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Life cycle of *Harmonia axyridis* in central Europe

Abstract

The development and reproduction, and maximum number of generations across seasons were ascertained for populations of *Harmonia* axyridis (Pallas) (Coleoptera: Coccinellidae) in Central Europe. Number of generations was calculated using the thermal characteristics of development and summation of daily average air temperatures, in 2007–2016. This species can produce 2–3 generations per year, however, there is insufficient time for it to achieve its full reproductive potential. Delayed emigration from hibernacula (late April) shortened the period of seasonal activity by 1–6%. Breeding occurred from May to mid September. Oviposition continued into late summer, which left insufficient time for the late-hatching immatures to complete their development before the onset of winter. A high mobility, opportunistic use of prey patches and weak tendency to enter dormancy provide the potential for population increase by extending the period of development of immatures at the risk of failure if the cold period comes early.

Key words

Coccinellidae; development; generation; temperature; voltinism

Introduction

Harmonia axyridis (Pallas) (Coleoptera: Coccinellidae) is an invasive non-native species that arrived in the Czech Republic in 2006 (Sprynar, 2008). In less than three years, from 2007–2009, it became a dominant ladybird species principally occurring on trees but frequently also on wild herbaceous plants and crops. *Harmonia axyridis* is not only an efficient predator of aphids (Roy et al. 2016) and other phytophagous insect pests (Qureshi and Stansly 2009) it is also an intraguild predator of native aphidophagous coccinellids (Ingels et al. 2013). As a consequence *H. axyridis* is considered to disrupt assemblages of native aphidophagous species (Pell et al. 2008). *Harmonia axyridis* is further accused of adversely affecting wine production and large aggregations in buildings of inducing allergic reactions and other medical conditions (Chakir et al. 2016). Consequently, the biology of *H. axyridis* has been intensively studied. However, despite this interest much of the basic life history data for this species has not been established with sufficient reliability.

Factors determining the number of generations per year (voltinism) are many and, despite intensive studies, still incompletely analyzed (Hodek 2012). This is also true of populations of *H. axyridis* in areas it has recently colonized. As in other coccinellids, its voltinism is specific for a particular geographic area with its specific climatic and biotic conditions (Roy et al. 2016). The temporal window for reproduction opens with leaving hibernacula in spring and closes with a return migration in autumn. The maximum number of generations they can complete during the vegetative period is controlled by abiotic conditions, temperature, which determines the pace of life and photoperiod, which governs the initiation of dormancy and may curtail the length of the period potentially available for reproduction. Further intrinsic (oviposition structure) and extrinsic factors (prey availability, mobility) limit the potential for reproduction. Assessments of voltinism in particular areas (Roy et al. 2016) differ as they were established by studies carried out in different years and using different methods of sampling and data analysis (Brown et al. 2008).

While aspects of migration (Nalepa et al. 2005) and overwintering (Raak-van den Berg et al. 2012) are well studied, the factors determining the time they leave and return to hibernacula remain to be studied with respect to local conditions. There are many studies on the factors determining reproduction within the „window“ of the breeding season. In this respect there are studies on species‘ thermal characteristics (Schanderl et al. 1985; LaMana and Miller 1998), temperature effects on development and reproduction (Zazycki et al. 2015, Guedes et al. 2016) and variation in development rate of native and invasive populations (Raak-van den Berg et al. 2017). Under natural conditions duration of development varies with the course of a season, along with changing temperature. Photoperiod influences duration of development and ovarian maturation (Raak-van den Berg 2013). Invasive populations are less sensitive to photoperiodic dormancy induction in the autumn (Ovchinnikova et al. 2016). Effect of food availability and quality on development and oviposition in coccinellids is obvious (Hodek and Evans 2012) and can determine the length of the larval period (Phoofolo et al. 2009) and oviposition in adults (Hukusima and Ohwaki 1972). As *H. axyridis* is attracted to both the odour of host plants and aphid prey (Rondoni et al. 2017) and can fly between host plants (Osawa 2000) it is capable of searching many host plants, aggregating at the most suitable sites and continuing reproduction for most of the season. The spatial and temporal redistribution of local populations in the landscape and its change during the course of a season, however, needs more study.

A synthesis of the following different kinds of information is needed for determining the voltinism of *H. axyridis*: the maximum number of generations based on local meteorological data, thermal characteristics of the development and oviposition of *H. axyridis* and the factors that set limits to the theoretically possible extent of their reproductive activity. We predict that the seasonal course of the life cycle of *H. axyridis* is (i) driven by thermal time (rate of summing of effective temperatures above lower development threshold), (ii) constrained by spring emigration from and autumn migration to hibernacula and (iii) limited by availability of prey necessary for reproduction. In this study we therefore first calculate the potential course of seasonal development as determined by ambient temperature and species thermal norms. Then we establish times of migration from and to hibernacula. Third we establish the temporal patterns in oviposition.

Material and Methods

Calculating potential life cycle

Thermal constants, lower development threshold LDT = 10.6 °C and sum of effective temperatures SET = 256 day degrees (dd) were used for calculating duration of the pre adult developmental period (LaMana and Miller 1998; Schanderl et al. 1985). Assuming the developmental rate is isomorphic (Jarosik et al. 2002), which is typical for coccinellids (Hodek and Honek 1996; p. 63), the same lower developmental threshold LDT = 10.6 °C was used to calculate the duration of the teneral and oviposition periods. Sum of effective temperatures were recalculated from data published by Guedes et al. (2016) who provide data on the teneral and oviposition periods of individuals of an invasive population of *H. axyridis* collected in Brazil and reared at 25 °C and fed *Brevicoryne brassicae* (L.). For the calculation we used a transformation coefficient calculated as [SET for development based on the data of Schanderl et al. (1985) and LaMana and Miller (1998)]/ [SET for development based on the data of Guedes et al. (2016)] = 256/325 = 0.790. By multiplying Guedes at al. (2016) data by this factor we get a SET = 69 dd for completing the teneral period (interval between adult moult and start of oviposition) and SET = 895 dd for the oviposition period. Sum of effective temperatures for the period from the beginning of development until beginning of oviposition is then SET = 325 dd (256 dd for development + 69dd for the teneral period).

The potential number of generations was calculated using average daily air temperatures measured at the meteorological station of the Crop Research Institute at Prague-Ruzyne (50.0852N, 14.2986E, 338 m a.s.l., http://www.vurv.cz/meteo/default.asp). Actual thermal time for individuals may differ slightly from the sum of temperatures based on sumation of daily averages because temperature minima may fall below LDT (c. 30% of days with average temperature above LDT) and maximum temperatures may rise above the 30°C, the upper developmental threshod (10% of days). Precise estimation of thermal time was impracticable because actual body temperatures of individuals determined by microclimate and thermoregulation were not available. The calculations were made for 2007–2016, the ten years when *H. axyridis* became established in the Czech Republic. Each year, the daily average temperatures above LDT = 10.6 °C threshold (TD) were summed starting from January 1, an arbitrary date based on diapause being terminated in December (Raak-van den Berg et al. 2013). As average temperatures in December were invariably below LDT, temperature summation of the SET for post-diapause development may have started from Januar 1 and the TD summed until the date when a sum of TD 69 dd had accumulated, which is the duration of the teneral period. This was also assumed necessary for the maturation of eggs during the pre-oviposition period of overwintered post-diapause females. Thermal requirements for both these life periods are likely to be similar (Hodek and Honek, 1996, p.79) provided that food conditions are optimum (Hukusima and Kamei, 1970). This day was considered to be the date on which the overwintered females, the parental (P) generation, started laying eggs and is used as the starting point for calculating the potential number of generations that may develop in the following season. Starting from this date TD were summed until 256 dd (indicating date of termination of development of the first generation

F1) and 325 dd (date of start of oviposition of F1 generation) had accumulated. Then following from this date the temperatures TD were summed again until 256 dd (terminating development of second generation F2) and 325 dd (start of oviposition of F2) had accumulated, and then repeated again to determine the date when development was finished and the oviposition of the third generation F3 started. The days necessary for the particular sums of dds to be accumulated indicated the earliest dates on which adults of the first (F1), second (F2) and third (F3) generations could have completed their development and started ovipositing.

For each of the generations P to F3 we calculated the percentage of the oviposition period (895 dd) that was realized in the course of a vegetative season before the onset of winter. For the P generation the summation of TD started from the day of the start of oviposition of overwintered females until the date when 895 dd were accumulated, which was considered to be the date on which the P generation ceased ovipositing. For the F1 generation summation of TD started from the date of the start of oviposition of the F1 generation and continued until the end of the vegetative season (the date when autumn temperatures decreased below 10.6 °C and further development was not possible). Each year this date came earlier than that necessary for the accumulation of the 895 dd needed for completing oviposition. The proportion of the oviposition period realized until end of vegetative season was calculated. The same process was repeated for F2 and F3 generations.

Leaving hibernacula in spring

Leaving artificial hibernacula was recorded in 2015 and 2016. Experimental adults were collected during the mass autumn migration and stored in plastic bottles at + 5 °C until the beginning of the experiments. On 10 November 2014 and 8 November 2015 they were put into 40 x 20 x 8 cm paper boxes perforated with holes enabling free access of beetles and filled with egg cartons, which provided hiding places. The boxes wrapped in nylon fabric bags and black plastic bags with small ventilation holes were put into an unheated shelter whose conditions may approach that of the hibernacula this species frequently uses in buildings. Each bag was connected via a transparent tube to a transparent plastic vial. In the spring, adults leaving the artificial hibernacula in paper boxes passed through the tube into the sampling vials where they were counted and removed at 3–4 day intervals, until all individuals had left.

Reproduction in the open

In 2015 and 2016, the percentage of ovipositing females and size of egg batches was established at 18 sites in the west of the Czech Republic situated in an 11 x 7 km area centred at 50.105N and 14.264E. The beetles were sampled on trees (*Acer platanoides* L., *A. pseudoplatanus* L., *A. campestre* L., *Betula pendula* Roth, *Prunus insititia* L., *Tilia cordata* Mill., *Tilia platyphylos* Scop.), herbaceous plants (*Tripleurospermum inodorum* (L.) Schultz-Bip., *Urtica dioica* L.) and crops (small grain cereals *Avena sativa* L., *Hordeum vulgare* L., *Triticum aestivum* L.), using a standard sweepnet (35 cm diam., 140 cm handle). Sampling sessions, collecting adults at particular sites and on particular host plants were repeated at 7–14 d intervals.

The course of oviposition was investigated using a method used previously for native species (Honek et al. 2007). Individual females were each put in an Eppendorf tube perforated for ventilation and kept for 48 h at 25 °C under a natural photoperiod. The number of eggs was counted and eggs were removed (to prevent cannibalism) at 2-6 h intervals. In most cases eggs were deposited in one batch, within the first day. The percentage of ovipositing females in a sample originating from a particular session and number of eggs deposited per female were recorded.

Proportion of females that oviposited was compared among months using GLM with binomial errors and logit link (GLM-b). The number of eggs laid (batch size) was compared among months using GLM with Poisson errors and log link (GLM-p). Quasibinomial and quasipoisson setting, respectively, was used due to overdispersion. Post hoc comparisons among months were made using contrasts.

Autumn migration

The dates of autumn mass flights to hibernacula were established by daily observations of migration activity made from September 20 until November 10. Landing of flying adults was checked on a 15 m section of the south-facing light coloured wall of the building of the Crop Research Institute at Prague-Ruzyne, every day at 13:00, for 15 minutes. The wall section was inspected visually and the coccinellids that landed were counted and removed. To determine the days on which a massive flight occurred a threshold flight activity of ≥3 individuals landing per 15 min. session was set. In fact, the numbers of beetles that landed was either much higher on days when they were migrating, or zero.

Results

Potential life cycle

In 2007–2016, the maximum potential number of generations that could be completed given the local thermal environment was three per year (Table 1). It was predicted that the overwintered population (probably a mixture of all generations that developed the previous year) started ovipositing in early May (average May 7 ± 2.9 d) and continued ovipositing until late August – early November (average September 8 ± 6.7 d). Adults of the 1st generation (F1) originating from the first egg batches laid by overwintered females may appear in late-June (average June 23 ± 2.2 d) and they started ovipositing seven days later (June 30 ± 2.1 d).

Adults of the 2nd generation (F2) were predicted to appear in late July (July 29 ± 1.2 d) and to start ovipositing one week later (Aug 4 ± 1.5 d). The first adults of the 3rd generation (F3) may start emerging in late August – September (September 5 ± 3.1 d) and ovipositing ten days later (September 15 ± 4.1 d). Not even the 1st generation has sufficient time to complete oviposition, with only 79 ± 2.6% of the potential oviposition period realized before the end of the vegetative season. Females of the second generation may realize only 43 ± 2.5% of their potential oviposition period. The 3rd generation was predicted to have oviposited in only seven out of the ten years considered and the females then may only have realized 15 ± 3.6% of their potential oviposition capacity. Towards the end of the vegetative season, development may be completed before the onset of winter only if eggs are laid earlier than 256 dd before the average temperature falls below 10.6 °C. In particular years this critical date occurred between Aug 12 and Aug 28, and on average on August 19 ± 2.0 d. The individuals that hatched from eggs deposited later are unlikely to survive.

Seasonal activity of adults

The time schedule indicates that the maximum number of generations that can develop during the course of a year is limited by biotic factors. The first is the length of time each year during which the adults are active, which is determined by when they leave hibernacula in spring and migrate to hibernacula in autumn. They began leaving artificial hibernacula (Figure 1) in mid-March and continued for c. 60 days until early May. April 20, the median date for emigration of 50% of the overwintering individuals in 2015 (April 16) and 2016 (April 23) was used as a corrected time for the start of the temperature summation. In all years this date was later than the beginning of the period with average temperatures exceeding 10.6 °C. Moving the start of temperature summation to April 21 postponed the start of thermal time summation in particular years by 8.4–65.6 dd, i.e. by 0.5–5.8% of the total annual temperature sum available in these years. In particular years this later start of temperature summation postponed the predicted time of oviposition of the overwintered generation by 1–20 days, the time of emergence of adults of the F1 generation by 1–11 d, F2 generation by 0–5 d and F3 generation by 0–5 d.

In autumn a large percentage of the adults cease foraging on plants and migrate to hibernacula. In 2009–2016 mass flights occurred between October 2 and October 19, and smaller flights were recorded between October 30 and November 3 (Figure 2). The days on which mass flight occurred were very sunny, the temperature was above the average recorded in the previous few days (daily maxima 19.2 ± 0.83 °C) and there was little or no wind (0.0–0.1 m s-1). The autumn migrations occurred before the end of the period when average daily air temperatures exceed 10.6 °C. In particular years this period finished on October 8 to November 11 (average October 23 ± 4.9 d).

Oviposition

The seasonal course of oviposition was recorded because it may modify seasonal course of activity as predicted by the temperature summation. In 2016, ovipositing females were recorded between May 9 (samples from *P. insititia* colonized by *Brachycaudus helichrysi* Kaltenbach) and September 14 (samples from *T. cordata* colonized by *Eucallipterus tiliae* (L.)). Proportion of ovipositing females in samples collected from natural populations on trees decreased significantly (GLM-b, $F_{4,58} = 7.7$, $P < 0.0001$) throughout the vegetative season from 49% in May and 57% in June to 20% in August and 19% in September (Figure 3). Batch size varied between 1–60 eggs (mean 19.8 ± 0.81 eggs, n = 238 batches, Figure 4) and was not significantly different each month throughout the season (GLM-p, $F_{4,233} = 0.18$, $P = 0.95$). Average size of the batches of eggs laid in the field (26 ± 3.6 eggs, n = 9, on *P. insititia*) was greater than that laid by the females in the samples collected in the field and then kept individually in tubes in a laboratory. In 2015, ovipositing females were recorded on *Acer*, *Betula* and *Tilia*. Oviposition occurred only between May 5–July 13 (although sampling continued until mid-October). Mean batch size was 21.7 ± 3.83 eggs (range 1–57 eggs, n = 77 batches), which is similar to that recorded in 2016.

Discussion

In this paper we determine when in the year *H axyridis* reproduces and develops, and how the potential number of generations it has is determined by local thermal conditions. We specify some of the factors that can modify this potential scenario: time of leaving and entering hibernacula and seasonal reproduction patterns. Calculations presented are of the fastest path for development: a sequence of life histories of the earliest developed individuals in each generation. This is an ideal sequence of successive generations, which may be modified by abiotic (microclimate, photoperiod) and biotic (thermoregulation, food) factors. The relationship between the predicted and actual species life cycle thus needs consideration.

Thermal limits of the life cycle

The temporal course of an insect's life history is shaped by temperature, which determines their pace of life (Dixon 2015; Trudgill et al. 2005). Our calculations (Table 1) using local temperature data predicts three generations per year, except in 2010 when only two generations were predicted. In seven of the years considered the thermal conditions remained suitable for even a 3rd generation to start reproducing. However, only overwintered females (P generation) have sufficient time to realize their full reproductive potential, on average ceasing to reproduce as late as September. None of the generations born during the course of a year (F1 – F3) achieved their full reproductive potential. Even for the F1 generation the vegetative season terminated earlier than the first born adults of this generation, which were predicted to complete their development in late June, leaving only 80% of the thermal time needed to realize their reproductive potential and even less thermal time for the second (42%) and third (10%) generations. These predictions based on laboratory established thermal requirements and standard meteorological measurements of temperature may be affected by two further factors.

First, active behavioural thermoregulation may increase body temperature above air temperature. Selection of warm places available within their habitats is an important factor determining the distribution of cocccinellids (Honek 1985). This thermoregulatory behaviour is typical of several species of coccinellids including *Coccinella septempunctata* L. (Honek 1982). Adults of *H. axyridis* also aggregate in the more sunny sections of tree crowns, where they make full use of high leaf temperatures and bask in sunshine. Active behavioural thermoregulation may be an efficient means of increasing the rate of thermal summation in adults, particularly in cool periods in spring and autumn (Michie et al. 2010). Consequently the reproductive potential of adults may be higher than predicted using meteorological data. Behavioural thermoregulation is used by adults of *Adalia bipunctata* (L.) to increase their body temperature several degrees above ambient temperature, depending on colour form and body size (Stewart and Dixon 1989). The different colour morphs of *H. axyridis* differ in their thermoregulatory properties, which is reflected in the geographical (Komai et al. 1950; Osawa and Nishida 1992) and seasonal variation (Dobzhansky 1924a; Komai 1956), and frequency of melanic (*conspicua* and *spectabilis*) and pale (*succinea*) morphs in local populations. Extent of melanism in the *succinea* morph is moreover affected by the number of spots on its elytra (genetically determined) and variation in their size, which increases with decreasing development temperature and may affect adult thermoregulation (Michie et al. 2010; Knapp and Nedved 2013). However, mating activity of melanic and pale morphs on cold mornings and warm afternoons do not differ (Awad et al. 2015). *Succinea* and *spectabilis* morphs also differ in their demographic parameters, intrinsic rate and finite rate of population increase, which are greater in the former morph (Zeki et al. 2015). As in *C. septempunctata* (Ohashi et al. 2005), thermoregulatory behaviour might also affect the selection of a pupation site. In the Czech Republic *H. axyridis* selects warm places for pupation, which may increase its survival and enable it to complete its development in cold autumns. Pupae of all morphs also display thermal melanism, which decreases differences in body temperature throughout the season. By contrast, development of eggs is less likely be affected by thermoregulation. In coccinellids, oviposition sites are selected with respect to availability of prey for the progeny and protecting eggs from intraguild predation (Seagraves 2009). Selecting oviposition sites based on these environmental characteristics leaves less freedom for selecting a more favourable thermal environment. Larvae spend most of their time foraging for prey. In cold weather coccinellid larvae often assemble on the insolated tops of leaves and aphids also move onto upper leaf surface to benefit from the warming rays of the sun (A.F.G. Dixon, unpublished). However, sections of crown where they gather are insolated for only a part of day and the larvae cannot keep pace with changing insolation as fast as adults, which move by flight. Larvae are therefore limited in making full use of active thermoregulation. The effect of thermoregulation on pre-adult development is thus probably smaller than on adult reproduction.

Second, there may be problems with the data on the thermal reactions of *H. axyridis* used in this study. The 895 dd available for oviposition calculated from Guedes et al. (2016) is the maximum estimate of the length of the oviposition period. Using the same method of recalculation and the results of Awad et al. (2013) and Zazycki et al. (2015) provided similar results (873 dd, 799 dd and 1051 dd, respectively) while the results of another study by Lanzoni et al. (2004) resulted in a much shorter oviposition period (183 dd). The thermal characteristics were calculated using data from experiments using strains from different geographic regions. Thermal requirements of populations native to particular geographic areas may be adapted to local conditions as has been demonstrated for several insect taxa (Kiritani 2012), such as Homoptera (Umeya and Yamada 1973), Heteroptera (Balashov and Kipyatkov 2008), Coleoptera (Lopatina et al. 2011) and Hymenoptera (Kipyatkov and Lopatina 2015). Differences among geographic populations are mostly small but nevertheless ecologically important. Whether this differentiation in thermal requirements exist in native populations of *H. axyridis*, and the extent to which it is already present in very recently spreading invasive populations of this species is difficult to estimate. Potentially, recalculating thermal constants using data of local populations may improve the prediction of the seasonal cycle of *H. axyridi*s.

Biotic modification of life cycle

There are several biotic factors that decrease the thermal time available for the development of *H. axyridis*. The annual life cycle starts when adults leave hibernacula. Although *H. axyridis* may overwinter on conifers (Holecova et al. in prep) and in hilltop hibernacula used by *C. septempunctata* and *Hippodamia variegata* Goeze (unpublished authors observation) there is good evidence of massive overwintering in buildings (Lucas et al. 2007; reports from the public). Our experiment using artificial hibernacula thus provides the timing of the spring migration typical for a large part of the *H. axyridis* population, which extends over two months. As for native species of coccinellid (Honek 1986) early emerging individuals may feed on alternative prey. The major peak of emigration in late April coincides with leaf expansion of their preferred tree hosts, *Tilia* spp. and *Acer* spp. and development of aphid populations on primary hosts (Leather and Walters 1984).

Low food specificity is typical (Weber and Lundgren 2009) and beneficial (Hodek and Evans 2012) for predaceous coccinellids, including *H. axyridis* (Lucas et al. 2004). Eating alternative prey, Homoptera, psyllids, aleyrodids, coccids, Heteroptera, Thysanoptera, Coleoptera, Lepidoptera and mites, or a mixed diet do not only enable adults to survive early and late in the vegetative season but supports development during the breeding period (Howe et al. 2016; Lucas et al. 2002). However, despite wide polyphagy, presence of aphids is the main factor determining the temporal distribution of *H. axyridis*. Prey abundance limits the percentage of individuals that realize their reproductive potential in particular generations and the length of the oviposition period at different sites. This limitation is substantial and may seriously distort the patterns of activity calculated using thermal data.

The average percentage of ovipositing females in populations (maximum c. 60% in June, Figure 3) was lower than in populations of *C. septempunctata* and *Propylea quatuordecimpunctata*, where it exceeds 80% (Honek et al. 2008). We propose that a high percentage of non-ovipositing females assures a more flexible strategy in which females may continue to move among host plant patches in search of other sites favourable for reproduction. The number of eggs ready to be laid (clutch size) is smaller in *H. axyridis* (~20 eggs) than in similarly sized *C. septempunctata* (~36 eggs) (Honek et al. 2007). Similar differences are reported in which the mean batch size for *H. axyridis* is 23–31 eggs (Dobzhansky 1924b; Takahashi 1987) and for *C. septempunctata* 33–50 eggs (Stewart et al. 1991; Takahashi 1987). This variation in batch size may reflect differences in the number of ovarioles, which is smaller in *H. axyridis* (62–70, mean 65 ± 1.3) than in *C. septempunctata* (74–149, mean 109 ± 9.6) (Nedved and Honek 2012). The partition of egg load into many small batches enables a species to lay eggs on many more host plants, thus decreasing the risk of failure to develop that threatens populations in any particular patch (den Boer 1981). Together with high mobility the tendency to partition oviposition in this way may assist *H. axyridis* in locating and exploiting small or more inaccessible patches of prey (Osawa 2000). This opportunistic strategy may have enabled *H. axyridis* to become a conspicuous and characteristic component of coccinellid communities in small patches of vegetation in urban areas (Honek et al. 2017).

In late summer females continued to oviposit until mid-September (Figure 3), far beyond the "critical date" for completing development before the onset of winter (August 19 ± 2.0d, Table 1) and near the ultimate date of oviposition established for native *H. axyridis* populations in Far East Russia (Telenga and Bogunova 1936). Despite their ability to thermoregulate some of these individuals are likely to be killed at the onset of cold weather. Development may occur also on days with low average temperatures if afternoon temperatures substantially exceed LDT, which is often the case in October. This may create conditions for completing development of some belated individuals even when forecasts using summation of average temperatures predict extinction. This poor adjustment of dormancy initiation in invasive populations of *H. axyridis* may be a consequence of a weak photoperiodic reaction and inability to respond to changing autumn conditions (Reznik et al. 2015). In this study females continued to lay eggs under a short dormancy inducing photoperiod (13h light:11h dark or 14h light:10h dark including twilight on September 15). In order to prevent late oviposition and its fatal consequences dormancy should be induced on August 15, i.e. by a 14.5h light:9.5h dark photoperiod (or 15.1h. light:8.9h dark photoperiod including twilight).

Mass migration of *H. axyridis* to overwintering sites occured in October. Each year there are few days suitable for migration. These days are characteristically warm, calm and sunny (Nalepa et al. 2005). These mass flights may be synchronized over large areas as on October 16, 2016 when massive flights were recorded simultaneously in Prague (50.1N, 14.3E, Figure 2), in southern Moravia (49.2N, 16.6E, S. Pekár) and central Slovakia (48.6N, 19.1E, Peter Zach, personal communication), that is at localities c. 400 km apart. Every year, *H. axyridis* is recorded on trees even after the mass migration, where they remain until leaf fall.

Our method of calculating the maximum number of generations and their share in the total of the offspring produced in a given year provides important information for assessing the impact of *H. axyridis* on aphid and intraguild prey populations in a particular area. The results presented indicate the enormous reproductive potential of *H. axyridis*. If prey is available its breeding period is limited only by thermal conditions. Populations of *H. axyridis* continue to reproduce in to late summer regardless of the risk of some of the individuals perishing when there is an unusually early onset of the cold autumn period. We propose that the source of success of this strategy is, paradoxically, a (still) poor adaptation to local climatic conditions of *H. axyridis* that has only recently colonized the Czech Republic (Reznik et al. 2015). This "audacious and risky" strategy may have contributed to making *H. axyridis* an extremely successful invasive species.

References

Awad M, Kalushkov P, Karabüyük F, Nedvěd O (2015) Non-random mating activity of colour morphs of ladybird *Harmonia axyridis* (Coleoptera: Coccinellidae). Acta Soc Zool Bohem 79:11–17

Awad M, Kalushkov P, Nedvědová T, Nedvěd O (2013) Fecundity and fertility of ladybird beetle *Harmonia axyridis* after a prolonged cold storage. BioControl 58:657–666

Balashov SV, Kipyatkov VE (2008) Study of intrapopulational variability of duration and temperature norms of development of the linden bug *Pyrrhocoris apterus* (Heteroptera, Pyrrhocoridae). J Evol Biochem Physiol 44:687–697

Brown PMJ, Roy HE, Rothery P, Roy DB, Ware RL, Majerus MEN (2008) *Harmonia axyridis* in Great Britain: analysis of the spread and distribution of a non-native coccinellid. BioControl 53:55–67

Chakir R, David M, Gozlan E, Sangare A (2016) Valuing the impacts of an invasive biological control agent: a choice experiment on the Asian ladybird in France. J Agric Econom 67:619–638

den Boer PJ (1981) On the survival of populations in a heterogeneous and variable environment. Oecologia 50:39–53

Dixon AFG (2015) Pace of life of insect natural enemies. Acta Soc Zool Bohem 79:45–50

Dobzhansky T (1924a) Die geographische und individuelle Variabilität von *Harmonia axyridis* Pall. in ihren Wechselbeziehungen. Biol Zent Bl 44:401–421

Dobzhansky T (1924b) Die weiblichen Generationsorgane der Coccinelliden als Artmerkmal betrachtet (Col.). Entomol Mitt 13:18–27

Guedes CFC, Almeida LM, Penteado SRC, Moura MO (2016) Effect of different diets on biology, reproductive variables and life and fertility tables of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae). Rev Bras Entomol 60:260–266

Hodek I (2012) Diapause/dormancy. In: Hodek I, van Emden HF, Honek A (eds) Ecology and behaviour of the ladybird beetles (Coccinellidae). Wiley-Blackwell, Chichester, pp 275–342

Hodek I, Evans EW (2012) Food relationships. In: Hodek I, van Emden HF, Honek A (eds) Ecology and behaviour of the ladybird beetles (Coccinellidae). Wiley-Blackwell, Chichester, pp 141–274

Hodek I, Honek A (1996) Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht, Boston, London

Honek A (1982) The distribution of overwintered *Coccinella septempunctata* L. (Col., Coccinellidae) adults in agricultural crops. Z Angew Entomol 94:311–319

Honek A (1986) Production of faeces in natural populations of aphidophagous coccinellids (Col.) and estimation of predation rates. Z Angew Entomol 102:467–476

Honek A, Dixon AFG, Martinkova Z (2007) Body size, reproductive allocation and maximum reproductive rate of two species of aphidophagous Coccinellidae exploiting the same resource. Entomol Exp Appl 1:1–11

Honek A, Dixon AFG, Martinkova Z (2008) Body size and the temporal sequence in the reproductive activity of two species of aphidophagous coccinellids exploiting the same resource. Eur J Entomol 105:421–425

Honek A, Dixon AFG, Soares AO, Skuhrovec J, Martinkova Z (2017) Spatial and temporal changes in the abundance and compostion of ladybird (Coleoptera: Coccinellidae) communities. Curr Opin Insect Sci 14:61–67

Howe AG, Ravn HP, Pipper CB, Aebi A (2016) Potential for exploitative competition, not intraguild predation, between invasive harlequin ladybirds and flowerbugs in urban parks. Biol Invasions 18:517–532

Hukusima S, Kamei M (1970) Effects of various species of aphids as food on development, fecundity and longevity of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). Res Bull Fac Agric Gifu Univ 29:53–66

Hukusima S, Ohwaki T (1972) Further notes on feeding biology of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). Res Bull Fac Agric Gifu Univ 33:75–82

Ingels B, Aebi A, Hautier L, van Leeuwen T, De Clercq P (2013) Molecular analysis of the gut contents of *Harmonia axyridis* (Coleoptera: Coccinellidae) as a method for detecting intra-guild predation by this species on aphidophagous predators other than coccinellids . Eur J Entomol 110:567–576

Jarosik V, Honek A, Dixon AFG (2002) Developmental rate isomorphy in insects and mites. Amer Nat 160:497–510

Kipyatkov VE, Lopatina EB (2015) Comparative study of thermal reaction norms for development in ants. Entomol Sci 18:174–192

Kiritani K (2012) The low development threshold temperature and the thermal constant in insects and mites in Japan (2nd edition). Bull Nat Inst Agro-environmental Sci 31:1–74

Knapp M, Nedved O (2013) Gender and timing during ontogeny matter: effects of a temporary high temperature on survival, body size and colouration in *Harmonia axyridis*. PLoS ONE 8(9): e74984

Komai T (1956) Genetics of ladybeetles. Adv Genet 8:155–188

Komai T, Chino M, Hosino Y (1950) Contributions to the evolutionary genetics of the lady-beetle, Harmonia. I. Geographic and temporal variations in the relative frequencies of the elytral pattern types and in the frequency of elytral ridge. Genetics 35:589–601

LaMana ML, Miller JC (1998) Temperature-dependent development in an Oregon population of *Harmonia axyridis* (Coleoptera: Coccinellidae). Environ Entomol 27:1001–1005

Lanzoni A, Accinelli G, Bazzocchi GG, Burgio G (2004) Biological traits and life table of the exotic *Harmonia axyridis* compared with *Hippodamia variegata*, and *Adalia bipunctata* (Col., Coccinellidae). J Appl Entomol 128:298-306

Leather SR, Walters KFA (1984) Spring migration of cereal aphids. Z Angew Entomol 97:431–437

Lopatina EB, Kipyatkov VE, Balashov SV, Dubovikoff DA, Sokolova IV (2011) Adaptive latitudinal variation of the duration and thermal requirements for development in a ground beetle *Amara communis* (Panz.) (Coleoptera, Carabidae). Entomol Rev 90:775–790

Lucas E, Demougeot S, Vincent C, Coderre D (2004) Predation upon the oblique-banded leafroller, *Choristoneura rosaceana* (Lepidoptera: Tortricidae), by two aphidophagous coccinellids (Coleoptera: Coccinellidae) in the presence and absence of aphids. Eur J Entomol 101:37–41

Lucas E, Gagné I, Coderre D (2002) Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegila maculata* (Coleoptera: Coccinellidae). Eur J Entomol 99:457–463

Lucas E, Vincent C, Labrie G, Chouinard G, Fournier F, Pelletier F, Bostanian NJ, Coderre D, Mignault MP, Lafontaine P (2007) The multicolored asian lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) in Quebec agroecosystems ten years after its arrival. Eur J Entomol 104:737–743

Michie LJ, Mallard F, Majerus MEN, Jiggins FM (2010) Melanic through nature or nurture: genetic polymorphism and phenotypic plasticity in *Harmonia axyridis*. J Evol Biol 23:1699–1707

Nalepa CA, Kennedy GG, Brownie C (2005) Role of visual contrast in the alighting behavior of *Harmonia axyridis* (Coleoptera: Coccinellidae) at overwintering sites. Environ Entomol 34:425–431

Nedved O, Honek A (2012) Life history and development. In: Hodek I, van Emden HF, Honek A (eds) Ecology and behaviour of the ladybird beetles (Coccinellidae). Wiley-Blackwell, Chichester, pp 54–109

Ohashi K, Sakuratani Y, Osawa N, Yano S, Takafuji A (2005) Thermal microhabitat use by the ladybird beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae), and its life cycle consequences. Environ Entomol 34:432–439

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, Nishida T (1992) Seasonal variation in elytral colour polymorphism in *Harmonia axyridis* (the ladybird beetle): the role of non-random mating. Heredity 69:297–307

Ovchinnikova AA, Ovchinnikov AN, Dolgovskaya MYu, Reznik SYa, Belyakova NA (2016) Trophic induction of diapause in native and invasive populations of *Harmonia axyridis* (Coleoptera: Coccinellidae). Eur J Entomol 113:469–475

Pell JK, Baverstock J, Roy HE, Ware RL, Majerus MEN (2008) Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives. BioControl 53:147–168

Phoofolo MP, Elliott NC, Giles KL (2009) Analysis of growth and development in the final instar of three species of predatory Coccinellidae under varying prey availability. Entomol Exp Appl 131:264–277

Qureshi JA, Stansly PA (2009) Exclusion techniques reveal significant biotic mortality suffered by Asian citrus psyllid *Diaphorina citri* (Hemiptera: Psyllidae) populations in Florida citrus. Biol Control 50:129–136

Raak-van den Berg CL, de Jong PW, Hemerik L, van Lenteren JC (2013) Diapause and post-diapause quiescence demonstrated in overwintering *Harmonia axyridis* (Coleoptera: Coccinellidae) in northwestern Europe. Eur J Entomol 110:585–591

Raak-van den Berg CL, Hemerik L, de Jong PW, van Lenteren JC (2012) Mode of overwintering of invasive *Harmonia axyridis* in the Netherlands. BioControl 57:71–84

Raak-van den Berg CL, Hemerik L, van der Werf W, de Jong PW, van Lenteren JC (2017) Life history of the harlequin ladybird, *Harmonia axyridis*: a global meta-analysis. BioControl 62:283–296

Reznik SYa, Dolgovskaya MYu, Ovchinnikov AN, Belyakova NA (2015) Weak photoperiodic response facilitates the biological invasion of the harlequin ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). J Appl Entomol 139:241–249

Rondoni G, Ielo F, Ricci C, Conti E (2017) Behavioural and physiological responses to prey-related cues reflect higher competitiveness of invasive vs. native ladybirds. Sci Rep 7:1–9

Roy HE, Brown PMJ, Adriaens T, Berkvens N, Borges I, Clusella Trullas S, Comont R, De Clercq P, Eschen R, Estoup A, Evans EW, Facon B, Gardiner MM, Gil A, Grez AA, Guillemaud T, Haelewaters D, Herz A, Honek A, Howe AG, Hui C, Hutchinson WD, Kenis M, Koch RL, Kulfan J, Lawson Handley L, Lombaert E, Loomans A, Losey J, Lukashuk AO, Maes D, Magro A, Murray KM, San Martin G, Martinkova Z, Minnaar IA, Nedved O, Orlova-Bienkowskaja MJ, Osawa N, Rabitsch W, Ravn HP, Rondoni G, Rorke SL, Ryndevich SK, Saethre MG, Sloggett JJ, Soares AO, Stals R, Tinsley MC, Vandereycken A, van Wielink P, Viglasova S, Zach P, Zakharov IA, Zaviezo T, Zhao Z (2016) The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology. Biol Invasions 18:997–1044

Schanderl H, Ferran A, Larroque MM (1985) Les besoins trophiques et thermiques des larves de la coccinelle *Harmonia axyridis* Pallas. Agronomie 5:417–421

Seagraves MP (2009) Lady beetle oviposition behavior in response to the trophic environment. Biol Control 51:313–322

Sprynar P (2008) Faunistic records from the Czech Republic - 252. Coleoptera: Coccinellidae. Klapalekiana 44:77–79

Stewart LA, Dixon AFG (1989) Why big species of ladybird beetles are not melanic. Funct Ecol 3:165–177

Stewart LA, Hemptinne JL, Dixon AFG (1991) Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. Funct Ecol 5:380–385

Takahashi K (1987) Differences in oviposition initiation and sites of lady beetles, *Coccinella septempunctata bruckii* Mulsant and *Harmonia axyridis* (Pallas) in the field. Japanese J Appl Entomol Zool 31:253–254

Telenga N, Bogunova MV (1936) The most important predators of coccids and aphids in the Ussuri region of Far East and their utilisation. Zashchita Rastenij 1939:75-87

Trudgill DL, Honek A, Li D, VanStraalen NM (2005) Thermal time - concepts and utility. Ann Appl Biol 146:1–14

Umeya K, Yamada H (1973) Threshold temperature and thermal constants for development of the diamond back moth, *Plutella xylostella* L., with reference to their local differences. Jap J Appl Entomol Zool 17:19–24

Weber DC, Lundgren JG (2009) Assessing the trophic ecology of the Coccinellidae: Their roles as predators and as prey. Biol Control 51:199–214

Zazycki LCF, Semedo RES, Silva A, Bisognin AZ, Bernardi O, Garcia MS, Nava DE (2015) Biology and fertility life table of *Eriopis connexa*, *Harmonia axyridis* and *Olla v-nigrum* (Coleoptera: Coccinellidae). Braz J Biol 75:969–973

Zeki E, Papanikolaou NE, Demiris N, Kontodimas DC (2015) Comparison of the demographic parameters and survival of two phenotypes of *Harmonia axyridis* (Coleoptera: Coccinellidae). Eur J Entomol 112:193–196

Table 1 Timing of the development of successive generations of *H. axyridis* based on meteorological data collected from 2007 to 2016 at Praha-Ruzyne and its thermal requirements for development and oviposition (see Material and Methods). The date of the start (SOVIP) and termination (EOVIP) of oviposition is indicated for the overwintered generation (P). For each generation (F1 – F3) that developed during the course of the vegetative season the dates for the completion of pre-adult development (DEV), start of oviposition (SOVIP) and the thermal time available for oviposition until the end of the vegetative season (REALT, number of day degrees (dd) and percentage of the total period available for reproduction) are indicated . Critical date (DCRIT) is the date after which pre-adult development cannot be completed because the thermal time to the onset of winter is shorter than that needed for pre-adult development. Mean dates were calculated after converting dates of particular years to Julian days.

Year	Generation														
	P		F1				F2				F3				
	SOVIP	EOVIP	DEV	SOVIP	REALT		DEV	SOVIP	REALT		DEV	OVIP	REALT		DCRIT
					dd	%			dd	%			dd	%	
2007	28-Apr	21-Aug	10-Jun	17-Jun	731.0	81.6	18-Jul	24-Jul	406.0	45.4	24-Aug	06-Sep	81.0	9.1	12-Aug
2008	17-May	06-Sep	24-Jun	01-Jul	639.0	71.4	01-Aug	07-Aug	309.0	34.5	09-Sep				13-Aug
2009	21-Apr	02-Sep	24-Jun	02-Jul	753.0	84.1	01-Aug	07-Aug	424.0	47.4	05-Sep	18-Sep	94.0	10.5	26-Aug
2010	22-May	04-Nov	01-Jul	08-Jul	575.0	64.2	01-Aug	10-Aug	246.0	27.5					12-Aug
2011	06-May	06-Sep	15-Jun	25-Jun	737.0	82.3	31-Jul	08-Aug	409.0	45.7	09-Sep	21-Sep	82.0	9.2	25-Aug
2012	02-May	26-Aug	19-Jun	27-Jun	736.0	82.2	26-Jul	01-Aug	423.0	47.6	27-Aug	08-Sep	95.0	9.5	20-Aug
2013	07-May	14-Sep	01-Jul	08-Jul	627.0	70.1	01-Aug	06-Aug	300.0	33.5	23-Sep				12-Aug
2014	06-May	14-Sep	24-Jun	05-Jul	688.0	76.9	30-Jul	06-Aug	359.0	40.1	17-Sep	10-Oct	32.0	3.6	21-Aug
2015	12-May	25-Aug	01-Jul	06-Jul	795.0	88.8	01-Aug	06-Aug	461.0	51.5	28-Aug	02-Sep	136.0	15.2	23-Aug
2016	14-May	01-Sep	23-Jun	30-Jun	790.0	88.3	27-Jul	04-Aug	454.0	50.7	04-Sep	11-Sep	123.0	13.7	28-Aug
Mean	07-May	08-Sep	23-Jun	30-Jun	707.1	79.0	29-Jul	04-Aug	379.1	42.4	05-Sep	15-Sep	91.9	10.1	19-Aug
SE	2.9d	6.7d	2.2d	2.1d	23.1	2.6	1.4d	1.5d	22.9	2.6	3.1d	4.1d	10.6	1.2	2.0d

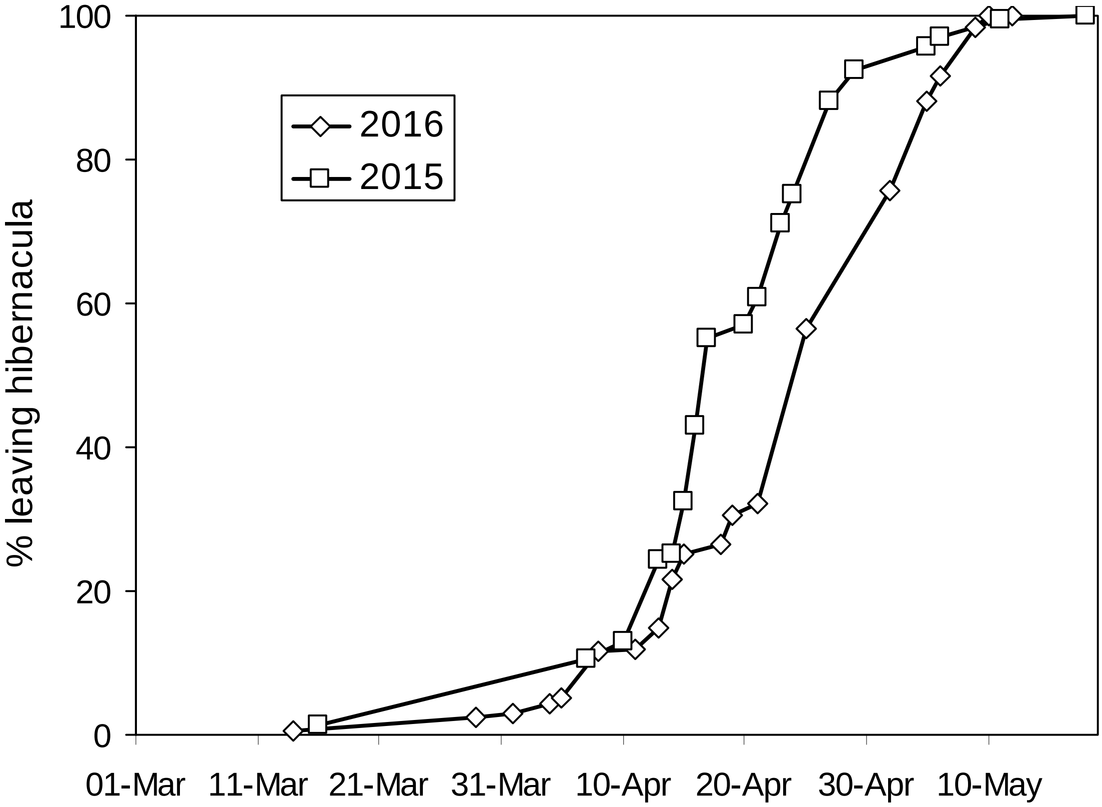

Figure 1 Cumulative percentage of *H. axyridis* individuals leaving an artificial overwintering site in 2015 (n = 238 individuals) and 2016 (n = 771).

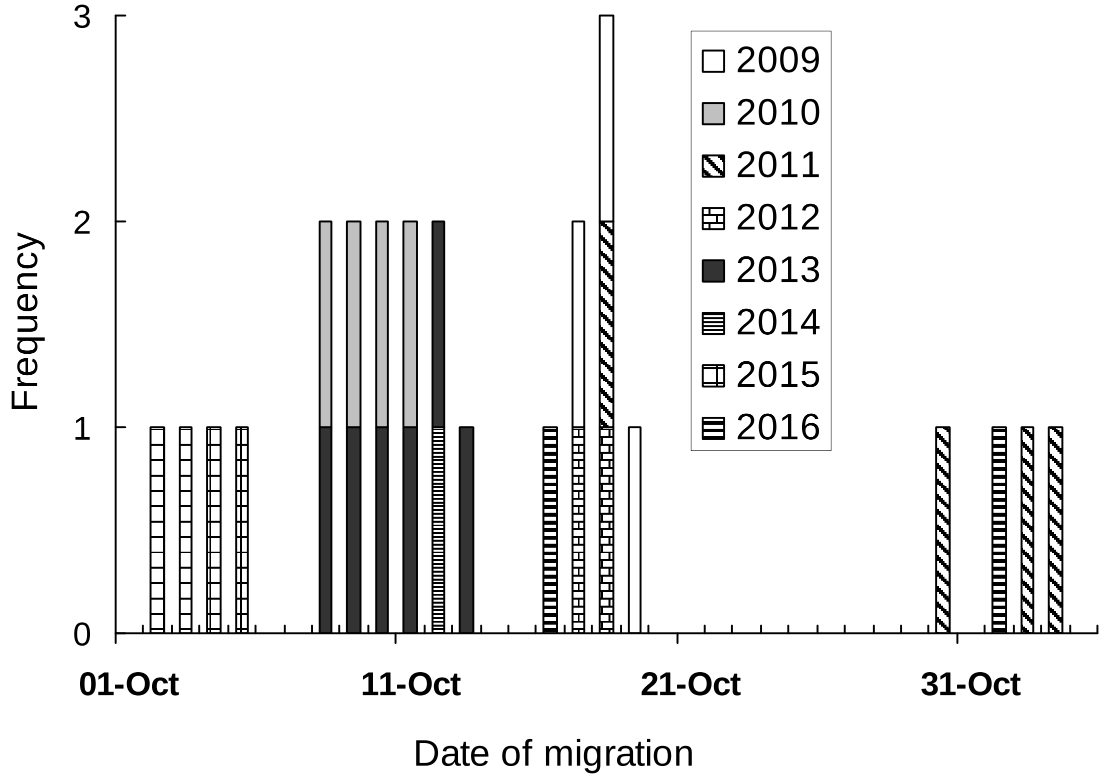

Figure 2 Frequency at which autumn migration of *H. axyridis* to hibernacula was recorded on particular days, at Prague-Ruzyně over the period 2009–2016. For each year dates on which migration was recorded is indicated by a column of the same size and columns are stacked vertically if flight activity occurred on the same date in different years.

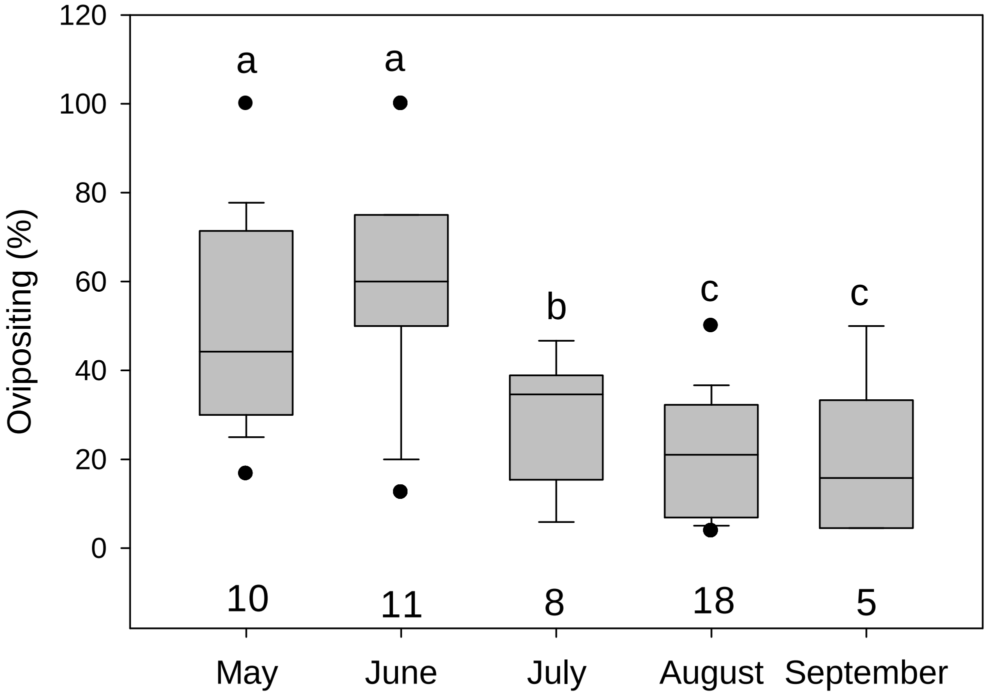

Figure 3 Percentage of females of *H. axyridis* in populations (number of populations is indicated by the number at the bottom) that oviposited. Boxes topped by different letters differ significantly at P < 0.05. Differences compared using contrasts following GLM with binomial errors. Boxes: median and 25% and 75% percentiles, whiskers are 1.5 times the interquartile range. Points outside whiskers are considered as outliers.

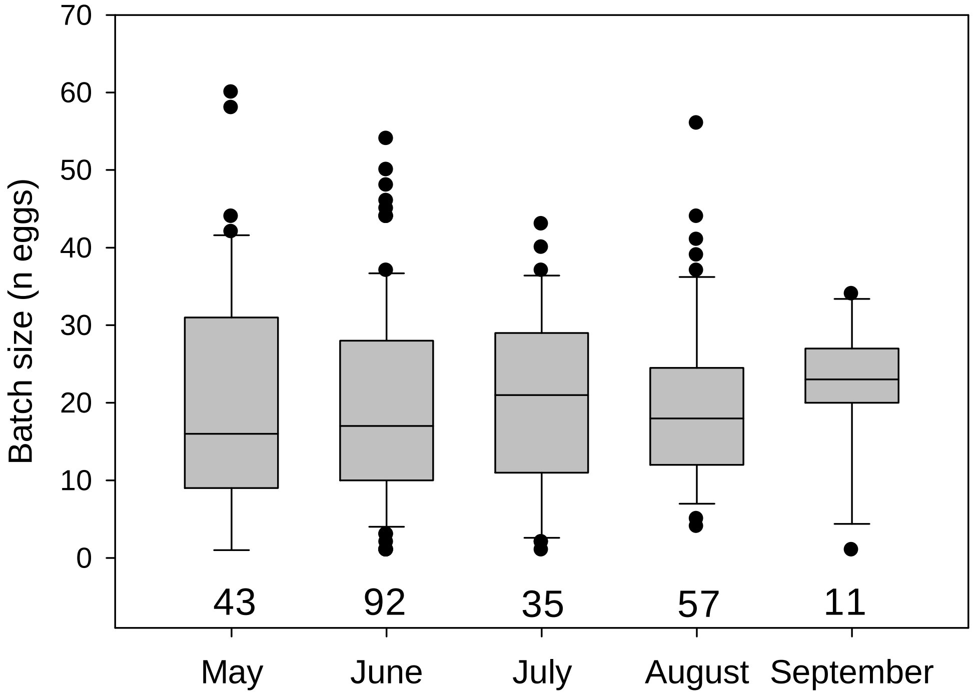

Figure 4 The sizes of the batches of eggs laid by females of *H. axyridis* (number of eggs laid by a female after collection from a natural population) in particular months in 2016 (number of batches is indicated by the number at the bottom). There was no significant differences in batch size among months. Differences compared using contrasts following GLM with Poisson errors. Boxes: median and 25% and 75% percentiles, whiskers are 1.5 times the interquartile range. Points outside whiskers are considered as outliers.