

## ORIGINAL CONTRIBUTION

**Weak photoperiodic response facilitates the biological invasion of the harlequin ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae)**S. Ya. Reznik<sup>1</sup>, M. Yu. Dolgovskaya<sup>1</sup>, A. N. Ovchinnikov<sup>1</sup> & N. A. Belyakova<sup>2</sup><sup>1</sup> Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia<sup>2</sup> All-Russian Institute of Plant Protection, Russian Academy of Agriculture, St. Petersburg, Russia**Keywords**aphidophagous coccinellids, diapause, *Harmonia axyridis*, *Harmonia yedoensis*, reproduction**Correspondence**

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**Abstract**

Photoperiodic regulation of reproductive diapause in two invasive and two native populations of *Harmonia axyridis* and in one native population of *Harmonia yedoensis* was investigated in laboratory at 20°C, five photoperiods (day length of 10, 12, 14, 16 and 18 h) and two diets: (i) eggs of the Angoumois grain moth *Sitotroga cerealella* and (ii) the green peach aphid, *Myzus persicae*. Laboratory strains originated from native populations of *H. axyridis* from Irkutsk province of Siberia and *H. yedoensis* from South Korea showed a strong photoperiodic response: under short photoperiods (10–14 h and 10–12 h for *H. axyridis* and *H. yedoensis*, correspondingly), all females which fed on eggs and most of those fed on aphids did not start to lay eggs during 40 days after emergence, while under long photoperiods, all females fed on aphids and most of those fed on eggs oviposited. The photoperiodic response of *H. axyridis* from South Korea was less strong: on the both diets, the range of the photoperiodic response (the difference in the proportion of ovipositing females between the treatments with long and short days) was ca 40%. In the European (Czech Republic) and in the Caucasian (Sochi region, Russia) invasive populations of *H. axyridis*, the photoperiodic response was very weak: the proportion of females that started oviposition (when fed on aphids) or at least reproductive maturation (when fed on eggs) during 40 days after emergence was close to 100%, independently of the photoperiodic conditions. Obviously, instead of a rapid micro-evolutionary adaptation of the critical day length to a new climate, the invasive populations of the harlequin ladybird decrease their dependence on photoperiod and thus the weak photoperiodic response of SE Asian population of *H. axyridis* can be considered as a pre-adaptation further developed during the invasion.

**Introduction**

Any insect species occasionally or intentionally introduced outside its native range inevitably faces a new set of environmental factors. Adaptation to new conditions is a necessary requirement for becoming a dangerous invader or (in the case of an intentional release) a successful classical biocontrol agent (Lee 2002; Gomi 2007; Lombaert et al. 2008; Szűcs et al.

2012; Urbanski et al. 2012; Laugier et al. 2013). However, adaptability of each species is limited and thus a potential invader (or biocontrol agent) should be to some extent 'pre-adapted'. Although the analysis of these pre-adaptations and their further evolution is very important both in the prevention of biological invasions and in the search for biocontrol agents, 'the knowledge of processes and factors explaining the invasion success is still rudimentary' (Williamson

2006). One of the methods of such analysis is the comparison of successful invaders with the closely related species (or populations) that failed to settle in new environment. In this context, the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) seems very promising (Sloggett 2012).

This predaceous coccinellid was introduced in the USA and Europe from South-East Asia. During many years, it has been successfully used for the biological control of insect pests. However, about 20 years ago, *H. axyridis* invaded natural ecosystems, and at present, it is considered an invasive insect in almost 40 countries (Koch and Galvan 2008; Roy and Wajnberg 2008; Lombaert et al. 2010; Brown et al. 2011). In Europe, this species moves to the north and to the east (Brown et al. 2008, 2011; van Lenteren et al. 2008; Berkvens et al. 2010; Raak-van den Berg et al. 2013), and quite recently, the invasive populations of *H. axyridis* were reported from the Russian part of the Caucasus (Belyakova and Reznik 2013; Ukrainsky and Orlova-Bienkowskaja 2013). On the other hand, *H. axyridis* is native to eastern Russia (more than 200 years ago this species was described from Siberia), but in spite of the heavy east–west traffic and the absence of natural borders, the representatives of the Siberian populations obviously were not able to invade European Russia (Belyakova and Reznik 2013). In addition, during last years, *H. axyridis* has been repeatedly introduced into the south of European Russia from the Russian Far East, but these introductions also never resulted in establishment (Brown et al. 2008, 2011; Lombaert et al. 2010; Belyakova and Reznik 2013; Ukrainsky and Orlova-Bienkowskaja 2013). In combination, these data support the conclusion made from the results of molecular genetic studies: the worldwide invasion of *H. axyridis* stemmed not directly from the native range, but from an invasive ‘bridgehead population’ where some ‘evolutionary shift’ have occurred (Lombaert et al. 2010; Brown et al. 2011; Sloggett 2012). This conclusion, in turn, raises two important questions. First, what preadaptations allow *H. axyridis* (in contrast to many other coccinellids) to evolve the bridgehead population? Second, what are the components of this evolutionary shift, what features differentiate the invasive populations from native populations of the same species? As seen from the recently published comprehensive review (Sloggett 2012) and from the later publications (e.g. Tayeh et al. 2012; Raak-van den Berg et al. 2013; Comont et al. 2014; Lombaert et al. 2014), various characters of *H. axyridis* have been suggested to be of importance for its invasion, including the rate of development, the diapause duration, cold

hardiness and some other features related to the climatic adaptations. However, the photoperiodic response of *H. axyridis* which is very important in life cycle synchronization with natural seasonal cycles (Tauber et al. 1986; Danks 1987; Zaslavski 1988; Denlinger 2002) has been extensively studied (Ongagna and Iperti 1994; Berkvens et al. 2008; Reznik and Vaghina 2011, 2013; Hodek 2012a; Belyakova and Reznik 2013) but, as far as we know, has not been specially considered in this aspect.

The photoperiodic regulation of diapause is based on the natural correlation between seasonal changes of day length and other environmental factors (temperature, precipitation, food availability, etc.). As the pattern of this correlation depends on geographical location, local populations of widely distributed insect species often differ in the critical day length. In addition, insects with a large geographical range may show a high intrapopulation variability in the parameters of the photoperiodic response or relative independence of the day length (in the last case, diapause may be induced by thermal or trophic cues). Although the above-listed adaptations are not mutually exclusive, stable populations of relatively short-dispersing insects are usually adapted to local climate (Tauber et al. 1986; Danks 1987; Zaslavski 1988; Denlinger 2002; Gomi 2007; Leisnham et al. 2011; Bean et al. 2012; Szűcs et al. 2012; Urbanski et al. 2012; Lankinen et al. 2013), while long-dispersing and, particularly, invasive species often show high individual variability and multifactorial regulation of diapause (Tauber et al. 1988; Lehmann et al. 2012; Izzo et al. 2014).

Thus, it can be expected that individuals from invasive populations of *H. axyridis* would show relatively weak photoperiodic effect on diapause induction (in comparison with that of native populations and closely related species). To check this hypothesis, we have conducted a comparative study on photoperiodic regulation of reproductive diapause in two invasive and two native populations of *H. axyridis* and in one (native) population of its sympatric sibling species *Harmonia yedoensis* Takizawa.

## Materials and Methods

The study was conducted with the following five laboratory populations.

1 *Harmonia axyridis* originated from 240 individuals from the native population collected in 2010 in the environs of Irkutsk (Russia, Southern Siberia, ca 52.3°N, 104.3°E). The climate of Irkutsk is temperate, rather continental, with a relatively warm

summer and very fast autumnal decrease in temperature: average temperatures of August, September and October are 15.8, 9.7 and 0.5°C, correspondingly; yearly average is 0.6°C (hereafter, data from <http://www.weatheronline.co.uk> are used).

- 2 *Harmonia axyridis* originated from 134 individuals from the native population collected in 2012 in the environs of Daegu (South Korea, ca 35.9°N, 128.6°E). The climate of Daegu is subtropical, and average temperatures of August, September and October are 27.2, 22.7 and 16.8°C, correspondingly; yearly average is 15.1°C.
- 3 *Harmonia axyridis* originated from 25 to 30 adults from the invasive population collected in 2010 in the environs of Pardubice (100 km E of Prague, Czech Republic, ca 50.0°N, 15.8°E). The climate of Prague is temperate oceanic, and average temperatures of August, September and October are 18.6, 14.0, and 9.5°C, correspondingly; yearly average is 9.1°C.
- 4 *Harmonia axyridis* originated from more than 120 individuals from the invasive population collected in 2012 in the environs of Sochi (Krasnodar Territory of Russia, ca 43.6°N, 39.6°E). The climate of Sochi is subtropical, and average temperatures of August, September and October are 24.7, 20.9 and 16.5°C, correspondingly; yearly average is 14.6°C.
- 5 *Harmonia yedoensis* originated from 40 individuals from the native population collected in 2009 in the environs of Nonsan (South Korea, ca 36.2°N, 127.0°E). The climate of Nonsan is similar to that of Daegu.

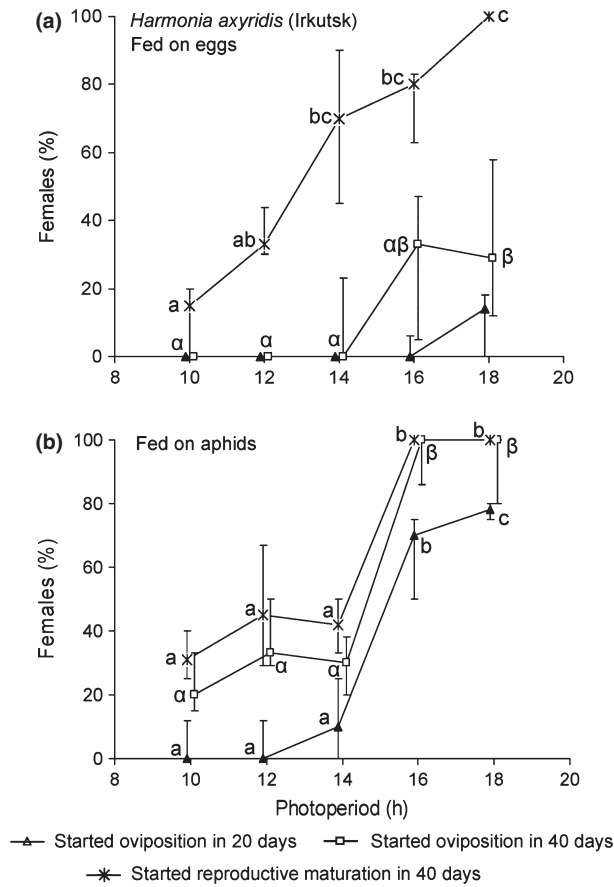
To start the experiment, a cohort of the first instar larvae hatched during 12 h from eggs laid by at least 20 females of the laboratory strain was randomly distributed between five photoperiodic regimens (chambers with day length of 10, 12, 14, 16 and 18 h in a thermostatic room at 20°C). This experiment was conducted using two diets: (i) frozen eggs of the Angoumois grain moth *Sitotroga cerealella* Oliv. glued to a small piece of hard paper with 10% honey solution and cotton ball soaked with water (hereafter 'eggs') and (ii) nymphs and adults of the green peach aphid, *Myzus persicae* (Sulz.) on the seedling of the broad bean, *Vicia faba* L. (hereafter 'aphids'). Both larvae and adults were reared in plastic Petri dishes (90 × 15 mm), and food was provided daily in excess. The larvae were reared individually, the emerged adults were sexed, and the pairs were kept under the same photoperiodic conditions as during their pre-imaginal development (in few cases, missing males were randomly selected from the main laboratory

strain). Each Petri dish was checked daily for eggs, and the duration of reproductive maturation was recorded as the number of days from female emergence to the laying of the first egg. Forty days after emergence, all non-ovipositing females were dissected and separated in two categories: 'diapause' (only germarium is present and follicles are absent) and 'reproductive maturation' (follicles or even mature oocytes are present).

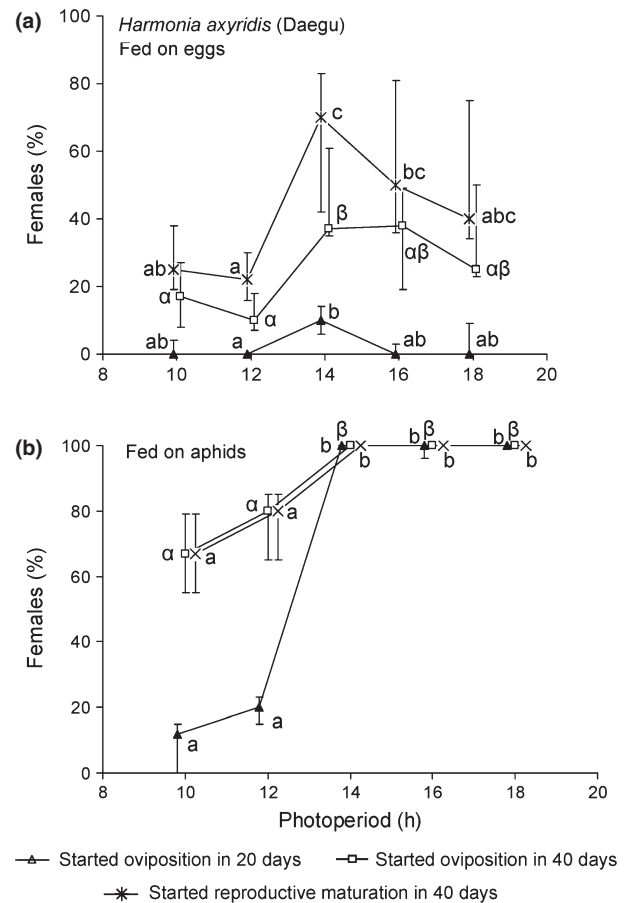
Each cohort included at least 10 larvae for each photoperiodic regimen. For each strain, five to seven cohorts were studied with each diet and position of photoperiodic chambers in the thermostatic room was periodically changed (by this means, the cohorts were separated both in time and space). To avoid pseudoreplication, cohorts (not individual females) were considered as experimental units. For each cohort, the proportion of females that started to lay eggs during 20 and during 40 days after emergence and the proportion of females that started reproductive maturation during 40 days after emergence were calculated, and these time periods were selected based on the results of our previous studies (Reznik and Vaghina 2011, 2013; Belyakova and Reznik 2013). For the statistical treatment, proportions were arcsine square-root-transformed, while figures show untransformed data (medians and quartiles). As the data for each cohort were not independent, the repeated measures ANOVA with orthogonal contrasts were used to compare treatments (McDonald 2009). All the calculations were made using SYSTAT 10.2 (Systat Software, Inc., San Jose, CA).

## Results

Preliminary analysis of the results showed that, as expected, diet markedly influenced on the proportions of egg-laying and maturing females of all of the studied populations. Thus, further analysis was conducted separately for individuals fed on eggs and on aphids. As seen in fig. 1, the photoperiodic response of *H. axyridis* from Irkutsk (Siberia) fed on both diets was statistically significant for all the three studied parameters, although in beetles fed on *Sitotroga* eggs, it was mostly manifested in the changes in the proportion of females that started reproductive maturation during 40 days after emergence. In the strain of the same species originated from individuals collected in Daegu (South Korea), the photoperiodic response was less strong although still statistically significant (fig. 2). In particular, when *H. axyridis* from Daegu were fed on aphids, day length mostly influenced the proportion of females that started oviposition during



**Fig. 1** Influence of photoperiod and diet on reproductive maturation of females of *Harmonia axyridis* population from Irkutsk (Siberia, Russia). (a) larvae and adults fed on frozen eggs of the Angoumois grain moth, (b) larvae and adults fed on the green peach aphid. Values with different letters in the same line are significantly different at  $P < 0.05$ . The absence of letters means the absence of any significant pairwise difference. The proportions of females that started to lay eggs during 20 days after emergence and the proportions of females that started reproductive maturation during 40 days after emergence are labeled with Latin letters, the proportions of females that started to lay eggs during 40 days after emergence are labeled with Greek letters.

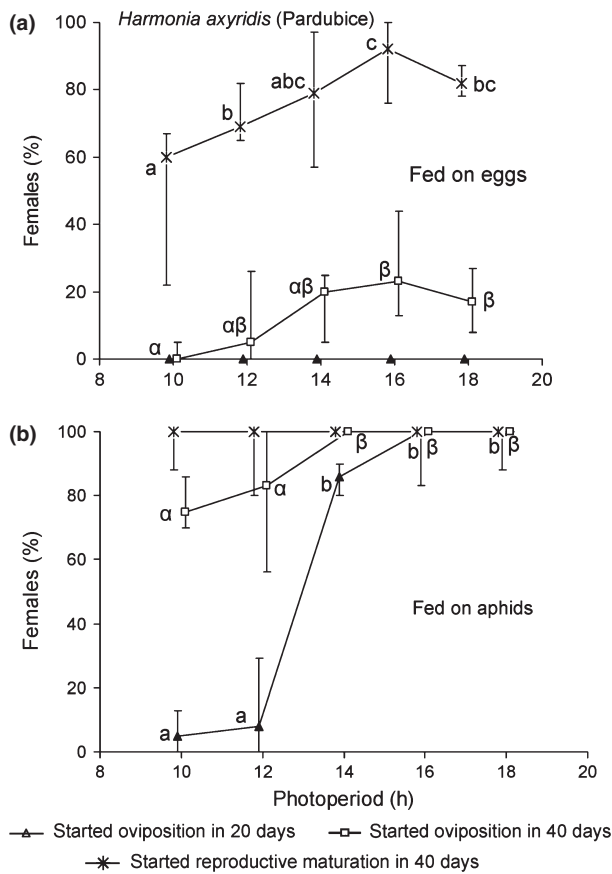


**Fig 2** Influence of photoperiod and diet on reproductive maturation of females of *Harmonia axyridis* population from Daegu (South Korea). Other explanations as in fig. 1.

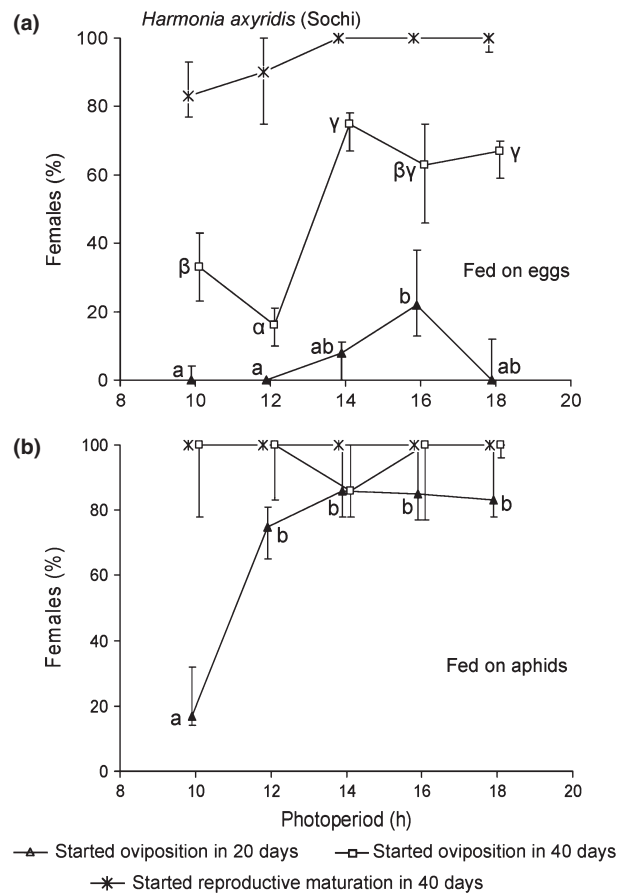
20 days after emergence, although the photoperiodic response was highly statistically significant for all the three parameters (fig. 2b). Note that critical day length constituted 14–16 h for the Siberian and 12–14 h for the Korean native populations (comp. figs 1 and 2).

In the two invasive populations of *H. axyridis* (figs 3 and 4), critical photoperiods were approximately the same as those in the Korean native population (fig. 2), but the photoperiodic response was weaker. When females of the strain originated from Pardubice were fed on eggs, the significant responses were observed in 40 days after emergence, but their ranges

did not exceed 20–25% (fig. 3a). If these beetles were fed on aphids, the photoperiodic effect on the proportion of ovipositing females, in contrast, was very clear in 20 days after emergence, but then it became less evident and the difference in the proportion of maturing females was not significant: almost all females fed on aphids started maturation independently of day length (fig. 3b). The results of the experiments with the females originated from Sochi were similar to those with the Czech population, but when adults were fed on aphids, both the proportion of females that started to lay eggs during 40 days after emergence and the proportion of those which started reproductive maturation were close to 100%, independently of the photoperiodic conditions (fig. 4b). When the females of this strain were fed on eggs, the photoperiodic effect on the proportion of maturing females was also weak although still statistically significant (fig. 4a). And, finally, the females of Korean *H. yedoensis* showed a very strong and clear-cut



**Fig 3** Influence of photoperiod and diet on reproductive maturation of females of *Harmonia axyridis* population from Pardubice (Czech Republic). Other explanations as in fig. 1.



**Fig 4** Influence of photoperiod and diet on reproductive maturation of females of *Harmonia axyridis* population from Sochi (Krasnodar Territory, Russia). Other explanations as in fig. 1.

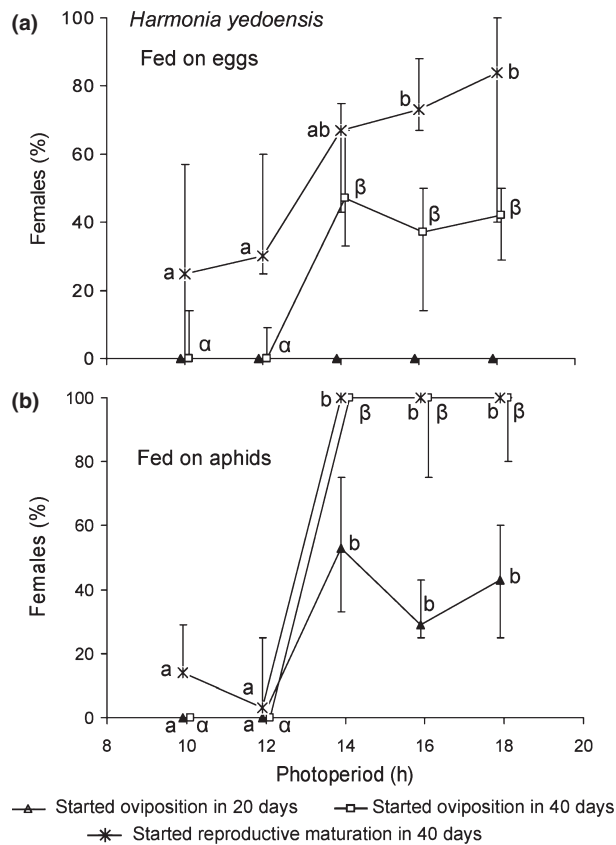
photoperiodic response similar to that of Siberian *H. axyridis*, but with shorter critical day length, which was almost the same as in Korean *H. axyridis* (comp. figs 1, 2 and 5).

### Discussion

Although our work was not aimed at assessing the effect of trophic factor, it should be noted that in all populations of the two studied *Harmonia* species, females fed on the green peach aphid more often began reproductive maturation and faster started oviposition than those fed on the grain moth eggs. It is well known that both the rate of pre-imaginal development and the reproductive maturation in *H. axyridis* strongly depend on diet (Evans and Gunther 2005; Osawa 2005; Soares et al. 2005; Berkvens et al. 2008; Agarwala and Bhowmik 2011; Stathas et al. 2011; Hodek 2012a; Hodek and Evans 2012). In particular, it has been demonstrated that although larvae and

adults of *H. axyridis* can develop and reproduce when fed on fresh or frozen eggs of *S. cerealella*, aphids are their preferred and more nutritionally suitable natural food (Chen et al. 2012; Dos Santos Rodrigues et al. 2013; Reznik and Vaghina 2013). In the present study, we first demonstrated the same difference between the suitability of these two diets for a closely related species, *H. yedoensis*.

As for the effect of day length, a typical long-day photoperiodic response, which was observed in our study, has been earlier shown for numerous coccinellids (Hodek 2012a) and, in particular, for several populations and laboratory strains of *H. axyridis* (Ongagna and Iperti 1994; Berkvens et al. 2008; Reznik and Vaghina 2011, 2013; Hodek 2012a; Belyakova and Reznik 2013), while the photoperiodic reaction of *H. yedoensis* was not investigated earlier. The observed differences in critical photoperiod between relatively northern (Siberian *H. axyridis*) and southern (Korean *H. axyridis* and *H. yedoensis*) populations and species



**Fig 5** Influence of photoperiod and diet on reproductive maturation of females of *Harmonia yedoensis* population from Nonsan (South Korea). Other explanations as in fig. 1.

also agree well with the results of earlier studies conducted on *H. axyridis* (Reznik and Vaghina 2011; Belyakova and Reznik 2013) and on many other insect species (Tauber et al. 1986; Saunders et al. 2002; Saunders 2010). The adaptive value of this latitudinal variation in critical day length is evident: in northern regions, the appropriate time to enter winter diapause coincides with longer days. Note, however, that in invasive populations, critical photoperiods do not differ from that in their source population, although, for instance, the climate of Daegu, South Korea, is much warmer than that of Pardubice, Czech Republic (see 'Materials and Methods').

However, the point we would like to emphasize is not the differences in the threshold, but the differences in the range of photoperiodic responses of the studied species and populations. *Harmonia axyridis* individuals from the Siberian population showed very strong and clear-cut photoperiodic response: when they were reared and kept under short photoperiods, most of the females fed on aphids did not even start to mature during 40 days after emergence. At the same

time, more than a half of females of the same species from South Korea reared and kept under the same conditions already laid eggs (comp. figs 1 and 2). This distinction cannot be explained only by the different climate conditions, because the photoperiodic response of *H. yedoensis* (also living in the Korean climate) was as strong as that of the Siberian *H. axyridis*, although the critical day length was shorter (comp. figs 1 and 5). Similar weak and short-term response to short photoperiods was also reported for *H. axyridis* from the Russian Far East (Reznik and Vaghina 2011, 2013): when the females were provided with their natural prey, short photoperiods did not totally prevent reproduction but only increased the duration of the pre-oviposition period. Furthermore, almost all females from the European and Caucasian invasive populations started to mature during 40 days and most of them laid eggs when fed on aphids almost independently of photoperiod. When applied to the natural conditions, this means that in the presence of preferred or at least suitable 'essential food' (Hodek and Evans 2012), they do not enter diapause independently of the astronomical season.

It is known that captive populations often lose photoperiodic response (e.g. Berkvens et al. 2008). However, all the studied strains were reared during <3–4 years under standard diapause-averting conditions (temperature of 20–25°C, day length of 18 h, feeding on aphids). As suggested by our earlier study (Reznik and Vaghina 2011), the peculiarities of the photoperiodic response of *H. axyridis* stay stable over several tens of generations of rearing under these conditions. Moreover, the weakest photoperiodic response was observed in the most recently collected Korean and Caucasian populations (see Materials and Methods).

As was noted in the Introduction, a fast-spreading invasive species encountering novel climatic conditions can use three strategies to survive in newly inhabited areas, namely (i) a continuous rapid micro-evolutionary adaptation to each new environment, (ii) a high genotypic diversity and polymorphism, ensuring survival of at least some individuals of a population under a wide range of environmental conditions, and (iii) a high phenotypic plasticity which, as applied to diapause regulation, means the dependence of the parameters of the photoperiodic response on other environmental factors such as temperature, humidity and diet (Facon et al. 2008; Lombaert et al. 2008; Sadakiyo and Ishihara 2011; Szűcs et al. 2012; Schilthuizen and Kellermann 2013; Su 2013; Díaz et al. 2014; Forsman 2014; Moran and Alexander 2014; Tanaka et al. 2014). Of course, in reality, these

strategies can be combined as, for example, in the Colorado potato beetle, *Leptinotarsa decemlineata* Say: its invasive European populations show a typical latitudinal cline of the critical day length combined with high intrapopulation variation in the tendency to diapause and, in addition, the proportion of diapausing adults depends not only on day length but also on temperature, food quality, etc. (Tauber et al. 1986, 1988; Yocum et al. 2011; Hodek 2012b; Lehmann et al. 2012; Izzo et al. 2014). The results of our study suggest that European and Caucasian invasive populations of *H. axyridis* used the last strategy to change the photoperiodic induction of the reproductive diapause: instead of adjusting the critical day length to a new climate the harlequin ladybirds decreased their dependence on photoperiod. The presence of 'essential food' is a necessary requirement for the reproductive maturation of *H. axyridis* (Osawa 2005; Berkvens et al. 2008; Hodek and Evans 2012; Dos Santos Rodrigues et al. 2013; Reznik and Vaghina 2013), and thus, the weakening of the photoperiodic response automatically placed the females under the control of the trophic factor. This evolutionary trend is common among aphidophagous coccinellids because 'unpredictable intermittent availability of aphid prey leads to a greater plasticity of diapause mechanisms' (Hodek 2012a). However, in the European invasive population of *H. axyridis*, the reproductive diapause under the natural conditions is particularly short-term and flexible (Iperti and Bertrand 2001; Berkvens et al. 2008) which 'may be an important factor that contributes to the invasive success' (Raak-van den Berg et al. 2013). This weak photoperiodic induction of diapause can also result from hybridization with European biocontrol populations (Lombaert et al. 2010; Turgeon et al. 2011) that have reportedly lost the photoperiodic response during numerous generations of mass rearing under laboratory conditions (Berkvens et al. 2008; Hodek 2012a). Note, however, that individuals from native South-East Asian population of *H. axyridis* (that was the source of the invasive population), when compared with the non-invasive Siberian population of *H. axyridis* and with the closely related South-East Asian species *H. yedoensis*, also show relatively weak photoperiodic response, which, consequently, can be considered as a pre-adaptation further developed during the invasion. Thus, the results of our study support our working hypothesis and, in addition, agree with the data on the increased phenotypic plasticity of various biological parameters that have been reported for European invasive populations of *H. axyridis* (Berkvens et al. 2008; Lombaert et al. 2008; Sloggett 2012; Raak-van den Berg et al. 2013).

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