



Warm Mesoclimate Advances the Seasonal Dynamics of *Harmonia axyridis* in Urban Habitats

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OPEN ACCESS

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Specialty section:

This article was submitted to
Population, Community,
and Ecosystem Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

Received: 15 June 2021

Accepted: 07 September 2021

Published: 30 September 2021

Citation:

Honek A, Skuhrovec J,
Martinkova Z, Kulfan J, Jauschova T
and Zach P (2021) Warm
Mesoclimate Advances the Seasonal
Dynamics of *Harmonia axyridis*
in Urban Habitats.
Front. Ecol. Evol. 9:725397.
doi: 10.3389/fevo.2021.725397

In 2016–2019, seasonal changes in the abundance of the harlequin ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) were established in the city center of Prague, Central Europe, and in its outskirts. Adults were sampled from lime trees (*Tilia* spp.) at regular intervals throughout the growing season. The abundance of *H. axyridis* paralleled the course of abundance of its prey, the aphid *Eucallipterus tiliae* L., which peaks either early or late in the season. As a result, the seasonal dynamics of *H. axyridis* were unimodal, with a peak in the early (late June—early July of 2017 and 2019) or late (late July—mid-September of 2016 and 2018) period of the season. In the early period, there was a small (1–4 days) difference in the timing of the peak of *H. axyridis* between the city center and the outskirts. In the late period, the peak occurred significantly earlier (by 13–21 days) in the city center due to the warmer climate there than in the outskirts. The difference in the timing of the population peak between both locations disappeared after recalculating the calendar to thermal time (number of day degrees above 10.6°C thresholds elapsed from the end of *H. axyridis* hibernation). The warm mesoclimate of the city center advances the seasonal dynamics of *H. axyridis*, contributing to the success of this invasive species in urban habitats.

Keywords: urban habitats, invasive, ladybirds, prey, temperature, mesoclimate, seasonal dynamics

INTRODUCTION

In Central Europe, *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) is a dominant invasive ladybird, although it is only a recently established component of aphidophagous coccinellid communities (Roy et al., 2016). This species occurs in urban (Adriaens et al., 2008; Purse et al., 2015; Mukwevho et al., 2017), agricultural (Musser and Shelton, 2003; Lucas et al., 2007; Riddick, 2017), and forest areas (Vandereycken et al., 2012) on trees, herbs and crops populated by a variety of aphid species. This adaptability to diverse habitats is due to the plasticity of its seasonal cycle. Overwintering adults leave the hibernation sites in April. During the vegetative season, 2–3 incomplete generations of offspring may be produced, depending on temperature. In the autumn, adults of all generations enter dormancy and overwinter together (Honek et al., 2019b). Dispersion of adults into and using host stands for reproduction is opportunistic since adults always occupy stands with high prey abundance (Honek et al., 2019b). Due to its plastic life cycle and high adaptability to local conditions, *H. axyridis* is a suitable subject for studying the effects of urban and rural environments on the life cycle (Dudek et al., 2015; Sloggett, 2017; Honek et al., 2018b).

Among the characteristics that differentiate urban and rural areas is a difference in their mesoclimate, which is typically warmer in city centers than in the outskirts (Bonan, 2002). As temperature determines the rate of development of exotherms, we hypothesize that differences in mesoclimate affect the pace of life of *H. axyridis* and predict that (i) the peak abundance will occur earlier in the city center than in the outskirts and (ii) this difference will level off if population development is plotted against thermal time. This hypothesis was tested in 2016–2019, when populations of *H. axyridis* were sampled from *Tilia* sp. infested with aphids in the city center and on the outskirts of Prague.

MATERIALS AND METHODS

Sampling

The abundance of *H. axyridis* was recorded in 2 areas situated at ~10 km distance in the western part of Prague, Central Europe. The beetles were sampled at 8 sites on the outskirts (situated between 50.081–50.094 N and 14.263–14.336 E) and at 4 sites in the city center (50.072–50.075 N, 14.454–14.465 E). The tree stands at particular sites consisted of ≥ 5 lime trees (*Tilia cordata* Mill. or *Tilia platyphyllos* Scop.) infested with the aphid *Eucallipterus tiliae* (L.) (Sternorrhyncha: Aphididae). This aphid species has a single peak of abundance, the timing of which varies from year to year (Dixon and Barlow, 1979; Dahlsten et al., 1999).

The lime trees were sampled throughout the whole period when *H. axyridis* adults were present on the lime trees (May to October) at 10-day intervals. Beetles were swept from the canopy up to a height of approximately 3 m. Sampling was standardized using a standard sweep net (35 cm diameter, 140 cm handle) operated by J.S. (city center) and A.H. (outskirts). All the days on which samples were collected were sunny and calm. The sampling (80–200 sweeps at each site) was performed, and *H. axyridis* abundance (number of adults caught per 100 sweeps) was established between 08.00 and 18.00 h. The abundance of aphids was classified according to an earlier elaborated scale (Honek et al., 2019b) into 4 degrees as follows based on the aphid counts: (1) 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 aphids per leaf, and (4) > 1.0 aphids per leaf. The difference in urbanization at the outskirts and city center areas was quantified as the percentage of the surrounding area (a circle with a 500-m radius centered at each sampling site) covered by impervious surfaces (buildings, streets, parking places, etc.) (Honek et al., 2018b). These values were $39 \pm 3.0\%$ in the outskirts and $71 \pm 5.6\%$ in the city center and were determined using maps available at <https://en.mapy.cz>.

Air temperature at 2 m above the ground was used to calculate the thermal time. The data for the outskirts were taken from the meteorological station of the Crop Research Institute (50.085N, 14.298E), and the data for the city center were taken from the meteorological station Klementinum (50.086N, 14.416E). The thermal time (expressed in day degrees dd) for *H. axyridis* was calculated as the sum of effective temperatures ($^{\circ}\text{C}$) above the 10.6°C lower development threshold (Honek et al., 2018a)

starting on 20 April, the date *H. axyridis* left the hibernation sites (Honek et al., 2018a). The thermal time (expressed in day degrees dd) for *E. tiliae* was calculated as the sum of effective temperatures ($^{\circ}\text{C}$) above the 5.0°C lower development threshold starting from the beginning of the year (Dixon et al., 1997; Brabec et al., 2014).

Data Analysis

For each year and site, the Julian day was determined when the maximum abundance of *H. axyridis* (population peak) was observed. Each year, the average terms of maximum abundance were calculated for the city center and the outskirts as the arithmetic mean (\pm SE) of the terms of population peaks at particular sites. Differences were tested using *t*-tests or (if the normality test failed) Mann-Whitney tests. Calculations were performed using SigmaStat 3.5 (Systat Software Inc, 2006).

For each site and year the relative frequency of *H. axyridis* was calculated so that the maximum abundance was rated 1 and the abundance on other dates as a proportion of this maximum. This data plotted against time (Julian day) was fitted by the Asymmetric Double Sigmoidal (ADS) function. Calculations were performed using TableCurve 2D (Systat Software Inc, 2002).

RESULTS

Each year, the course of change in the abundance of *H. axyridis* adults was unimodal. The term of peak abundance varied among years. In both areas, abundance peaked early in 2017 (22 June and 23 June) and 2019 (5 July and 9 July) and late in 2016 (29 August and 19 September) and 2018 (15 July and 28 July), with the peak occurring earlier every year in the city center than in the outskirts (Figure 1). The interval dividing the population peak in the city center and the population peak in the outskirts increased with the time that had elapsed since the beginning of the season (Figure 2). The difference was statistically significant in the years when abundance peaked late (2016 and 2018) (Table 1). The obvious difference on Julian days leveled off after the calendar time was transformed to thermal time (except 2017, when the population peak occurred very early). Differences in the timing of the population peak thus arose due to differences in the thermal conditions of the city center and the outskirts.

DISCUSSION

Mesoclimate Factors That Affect Population Development

Divergence in the quality of urban (downtown area) and rural (outskirt area) environments is well established and is associated with a variety of environmental characteristics. Urban centers differ from the outskirts in terms of excessive light pollution, decreased humidity, modified schedules of precipitation and variations in wind direction and speed (Bonan, 2002). The differences increase with the size of the town and are appreciable in cities whose human population exceeds 1 million (Karl et al., 1988), as is the case for Prague. Urban conditions affect

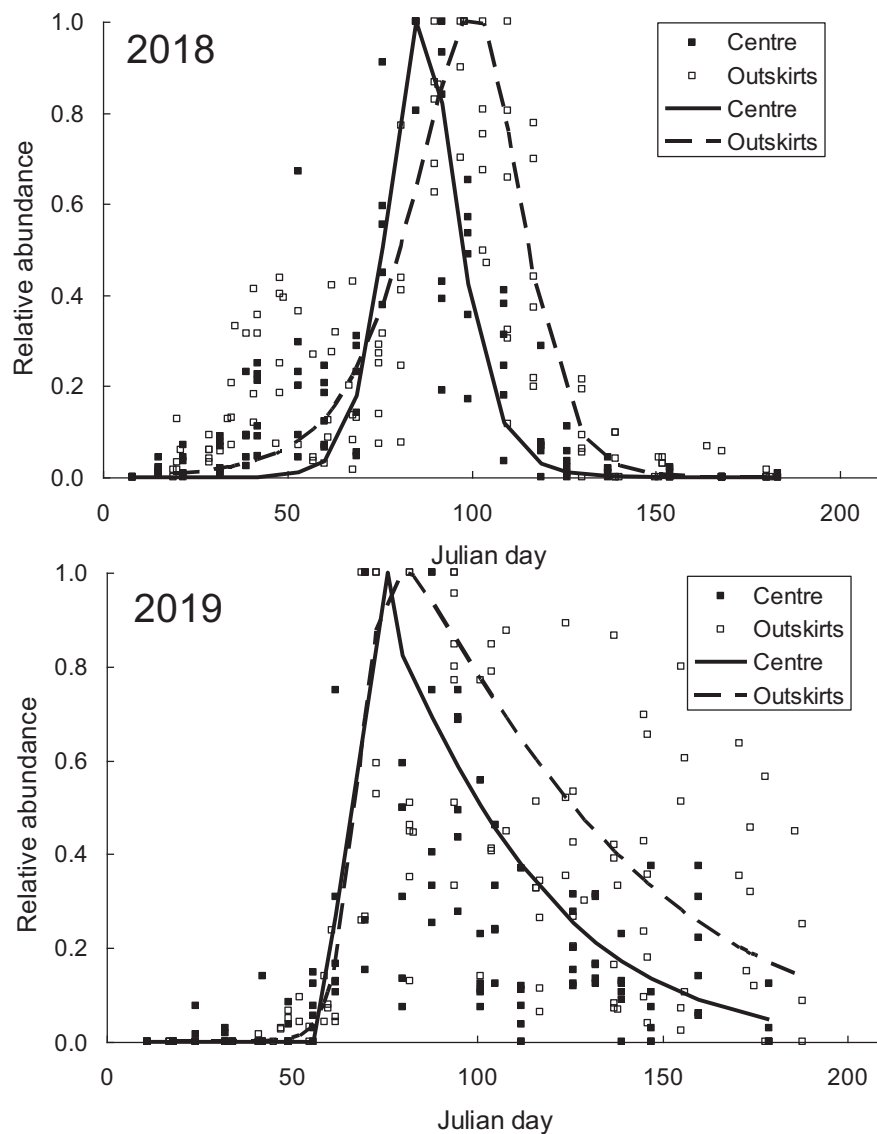


FIGURE 1 | Changes in the relative abundance of *Harmonia axyridis* in the city center and the outskirts of Prague plotted against calendar time (Julian days from leaving their hibernacula on 20 April). The maximum abundance at each locality is scored 1. The data were fitted to the asymmetric double sigmoidal (ADS) equation. The figure shows example of a year when population peak occurred late in the season (2018) and of a year when population peak occurred early in the season (2019).

vegetation (Pyšek, 1998), its insect phytophagans and their predators (Bolger et al., 2000; McIntyre, 2000; Pickett et al., 2001), as well as their pathogens (Dudek et al., 2017a,b). Apart from light pollution, divergent ambient temperature is the most important difference between urban and rural environments. The warm temperature of urban areas compared to that of rural areas accelerates the rate of life processes of exotherm organisms. Differences in their duration are compensated when calendar time is converted to thermal time (Trudgill et al., 2005).

The agreement between the term of the population peak in the city center and the term of the population peak in the outskirts resulting from this transformation (**Table 1**) indicates that the timing of peaks depends on the sum of a definite amount of heat.

Increased ambient temperature accelerates the life processes of *H. axyridis* and shifts the peak of its seasonal cycle of abundance if sufficient prey is available to support an acceleration. This is a necessary consequence of the influence of urban centers on populations of exothermic organisms.

The effect of ambient temperature could be modified by thermoregulation, which can shift body temperature against ambient temperature, albeit slightly. A decrease in body temperature can be achieved by searching for and hiding in cool places. Coccinellids living in the city center on trees surrounded by buildings and roads that are severely heated in the sunshine (Parlow, 2011) have little chance of decreasing their pace of life. Additionally, they have no reason to decrease their body

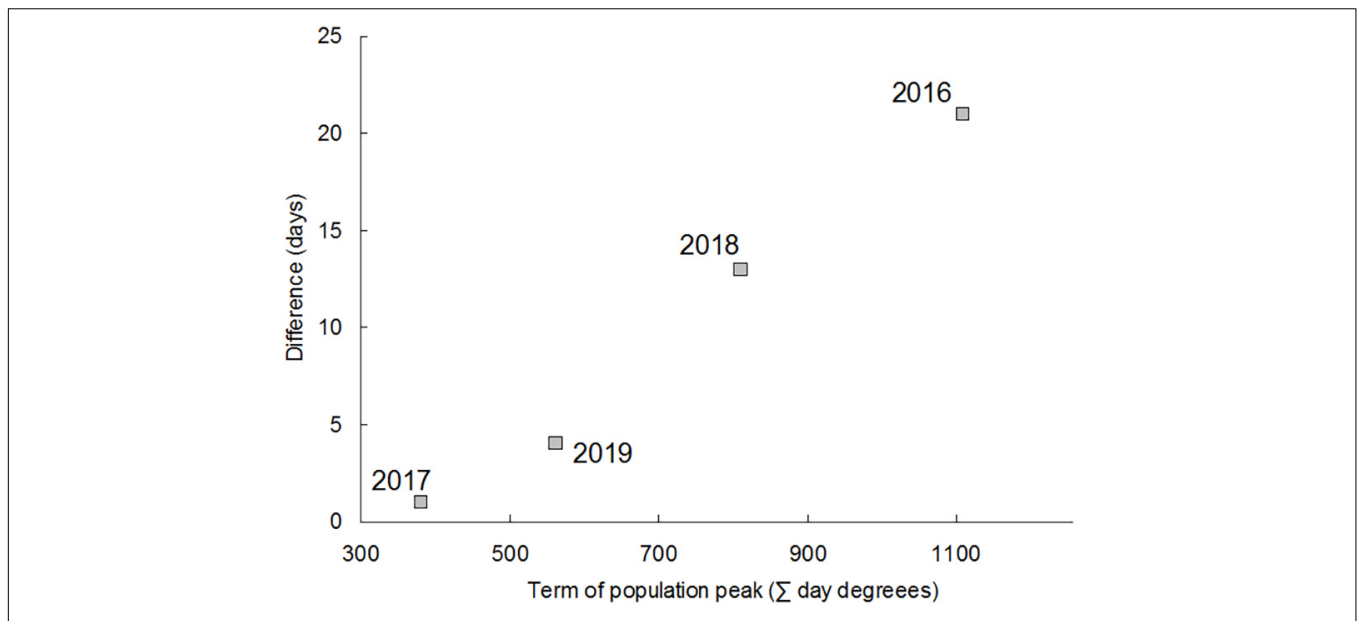


FIGURE 2 | Difference (days) between the term of the population peak in the city center and the term of the population peak in the outskirts of Prague plotted against the thermal time (day degrees) when the maximum abundances were observed (average of the thermal time value in the city center and the outskirts).

temperatures because the ambient temperature remains mostly below the upper temperature threshold of 30°C (Honek et al., 2018a). The temperature maxima in the city center exceeded this limit by 14 times (2016) to 29 times (2019), in most cases (64%) by less than 2°C.

An increase in body temperature above ambient temperature is realized by basking in the sunshine (Sloggett and Honek, 2012; Sloggett, 2021). The capacity to increase body temperature also exists in *H. axyridis* (Michie et al., 2010), but evidence of thermoregulation under natural conditions is indirect. This evidence consists of the geographic variation of the ratio of

dark and light color forms that changes in parallel with climate (Dobzhansky, 1924; Komai, 1956). The mechanisms affecting morph distribution include differences in thermoregulation, assortative mating and winter mortality of color morphs (Osawa and Nishida, 1992; Su et al., 2009). This geographic variability is important in some parts of the native area of *H. axyridis*; however, in recently colonized regions of Europe, this phenomenon cannot be reliably demonstrated, as a significant geographic or temporal variation in proportional representation of dark and light forms was not established (Honek et al., 2020a), and thus, the effect of thermoregulation on the life cycle of *H. axyridis*

TABLE 1 | Timing of the peak density of *Harmonia axyridis* in calendar time (Julian days since the release of hibernacula set at 20 April), thermal time calculated using thermal constants of *H. axyridis* as the number of day degrees (dd) above the 10.6°C threshold (Thermal time HA), and thermal time calculated using thermal constants for *E. tilliae* as the number of day degrees (dd) above the 5.0°C thermal threshold (Thermal time ET).

| | | N | Calendar time Julian days | Thermal time HA dd | Thermal time ET dd |
|------|-----------|---|-------------------------------|--------------------------------|-----------------------------------|
| 2016 | Center | 4 | 131 ± 18.3 | 1,126 ± 187.6 | 2,084 ± 143.3 |
| | Outskirts | 7 | 152 ± 8.7 $P_t = 0.028$ | 1,092 ± 67.2 $P_t = 0.663$ | 2,056 ± 42.8 $P_t = 0.820$ |
| 2017 | Center | 6 | 63 ± 3.7 | 423 ± 44.3 | 1,037 ± 26.9 |
| | Outskirts | 7 | 64 ± 4.3 $P_t = 0.557$ | 341 ± 45.2 $P_t = 0.007$ | 845 ± 25.7 $P_{MW} = 0.006$ |
| 2018 | Center | 6 | 86 ± 2.9 | 807 ± 37.4 | 1,571 ± 47.1 |
| | Outskirts | 7 | 99 ± 6.1 $P_{MW} = 0.002$ | 815 ± 88.9 $P_{MW} = 0.534$ | 1,570 ± 47.1 $P_{MW} = 0.160$ |
| 2019 | Center | 6 | 76 ± 9.3 | 603 ± 96.8 | 1,303 ± 146.4 |
| | Outskirts | 8 | 80 ± 10.1 $P_{MW} = 0.491$ | 522 ± 87.7 $P_{MW} = 0.345$ | 1,124 ± 146.0 $P_{MW} = 0.042$ |

N—number of populations used in the study. P—the significance of differences calculated using the t-test (P_t) or the Mann-Whitney test (P_{MW}).

cannot be reliably demonstrated. Thus thermoregulation likely does not significantly alter the effect of ambient temperature on the population dynamics of *H. axyridis* in the city center and its outskirts.

Ultimate Cause of Variation in the Timing of the Seasonal Peak of Abundance

In *Tilia*, the change in abundance of adult *H. axyridis* parallels that of the abundance of its prey, the monophagous anholocyclic aphid *Eucallipterus tiliae* (Honek et al., 2019a). Aphid abundance estimated in a period of 10–20 days around the peak of *H. axyridis* abundance (Alois Honek and Jiri Skuhrovec, unpublished) exceeded the threshold density of 1 aphid per leaf area necessary for the start of *H. axyridis* oviposition (Honek et al., 2020b). The dependence of *H. axyridis* on its prey determines the early (2017 and 2019) or late (2016 and 2018) timing of the population peaks in particular years. The annual variation in the timing of the peak abundance of *E. tiliae* is well known (Dixon and Barlow, 1979; Dahlsten et al., 1999), likely determined by the size of the overwintering population. The population peak occurs early in the vegetative season if hibernating eggs are abundant; if not, the population peak occurs late in the season (Dixon and Barlow, 1979). As a consequence, the population peaks of *E. tiliae* in the city center and the outskirts in particular years occurred approximately in the same period of the season. The ultimate cause of the timing of the *H. axyridis* population peak is the population dynamics of its prey, *E. tiliae*, which does not depend on the thermal conditions of the season.

Proximate Cause of the Difference in Timing of the Population Peaks in the City Center and the Outskirts

The magnitude of the difference between the *H. axyridis* population peaks in the city center and the outskirts increases with the time that has elapsed since the beginning of the season. The difference in the timing of the population peak levels after the recalculation of the calendar time to thermal time, which passes faster in warm city centers than in colder outskirts. The question remains whether the main factor of the origin of this difference is the temperature effect on the development of the aphid population or, alternatively, is the main factor directly the effect on the predator population? Using our data, this question cannot be reliably resolved, but the assumption of a direct effect on *H. axyridis* populations appears more probable. The effect on *H. axyridis* is significant because temperatures are below the maximum temperature for development, which is approximately 30°C (Aquad et al., 2014; Barahona-Segovia et al., 2016) and in this range ambient temperature affects the rate of development of *H. axyridis* populations positively. Temperature also affects the rate of development of aphid populations, but in a different way than in *H. axyridis*. This is because the development threshold for aphid populations is 5°C (Honek and Kocourek, 1990; Honek, 1996), and temperature maximum is then $\leq 25^\circ\text{C}$ (Dixon et al., 2009). The temperature in summer often exceed the temperature maxima for aphids, and in this range, does not influence the rate of development of *E. tiliae* positively. It can therefore be

assumed that the main reason for the difference in population peak timing is the effect of temperature on populations of *H. axyridis* and not the effect of temperature on the population development of prey.

Significance of the Flexibility of Timing of the *H. axyridis* Life Cycle

This 4-year study enabled us to determine the causes of annual and local variability in the timing of the population peak of adult *H. axyridis*. In particular years, the peak occurred early or late in the season depending on variations in prey abundance. The results corroborated the hypothesis that differences in mesoclimate affect the pace of life of *H. axyridis* and supported the predictions (i) that the increased temperature of the city center, compared to that in the outskirts, advanced the onset of the population peak and (ii) that this difference will level off if population development is plotted against thermal time. Minor differences in the timing of the population peak were due to differences in the mesoclimate in the Prague city center and the outskirts, and the magnitude of the difference increased with the length of time that had elapsed since the beginning of the season. The flexibility of the timing of population development contributes to the success of *H. axyridis* invasion into the non-native area of Central Europe because it enables the effective utilization of prey resources whose location varies in space and time.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

AH and JS designed the experiments and collected data. ZM coordinate all work. AH and PZ analyzed the data and performed the statistical analyses. All authors wrote and edited the manuscript.

FUNDING

The work was supported by the program VES19 INTER-COST No. MSMT-15739/2019-6 (MŠMT ČR), Grant No. QK 1910281 from the National Agency for Agricultural Research (NAZV) of the Czech Republic and the grant VEGA 2/0032/19 of the Scientific Grant Agency of Ministry of Education, Science, Research and Sport of the Slovak Republic.

ACKNOWLEDGMENTS

We thank Ms Helena Uhlířová, Jana Kohoutová, and Hana Smutná for their excellent technical assistance.

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