed the larval peaks. The patterns in the coincidence of larval and adult population peaks differed with the timing of aphid and *H. axyridis* occurrence. In 2015 when *H. axyridis* populations peaked early in the season (Fig. 7A), adults assembled and immatures developed in synchrony with the increase in the aphid populations. Larval populations peaked early, 1 to 1.5 months after the arrival of the adults. Abundance of adults peaked 8 d after the larval peak (ADS function: $R^2 = 0.5233$, $F = 18.4451$). Adults then stayed at sites long after the decline in aphid abundance (3–5 months). In 2016 when *H. axyridis* peaked late in the season (Fig. 7B), adults started to assemble, in small numbers, long before the increase in aphid abundance (at some sites > 50 days earlier) and the larval population peak (4 to 5 months), apparently feeding on alternative prey. Abundance of adults peaked 23 d after the larval peak (ADS function: $R^2 = 0.7062$, $F = 38.4549$). The adults did not persist long after the peak since they left the trees and flew to hibernacula.

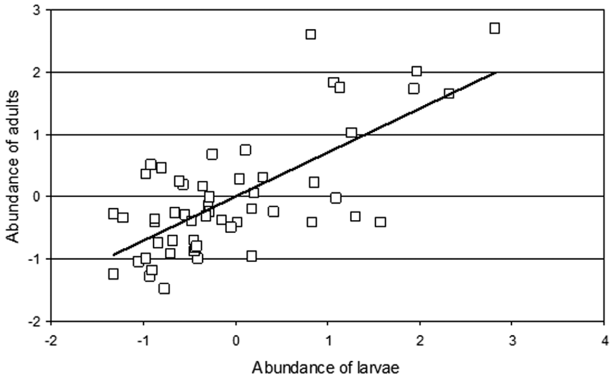

**Fig. 6.** The regression of modal values (maximum abundances) for *H. axyridis* adults on modal values for the larvae. Data for *Tilia* in 2012–2016. To compensate for the annual variation in abundance the data were standardized within years. The graph thus shows abundance as a population mean 0 ± SD. $R^2 = 0.5030$, $p < 0.0001$.

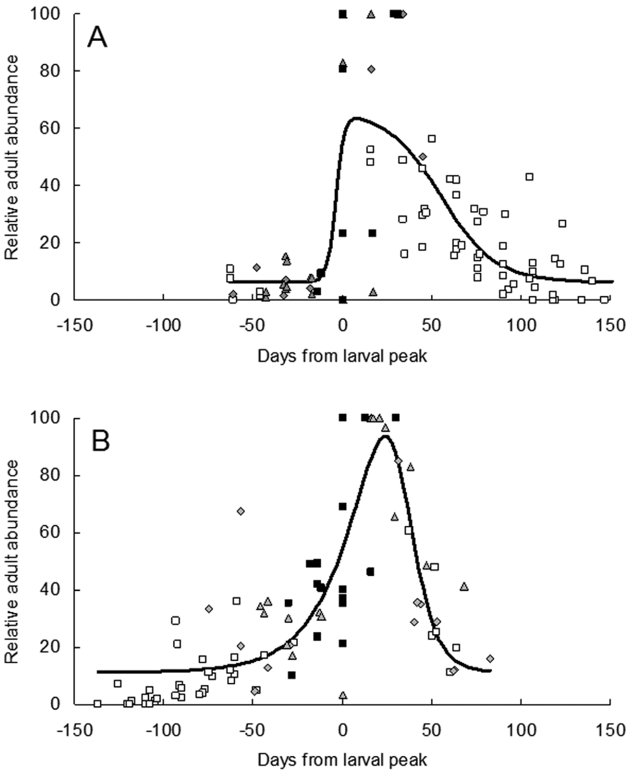

**Fig. 7.** Seasonal variation in the abundance of adult *H. axyridis* on *Tilia*. Adult abundance (percentage of maximum at each site) is plotted against the time (days) that elapsed from the date when larval abundance was at its maximum (0). A – data for 2015 when population dynamics peaked early in the season, B – data for 2016 when population dynamics peaked late in the season. The symbols indicate different degrees of aphid (*Eucallipterus tiliae*) abundance at the time of sampling: □ no aphids ▲ < 0.002 aphids per leaf ♦ ≥ 0.002 to 1.0 aphid per leaf ■ > 1.0 aphid per leaf. The data were fitted using the Asymmetric Double Sigmoidal (ADS) function.

## DISCUSSION

Seasonal dynamics of coccinellids have been studied over a long period of time by many researchers (e.g. Skuhravy & Novak, 1957; Radwan & Lövei, 1983; Hoffmann et al., 1997; Vandereycken et al., 2013; Kawakami et al., 2016). Evaluation of their results reveals that for the safe interpretation of the seasonal dynamics of coccinellids observations should be replicated in space (sites, hostplants) and over time (years), as in our study.

### Factors determining the seasonal variation in abundance

The six year census of abundance revealed constant and variable characteristics in the seasonal dynamics of *H. axyridis*. The seasonal profiles of larvae and adults were unimodal and their size, timing and shape varied among sites and years. Throughout the growing season, the adult population consists of mainly overwintered individuals that produce up to three generations of offspring in Central Europe (Honek et al., 2018a). Thermal conditions enable the overwintered adults of this species to start reproducing at the end of April, the first generation, which may start laying eggs in late June, the second generation in late July and the third one as late as in early September (Honek et al., 2018a). Oviposition by the second and third generations (i.e. under shortening day length) is possible because they only have a weak tendency to winter diapause (Reznik & Vaghina, 2013; Reznik et al., 2015). Since adult life is long, individuals of all generations born during a growing season may survive into autumn and overwinter (Honek et al., 2018a). It is unknown in what proportions the individuals of the successive generations contribute to adult seasonal profiles in particular years and sites. Determining the age structure of natural populations requires information not yet available for *H. axyridis*; such as the length of their reproductive period, time of dormancy induction and percentage of individuals that enter diapause in each generation (Hagen, 1962; Hodek, 2012).

Essential prey are a crucial factor limiting reproductive activity. It is a prerequisite for attracting adults and development of larval populations. This is not surprising considering the food specialization of coccinellids (Hodek & Evans, 2012), but we expect that *H. axyridis* is limited less than native species because it is very polyphagous. *Harmonia axyridis* arrival before aphids was observed in years when aphid abundance on *Tilia* peaked late (Fig. 7), however, they did not reproduce. Threshold aphid population densities necessary for oviposition under natural conditions are unknown but may be quite low, as in *Coccinella septempunctata* L. (Honek, 1980). The adults thus aggregate in large numbers at the very beginning of aphid population development. Towards the end of a season low numbers of adults (Fig. 1) may persist for long periods because they can feed on alternative prey. In contrast to adult seasonal profiles the range in larval profiles was narrow, usually ~ 1 month, probably because oviposition is limited to a "window" (Doumbia et al., 1998; Hemptinne & Dixon, 2000), which ensures there is usually sufficient aphids for the larvae and for *H. axyridis* to lay eggs during the "window" just before aphid numbers peak (Kajita & Evans, 2010).

### Timing of reproduction

In many potentially polyvoltine species of native coccinellids including *Adalia bipunctata* (L.), *Hippodamia variegata* (Goeze), *Ceratomegilla undecimnotata* (Schneider), *Coccinella septempunctata* L. and *Propylea quatuordecimpunctata* (L.) breeding does not occur late in the season. Reproduction in these native species is limited to the first half of the growing season probably because reproduction mainly occurs in stands of herbaceous plants (Hodek, 1960). In contrast, that of some native species developing on trees such as *Calvia decemguttata* (L.), *C. quatuordecimguttata* (L.) and *Oenopia conglobata* (L.), may extend into autumn (Honek et al., 2019) and their larvae may feed on populations of monoecious species of aphids that persist until late in the season. Seasonal profiles of larvae of *H. axyridis*, however, extend to as late as November (Honek et al., 2018a). A prolongation of larval development into autumn is hazardous if winter comes early. However, at least in warm years, late larval development may be successful. This extension of the period available for development, although risky, may contribute to the success of invasive species such as *H. axyridis* in extending the area colonized.

### Demographic processes

Seasonal profiles of coccinellids are shaped by demographic processes, natality and mortality, and movements of individuals (dispersal/migration). A significant positive correlation between larval and adult seasonal profiles (Fig. 7) indicates that local reproductive activity is an important determinant of adult population size. At least two facts indicate that dispersal (movement of adults between sites) is also important in determining adult population size. First, temporal disconnection between peak larval and adult occurrence, which was recorded in a few cases, when the timing of the mode in adult occurrence was delayed by > 1 month after the larval peak. These late peaks may be composed of "autochthonous" individuals that developed locally plus immigrants from surrounding areas. The source populations of immigrants is likely to be stands of herbaceous plants (Honek et al., 2019) on which the abundance of *H. axyridis* declined because of plant senescence. Abundance of *H. axyridis* in stands of herbaceous plants and crops is low but their area in agricultural landscapes is much bigger than the area covered by stands of trees, their preferred habitat. The role of migration in the seasonal dynamics of *H. axyridis* is important. In native populations in East Asia, adults fly continuously between sub-populations (Osawa, 2000). Adults in invasive populations also fly regularly (Nalepa, 2013) perhaps in search of new hostplant stands and thus increase the probability of finding habitats populated by aphids. Flights supported by wind may cover several kilometres (Jeffries et al., 2013). This high mobility results in the opportunistic location and exploitation of small patches of prey (With et al., 2002) and contrasts with the sedentary behaviour of native species of coccinellid, which tend to remain at sites where they reproduce until the prey become extinct (Kokubu, 1986).

Although it was impossible to survey all the habitats where this species occurs, those studied included the hostplants they prefer (Adriaens et al., 2008; Viglasova et al., 2017). On *Tilia,* abundant assemblages of adults followed peaks in aphid abundance, whereas the adults that assembled on *Acer* and *Betula* bore no relation to the numbers that bred there. Adults are able to exploit aphid outbreaks whose timing is unpredictable by surviving in relatively high numbers at sites where aphid prey abundance is insufficient for breeding, or even at sites where there is only alternative prey. Occupation of such transient habitats depends on a high dispersal capacity and is no less important than breeding locally.

### Short- and long-term population trends

The results contradict intuitive expectations concerning seasonal and long-term trends in *H. axyridis* abundance. Numbers of *H. axyridis* adults in particular sub-populations on trees (this study) and other hostplants (Honek et al., 2019), which make up its metapopulation, should increase over the course of a season as a consequence of polyvoltinism and an increase in the number of individuals that reproduce (Honek et al., 2018a). Adults, therefore, should be more abundant in autumn than in spring. However, this trend was not reflected in our data (Fig. 1) as there was no systematic difference in the modal height (maximum abundance) of the early (2012, 2015) and late (2011, 2016) adult peaks (Fig. 2C, D). Our six year study of the population dynamics of *H. axyridis* encompasses more than half of the period of its occurrence in the Czech Republic, where this species became established in 2006 (Sprynar, 2008). During this period we expected this species to increase in abundance if it was still continuing to spread or no trend if it had reached the „carrying capacity“ of this newly occupied area. This analysis did not reveal a monotonic increase in the size of the seasonal profiles (Fig. 2A).

The results point to the importance of long-term studies for understanding the mechanisms of population development in *H. axyridis*. Annual variation in seasonal profiles revealed that *H. axyridis* is plastic in its response to environmental conditions. This flexible response to trophic and climatic conditions (Honěk et al., 2018b) is apparently an important factor in the invasive success of this species. Other factors determining the abundance of *H. axyridis*, e.g. metapopulation size and landscape quality, await clarification.

**ACKNOWLEDGEMENTS.** A.H., Z.M. and J.S. were supported by the Ministry of Agriculture of the Czech Republic, institutional support MZE-RO0418 and from program NAZV No. QK1910281 (MZe ČR). M.B. by the long-term strategic development financing of the Institute of Computer Science (Czech Republic RVO 67985807), A.F.G.D. by Grant No. CZ.1.05/ 1.1.00/02.0073 of the Ministry of Education of the Czech Republic. We thank J. Kohoutová and H. Uhlířová for excellent technical assistance.

## REFERENCES

Adriaens T., San Martin y Gomez G. & Maes D. 2008: Invasion history, habitat preferences and phenology of the invasive ladybird *Harmonia axyridis* in Belgium. — *BioControl* **53**: 69–88.

Brown P.M.J. & Roy H.E. 2018: Native ladybird decline caused by the invasive harlequin ladybird *Harmonia axyridis*: evidence from a long-term field study. — *Insect Conserv. Divers.* **11**: 230–239.

Brown P.M.J., Ingels B., Wheatley A., Rhule E.L., De Clercq P., van Leeuwen T. & Thomas A. 2015: Intraguild predation by *Harmonia axyridis* (Coleoptera: Coccinellidae) on native insects in Europe) molecular detection from field samples. — *Entomol. Sci.* **18**: 130–133.

Dahlsten D.L., Zuparko R.L., Hajek E.A., Rowney D.L. & Dreistadt S.H. 1999: Long-term sampling of *Eucallipterus tiliae* (Homoptera: Drepanosiphidae) and associated natural enemies in a northern California site. — *Environ. Entomol.* **28**: 845–850.

Dixon A.F.G. & Barlow N.D. 1979: Population regulation in the lime aphid. — *Zool. J. Linn. Soc.* **67**: 225–237.

Dixon T. & Thieme T. 2007: *Aphids on Deciduous Trees*. The Richmond Publishing Co., Slough, UK, 138 pp.

Dixon A.F.G., Wellings P.W., Carter C. & Nichols J.F.A. 1993: The role of food quality and competition in shaping the seasonal cycle in the reproductive activity of the sycamore aphid. — *Oecologia* **95**: 89–92.

Doumbia M., Hemptinne J.L. & Dixon A.F.G. 1998: Assessment of patch quality by ladybirds): role of larval tracks. − *Oecologia* **113**: 197–202.

Fluckiger W. & Braun S. 1999: Stress factors of urban trees and their relevance for vigour and predisposition for parasite attacks. — *Acta Hortic.* **496**: 325–334.

Gagnon A.E. & Brodeur J. 2014: Impact of plant architecture and extraguild prey density on intraguild predation in an agroecosystem. — *Entomol. Exp. Appl.* **152**: 165–173.

Hagen K.S. 1962: Biology and ecology of predaceous Coccinellidae. — *Annu. Rev. Entomol.* **7**: 289–326.

Hemptinne J.L. & Dixon A.F.G. 2000: Defence, oviposition and sex) semiochemical parsimony in two species of ladybird beetles (Coleoptera, Coccinellidae)? A short review. — *Eur. J. Entomol.* **97**: 443–447.

Hodek I. 1960: Hibernation-bionomics in Coccinellidae. — *Čas. Čs. Spol. Entomol.* **57**: 1–20.

Hodek I. 2012: Diapause/dormancy. In Hodek I., van Emden H.F. & Honek A. (eds): *Ecology and Behaviour of the Ladybird Beetles (Coccinellidae).* Wiley-Blackwell, Chichester, pp. 275–342.

Hodek I. & Evans E.W. 2012: Food relationships. In Hodek I., van Emden H.F. & Honek A. (eds): *Ecology and Behaviour of the Ladybird Beetles (Coccinellidae).* Wiley-Blackwell, Chichester, pp. 141–274.

Hoffmann M.P., Orfanedes M.S., Pedersen L.H., Kirkwyland J.J., Hoebke E.R. & Ayyappath R. 1997: Survey of lady beetles (Coleoptera: Coccinellidae) in sweet corn using yellow sticky cards. — *J. Entomol. Sci.* **32**: 358–369.

Honek A. 1980: Population density of aphids at the time of settling and ovariole maturation in *Coccinella septempunctata* (Col., Coccinellidae). — *Entomophaga* **25**: 427–430.

Honek A., Martinkova Z., Kindlmann P., Ameixa O.M.C.C. & Dixon A.F.G. 2014: Long-term trends in the composition of aphidophagous coccinellid communities in Central Europe. − *Insect Conserv. Divers.* **7**: 55–63.

Honek A., Martinkova Z. & Dixon A.F.G. 2015: Detecting seasonal variation in composition of adult Coccinellidae communities. — *Ecol. Entomol.* **40**: 543–552.

Honek A., Martinkova Z., Dixon A.F.G., Roy H.E. & Pekar S. 2016: Long-term changes in communities of native coccinellids: population fluctuations and the effect of competition from an invasive non-native species. — *Insect Conserv. Divers.* **9**: 202–209.

Honek A., Martinkova Z., Dixon A.F.G., Skuhrovec J., Roy H.E., Brabec M. & Pekar S. 2018a: Life cycle of *Harmonia axyridis* (Coleoptera: Coccinellidae) in central Europe. — *BioControl* **63**: 241–252.

Honěk A., Martinková Z. & Štrobach J. 2018b: Effect of aphid abundance and urbanization on the abundance of *Harmonia axyridis* (Coleoptera: Coccinellidae). — *Eur. J. Entomol.* **115**: 703–707.

Honek A., Martinkova Z., Roy H.E., Dixon A.F.G., Skuhrovec J., Pekar S. & Brabec M. 2019: Differences in the phenology of *Harmonia axyridis* and native coccinellids on plants in central Europe (Coleoptera: Coccinellidae). — *Environ. Entomol.* **48**: 80–87.

Jeffries D.L., Chapman J., Roy H.E., Humphries S., Harrington R., Brown P.M.J. & Lawson Handley L.J. 2013: Characteristics and drivers of high-altitude ladybird flight: insights from vertical-looking entomological radar. — *PLoS ONE* **8**: e82278, 12 pp.

Johnson S.N., Elston D.A. & Hartley S.E. 2003: Influence of host plant heterogeneity on the distribution of a birch aphid. — *Ecol. Entomol.* **28**: 533–541.

Kajita Y. & Evans E.W. 2010: Alfalfa fields promote high reproductive rate of an invasive predatory lady beetle. — *Biol. Invas.* **12**: 2293–2302.

Kawakami Y., Yamazaki K. & Ohashi K. 2016: Population dynamics, seasonality and aphid prey of *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae) in an urban park in central Japan. — *Eur. J. Entomol.* **113**: 192–199.

Kidd N.A.C. 1976: Aggregation in the lime aphid (*Eucallipterus tiliae* L.) 2. Social aggregation. — *Oecologia* **25**: 175–185.

Kindlmann P., Honek A. & Martinkova Z. 2017: Spreading of alien species and diversity of communities. — *BioControl* **62**: 397–407.

Koch R.L., Hutchinson W.D., Venette R.C. & Heimpel G.E. 2003: Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danainae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). — *Biol. Contr.* **28**: 265–270.

Koch R.L., Burkness E.C., Wold Burkness S.J. & Hutchinson W.D. 2004: Phytophagous preferences of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) for autumn-ripening fruit. — *J. Econ. Entomol.* **97**: 539–544.

Kokubu H. 1986: *Migration Rates, in Situ Reproduction, and Flight Characteristics of Aphidophagous Insects (Chrysopidae, Coccinellidae, and Syrphidae) in Cornfields.* PhD Thesis, University of Basel, 186 pp.

Lincoln R., Boxshall G. & Clark P. 1998: *A Dictionary of Ecology, Evolution and Systematics*. Cambridge University Press, Cambridge, UK, 361 pp.

Lucas E., Coderre D. & Vincent C. 1997: Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*. — *Entomol. Exp. Appl.* **85**: 151–159.

Lundgren J.G., Razzak A.A. & Wiedenmann R.N. 2004: Population responses and food consumption by predators *Coleomegilla maculata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) during anthesis in an Illinois cornfield. — *Environ. Entomol.* **33**: 958–963.

Mackos-Iwaszko E., Lubiarz M. & Karczmarz K. 2015: The impact of urban conditions on the occurrence of aphids on *Acer platanoides* L. — *Acta Sci. Pol. / Hortorum Cultus* **14**: 189–207.

Mathews C.R., Brown M.W. & Wäckers F. 2016: Comparison of peach cultivars for provision of extrafloral nectar resources to *Harmonia axyridis* (Coleoptera: Coccinellidae). — *Environ. Entomol.* **45**: 649–657.

McClure M.S. 1987: Potential of the Asian predator, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), to control *Matsucoccus resinosae* Bean and Godwin (Homoptera: Margarodidae) in the United States. — *Environ. Entomol.* **16**: 224–230.

Michaud J.P. & Olsen L.E. 2004: Suitability of Asian citrus psyllid, *Diaphorina citri*, as prey for ladybeetles. — *BioControl* **49**: 417–431.

Nalepa C.A. 2013: Coccinellidae captured in blacklight traps, seasonal and diel pattern of the dominant species *Harmonia axyridis* (Coleoptera: Coccinellidae). — *Eur. J. Entomol.* **110**: 593–597.

Nedved O. 2014: [Harmonia axyridis – *Useful Agent in Biological Control or Threat of Biodiversity?*] University of South Bohemia, Ceske Budejovice, 67 pp. [in Czech].

Osawa N. 2000: Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): resource tracking and population characteristics. — *Popul. Ecol.* **42**: 115–127.

Osawa N. 2005: The effect of prey availability on ovarian development and oosorption in the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). — *Eur. J. Entomol.* **102**: 503–511

Osawa N. 2011: Ecology of *Harmonia axyridis* in natural habitats within its native range. — *BioControl* **56**: 613–621.

Pell J.K., Baverstock J., Roy H.E., Ware R.L. & Majerus M.E.N. 2008: Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives. — *BioControl* **53**: 147–168.

Radwan Z. & Lövei G.L. 1983: Structure and seasonal dynamics of larval, pupal, and adult coccinellid (Col., Coccinellidae) assemblages in two types of maize fields in Hungary. — *Z. Angew. Entomol.* **95**: 396–408.

Reznik S.Ya. & Vaghina N.P. 2013: Effects of photoperiod and diet on diapause tendency, maturation and fecundity in *Harmonia axyridis* (Coleoptera: Coccinellidae). — *J. Appl. Entomol.* **137**: 452–461.

Reznik S.Ya., Dolgovskaya M.Yu., Ovchinnikov A.N. & Belyakova N.A. 2015: Weak photoperiodic response facilitates the biological invasion of the harlequin ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). — *J. Appl. Entomol.* **139**: 241–249.

Reznik S.Ya., Ovchinnikov A.N., Ovchinnikova A.A., Belyakova N.A. & Barabanova L.V. 2017: On the photoperiodic induction of diapause in first generation hybrids of *Harmonia axyridis* (Pall.) (Coleoptera, Coccinellidae). — *Russ. J. Genet. Appl. Res*. **7**: 717–720.

Roy H.E., Brown P.M.J., Adriaens T., Berkvens N., Borges I., Clusella Trullas S., Comont R., De Clercq P., Eschen R., Estoup A. et al. 2016: The harlequin ladybird, *Harmonia axyridis* global perspectives on invasion history and ecology. — *Biol. Invas.* **18**: 997–1044.

Skuhravy V. & Novak K. 1957: [Insect fauna of potato field and its seasonal development.] — *Rozpr. Čsl. Akad. Věd* **67**: 1–50 [in Czech].

Sprynar P. 2008: Faunistic records from the Czech Republic – 252. Coleoptera: Coccinellidae. — *Klapalekiana* **44**: 77–79.

Stuart R.J., Michaud J.P., Olsen L. & McCoy C.W. 2002: Lady beetles as potential predators of the root weevil *Diaprepes abbreviatus* (Coleoptera: Curculionidae) in Florida citrus. — *Fla Entomol.* **85**: 409–416.

Systat Software 2002: *TableCurve 2D 5.01 for Windows User's Manual.* Richmond, VA, 660 pp.

Tillman P.G. 2013: Stink bugs (Heteroptera: Pentatomidae), a leaffooted bug (Hemiptera: Coreidae), and their predators in sorghum in Georgia. — *J. Entomol. Sci.* **48**: 9–16.

Vandereycken A., Brostaux Y., Joie E., Haubruge E. & Verheggen F.J. 2013: Occurrence of *Harmonia axyridis* (Coleoptera) Coccinellidae) in field crops. — *Eur. J. Entomol.* **110**: 285–292.

Viglasova S., Nedved O., Zach P., Kulfan J., Parak M., Honek A., Martinkova Z. & Roy H.E. 2017: Species assemblages of ladybirds including the harlequin ladybird *Harmonia axyridis*: a comparison at large spatial scale in urban habitats. — *BioControl* **62**: 409–421.

With K.A., Pavuk D.M., Worchuck J.L., Oates R.K. & Fisher J.L. 2002: Threshold effects of landscape structure on biological control in agroecosystems. — *Ecol. Appl.* **12**: 52–65.

Zhang G.F., Wu X., Zhou Z.X., Meng X.Q. & Wan F.H. 2014: A one-step, single tube, duplex PCR to detect predation by native predators on invasive *Bemisia tabaci* MEAM1 and *Frankliniella occidentalis*. — *Entomol. Exp. Appl.* **150**: 66–73.

Received October 25, 2018; revised and accepted March 19, 2019