Eur. J. Entomol. **112**(4): 642–647, 2015
doi: 10.14411/eje.2015.081
ISSN 1210-5759 (print), 1802-8829 (online)

Effect of photoperiod on adult size and weight in *Harmonia axyridis* (Coleoptera: Coccinellidae)

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Key words. Coleoptera, Coccinellidae, *Harmonia axyridis*, photoperiod, development, weight, size, maturation, diapause

Abstract. Short photoperiods often accelerate preimaginal development in insects that overwinter as adults and thus ensure the timely development of the diapausing stage. However, fast development usually results in small adults with few reserves whereas successful overwintering is dependent on sufficient reserves of nutrients. Thus, an insect faces two opposite challenges: increase adult weight or speed up pre-adult development. One solution to this "time-size trade-off" is fast development resulting in relatively light-weight but not too small adults, which are able to survive if there is an early onset to winter and have the possibility of further increasing their weight if conditions in autumn remain favourable for longer than usual. To test this hypothesis, we determined the effect of different photoperiods (day lengths of 12 and 18 h at 20°C) on the duration of preimaginal development, size of emerging adults and dynamics of adult weight in *Harmonia axyridis*. The larvae reared under short-day conditions tended to develop faster and invest resources in structural growth rather than in increasing weight: the daily rate of increase in size under a 12 h long photoperiod was greater than that under a 18 h long photoperiod, whereas the rate of gain in weight showed the opposite tendency. This resulted in a significant decrease in the weight/size ratio of emerging adults. However, their low initial nutritional status was partly compensated for by adult feeding: the relative gain in adult weight of "short-day individuals" was greater than that of the beetles that developed under long day conditions.

INTRODUCTION

It is known that short day length often accelerates preimaginal development in insects that overwinter as adults, which ensures the timely development of the diapausing stage prior to the beginning of winter (Tauber et al., 1986; Nylin & Gotthard, 1998; Saunders et al., 2002; Musolin et al., 2004; Lopatina et al., 2007). However, the species-specific growth rate is naturally limited and hence fast development often results in small and light adults (Abrams et al., 1996; Kingsolver & Huey, 2008; Nijhout et al., 2010; Dmitriew, 2011; Pöykkö & Hyvärinen, 2012; Salminen et al., 2012; Chen et al., 2014). On the other hand, successful overwintering depends on sufficient fat and glycogen reserves, which are often positively correlated with body weight (Hahn & Denlinger, 2011; Hodek, 2012; Clemmensen & Hahn, 2015). In addition, large females have a greater potential fecundity and some other selective advantages (Honěk, 1993; Abrams et al., 1996; Nylin & Gotthard, 1998; Nakamura, 2002; Dmitriew, 2011; Nedvěd & Honěk, 2012). Thus, an insect faces two seemingly opposite challenges: increase adult weight or speed up pre-adult development. Although in some species both goals are achieved (Leimar, 1996; Kutcherov et al., 2011), in most cases a compromise is adopted.

However, even in adult insects the correlation between weight and size is strong but not absolute. Although the weight of emerging adults is limited by the final larval weight, the size can vary. In addition, adult size is fixed at emergence, whereas adult weight can change during its lifetime. As the natural seasonal dynamics of temperature, in contrast to that of day length, is quite variable, one solution to this "time-size trade-off" (Nylin & Gotthard, 1998) is the rapid development of a relatively light-weight but not too small adult, in case winter arrives early, with the possibility of further weight increase if conditions remain favourable for longer than usual. Similar accelerated development (constant size with low weight) is predicted by the "optimality model" (Abrams et al., 1996) and recorded in some insects (Nylin & Gotthard, 1998; Strobbe & Stoks, 2004).

Accelerated development has been studied in many insects, but in the overwhelming majority of cases the correlation between the duration of development and either structural size or weight of the adults was considered, whereas the "size/weight" relations are rarely investigated (Strobbe & Stoks, 2004; Dmitriew & Rowe, 2007; Knapp & Nedvěd, 2013). In the present study, we determined the effect of photoperiod on the duration of development, size, and weight of the emerging adults, and the dynamics of adult weight in *Harmonia axyridis* (Pall.) (Coleoptera: Coccinellidae). The main aim of this study was to test the above hypothesis that individuals which develop fast tend to invest resources in structural growth rather than in weight gain and have the possibility of at least a partial compensation for their small adult size by increasing their adult weight.

This study was carried out using the predatory lady beetle *H. axyridis,* which has been the subject of many investigations, first on its effectiveness as a biological control agent of insect pests and more recently as an invasive alien species (Koch & Galvan, 2008; Roy & Wajnberg, 2008; Lombaert et al., 2010; Brown et al., 2011). It is well known that short photoperiods not only slow down the reproductive maturation of *H. axyridis* females but also speeds up preimaginal development (Ongagna & Iperti, 1994; Iperti & Bertrand, 2001; Berkvens et al., 2008; Reznik & Vaghina, 2011; Hodek, 2012; Reznik et al., 2015). However, the influence of day length on the weight and size of adults has not been studied in this species.

MATERIAL AND METHODS

In our study we used a laboratory strain of *H. axyridis* that originated from adults collected in the Khasanskiy region (Primorskiy territory, Far East of Russia, 43.1°N, 131.5°E) and then reared for several tens of generations under laboratory conditions (temperature of 20–25°C, day length of 18 h). Larvae and adults were fed on the green peach aphid, *Myzus persicae* (Sulz.) (Aphididae) reared on broad bean, *Vicia faba* L. seedlings.

To begin the experiment, 1st instar larvae that have just hatched from eggs laid over a period of 24 h by more than 50 females from the laboratory culture were evenly distributed between two different photoperiodic treatments (day length of 12 and 18 h at a temperature of 20°C). These treatments were selected because earlier studies revealed that under a 12 h long day preimaginal development was significantly faster and reproductive maturation markedly slower than under a 18 h long day (Reznik & Vaghina, 2011, 2013). In addition, the proportion of females that entered diapause under a 12 h long day was much higher than that under a 18 h long day, which was expected because after the autumnal equinox in the Primorskiy territory of Russia temperature decreases rapidly: average temperatures in September, October, and November are 15°, 10° and 0°C, respectively (data from http://www.weatheronline.co.uk). The larvae were reared individually in plastic Petri dishes (60 × 15 mm). Larvae were fed frozen eggs of the grain moth *Sitotroga cerealella* Oliv. (Lepidoptera: Gelechiidae), which were glued to card by means of a honey solution. This food was provided daily in excess. In addition, a 10% sugar solution was provided in Eppendorf test tubes plugged with cotton wool. Earlier experiments indicated that this diet is not preferred but still moderately suitable for the development and reproductive maturation of *H. axyridis* (Reznik & Vaghina, 2013; Reznik et al., 2015).

Pupation and adult emergence were recorded daily. Newly emerged adults that have not yet fed were sexed, weighed to an accuracy of 0.1 mg using a torsion balance (we used the wet rather than the dry weight of adults because this method allows the weight changes of individual beetles to be estimated), and once again evenly distributed between the same two photoperiodic regimes. Thus, the experiment included four photoperiodic treatments, i.e. combinations of two larval (12 and 18 h) and two adult (12 and 18 h) photoperiods. The adults were kept individually in the same Petri dishes, and food and sugar solution were provided in the same way as for larvae. Forty days after emergence, all the individuals that survived were weighed again and the left hind femur of each individual measured to an accuracy of 0.025 mm using a stereo microscope (the length of femur is easy to measure using a microscope and thus it is often used to estimate the structural size of an adult insect). Then the beetles were dissected and the state of their fat body was recorded using the following scale: (i) "poorly developed" (active stage fat body is arranged in thin lobes interspersed around the internal organs) or (ii) "well developed" (dormant stage fat body is composed of well-formed globules and interconnected stringy lobes and the internal organs are completely or nearly completely hidden) (Kono, 1982; Raak-van den Berg et al., 2012). In addition, the state of the ovaries of females was described as (i) "diapausing" (only germaria are present, follicles are absent, no visible oocytes) or (ii) "active" (stage I–II follicles or mature oocytes are present) (Kono, 1982; Sakurai et al., 1992; Raak-van den Berg et al., 2013). Thus, for each adult beetle, the duration of larval and pupal development, size (estimated as the length of the hind femur), initial weight (at emergence), final weight (40 days after emergence), and the state of the fat body (in all beetles) and ovaries (in females) 40 days after emergence were recorded.

Then five derivate parameters were calculated for each individual:

1. The daily rate of increase in size (length of the hind femur divided by the duration of larval development).
2. The daily gain in larval weight (initial adult weight divided by the duration of larval development).
3. The relative (percentage) gain in adult weight over a period of 40 days (the difference between the initial and final weight divided by the initial weight).
4. Initial nutritional status of emerged adults estimated as the weight divided by the length of the hind femur to the power of 2.5. This index was used because preliminary treatment of the data showed that adult weight was proportional to the 2.5 power of its size. Although the parameters of this regression varied with photoperiod and sex, the pooled data revealed a very close correlation ($R = 0.99$). A similar equation has been published for other Coccinellidae (Nedvěd & Honěk, 2012).
5. Final nutritional status 40 days after emergence using the same method as used for recently emerged adults.

The difference in temperature between chambers never exceeded 0.1°C. In addition, photoperiodic chambers were periodically replaced within a thermostatically controlled room. Individuals that died during the larval, pupal or adult stages, as well as the occasional malformed adult were not included in the analysis. Preimaginal mortality (mostly first instar larvae) was 25.2%, adult mortality during 40 days of the experiment was 6.4% and both were independent of photoperiod. The main aim of our work was to determine age-related changes in the different parameters of individual beetles. Therefore, each individual was considered as an experimental unit. In total, the experiment included 606 individuals (75–80 males and 70–75 females in each of the 4 photoperiodic treatments). Statistical analysis of parametric data included ANOVA followed by Student t-tests and the Bonferroni test for multiple comparisons. Means with SD were used as descriptive statistics. For non-parametric data, percentages with 0.95 confidence intervals and Chi-square tests were used. All the calculations were made using SYSTAT 10.2.

RESULTS

Two-way ANOVA revealed that the difference between photoperiods was significant ($P < 0.001$) for all parameters, except the duration of pupal development. The difference between sexes was significant ($P < 0.001$) for all parameters, except the duration of larval, pupal and total development. The interaction of the factors "Sex" and "Photoperiod" was not statistically significant for all parameters suggesting that the photoperiodic responses of males and females were the same or at least very similar. Indeed, under short day conditions, development of both males and females was faster, weight lower and size smaller than under long day conditions (Table 1). However, the difference in weight was greater than that in the length of the hind femur and therefore the initial nutritional status (weight / size ratio) of emerging males and females was significantly greater under long than under short day conditions. The

TABLE 1. The duration of preimaginal development, size and weight of the emerging male and female adults of *Harmonia axyridis* reared under short (12 h) and long day (18 h) conditions.

Sex	Males			Females		
Photoperiod during preimaginal development and sample size (n)	12 h (n = 161)	The significance of the difference between the preimaginal photoperiods[1]	18 h (n = 156)	12 h (n = 146)	The significance of the difference between the preimaginal photoperiods[1]	18 h (n = 143)
The duration of larval development (days)[2]	20.7 ± 2.7	P < 0.001	22.1 ± 2.6	20.8 ± 2.3	P < 0.001	22.7 ± 2.5
The duration of pupal development (days)[2]	7.6 ± 0.6	P = 0.160	7.7 ± 0.6	7.5 ± 0.5	P = 0.156	7.6 ± 0.5
The total duration of larval and pupal development (days)[2]	28.3 ± 2.3	P < 0.001	29.8 ± 2.8	28.3 ± 2.4	P < 0.001	30.3 ± 2.7
The length of the hind femur (mm)[2]	1.74 ± 0.11	P = 0.034	1.77 ± 0.10	1.82 ± 0.11	P = 0.001	1.86 ± 0.11
The initial weight of emerging adults (mg)[2]	22.7 ± 2.3	P < 0.001	26.1 ± 2.2	25.3 ± 2.7	P < 0.001	28.3 ± 2.8
The initial nutritional status of emerging adults (mg/mm$^{2.5}$)[2]	5.74 ± 0.90	P < 0.001	6.37 ± 0.91	5.74 ± 0.89	P = 0.001	6.08 ± 0.95
The daily rate of increase in size (μm/day)[2]	84.9 ± 8.9	P < 0.001	80.7 ± 8.6	88.2 ± 9.3	P < 0.001	82.7 8.6
The daily increase in weight (mg/day)[2]	1.12 ± 0.20	P < 0.001	1.20 ± 0.19	1.24 ± 0.24	P = 0.244	1.27 ± 0.22

[1] Student t- test; [2] (mean ± SD).

daily rate of increase in size under a 12 h long photoperiod was greater than that under a 18 h long photoperiod, whereas the rate of gain in weight showed the opposite tendency (Table 1).

Three-way ANOVA revealed that the final weight and final nutritional status of 40-day-old beetles, as well as their relative weight gain during 40 days after emergence, significantly ($P < 0.001$) depended on the photoperiod experienced by the adult. The final weight and relative weight gain were also strongly ($P < 0.001$) dependent on the photoperiod experienced during preimaginal development, but for the final nutritional status this effect was only marginally significant ($P = 0.040$). The effect of sex was also significant in terms of the final weight and adult weight gain ($P < 0.001$), but not for the final nutritional status ($P = 0.137$). All the interactions of factors (larval photoperiod, adult photoperiod and sex) were not or only marginally ($P > 0.04$) significant.

Forty days after emergence the individuals that developed under the long day conditions were still heavier than those that developed under short day conditions (Table 2; compare columns). The photoperiod experienced by the adults, however, had the opposite effect (Table 2, compare lines). Although practically all adults gained weight during the 40 days after emergence, the relative weight gain was greater under short larval and adult photoperiods. The effect of photoperiod experienced during preimaginal development on the final nutritional status was weak (significant only for males kept under short-day conditions).

TABLE 2. The dynamics of the weight of male and female adults of *Harmonia axyridis* reared under short (12 h) and long day (18 h) conditions as larvae and either short or long day conditions as adults.

Sex		Males			Females		
Photoperiod during preimaginal development		12 h	The significance of the difference between the preimaginal photoperiods[1]	18 h	12 h	The significance of the difference between the preimaginal photoperiods[1]	18 h
Sample size (n)	Adult photoperiod = 12 h	80		76	74		72
	Adult photoperiod = 18 h	81		80	72		71
The final weight of 40-day-old adults (mg)[2]	Adult photoperiod = 12 h	31.3 ± 3.5	P < 0.001	35.0 ± 4.7	36.9 ± 3.9	P < 0.001	40.9 4.6
	The significance of the difference recorded in the two photoperiods[1]	P = 0.010		P < 0.001	P = 0.163		P = 0.003
	Adult photoperiod = 18 h	29.8 ± 3.9	P < 0.001	32.0 ± 3.4	35.9 ± 4.8	P = 0.001	38.5 4.9
The relative increase in adult weight over 40 days (%)[2]	Adult photoperiod = 12 h	38.0 ± 10.4	P = 0.207	35.4 ± 15.0	46.5 ± 10.7	P = 0.077	43.3 ± 11.0
	The significance of the difference recorded in the two photoperiods[1]	P = 0.001		P < 0.001	P = 0.014		P = 0.007
	Adult photoperiod = 18 h	31.9 ± 13.0	P < 0.001	21.8 ± 11.2	41.4 ± 13.7	P = 0.086	37.2 ± 15.4
The final nutritional status of 40-day-old adults (mg/mm$^{2.5}$)[2]	Adult photoperiod = 12 h	7.90 ± 1.47	P = 0.008	8.62 ± 1.80	8.48 ± 1.54	P = 0.272	8.75 ± 1.44
	The significance of the difference recorded in the two photoperiods[1]	P = 0.183		P = 0.001	P = 0.060		P = 0.025
	Adult photoperiod = 18 h	7.60 ± 1.41	P = 0.358	7.79 ± 1.27	8.03 1.28	P = 0.289	8.25 ± 1.17

[1] Student t- test; [2] (mean ± SD).

Table 3. Weight (mg) of 40-day-old female and male adults of *Harmonia axyridis* and the state of development of their fat body and ovaries.

Fat body	Females (ovaries state)		Males
	Diapausing	Active	
Poorly developed	30.0 ± 3.9 a [1] (n = 4)	37.1 ± 4.8 b (n = 112)	30.1 ± 4.0 a (n = 168)
Well developed	39.0 ± 4.4 c (n = 134)	37.8 ± 5.6 bc (n = 39)	33.6 ± 3.9 b (n = 149)

[1] Mean ± SD and sample size, values for a given sex labelled with different letters are statistically different ($P < 0.05$ by the Bonferroni test).

A short photoperiod induced diapause: the percentages and 0.95 confidence intervals of beetles with a well developed fat body were 93.0% (88.9–95.9%) and 19.7% (14.8–25.3%) under 12 h and 18 h long photoperiods, respectively ($P < 0.001$; Chi-square test). Although the overwhelming majority of females had either a well developed fat body or active ovaries, some individuals (possibly those activated after a short-term reproductive diapause) had both, whereas sporadic (weak, under-sized) females had neither (Table 3). Diapausing females (as well as males) were heavier than those with a poorly developed fat body, whereas activated females were of an intermediate weight.

DISCUSSION

The duration of development and the wet weight of adults of *H. axyridis* recorded in the present study are close to those recorded in our earlier experiments (Reznik & Vaghina, 2011, 2013; Belyakova & Reznik, 2013) and reported by other authors (Ongagna & Iperti, 1994; Dmitriew & Rowe, 2007; Berkvens et al., 2008; Ungerová et al., 2010; Nedvěd & Honěk, 2012; Kalushkov et al., 2013; Knapp & Nedvěd, 2013; Nedvědová et al., 2013; Knapp, 2014). The average values of the initial weight and the daily gain in weight indicated that *S. cerealella* eggs are a moderately suitable food for *H. axyridis* larvae, but this may be because we used smaller Petri dishes than those used by Ungerová et al. (2010). In addition, feeding on frozen eggs of the grain moth resulted in high larval mortality, which was recorded but not reported in our earlier paper (Reznik et al., 2015).

Effect of day length on the size and weight of emerging adults, as far as we know, has not been studied in *H. axyridis*, although this kind of quantitative photoperiodic response is reported for the red poplar leaf beetle, *Chrysomela populi* L. (Kutcherov et al., 2011), the northern malt fly, *Drosophila montana* Stone, Griffen & Patterson (Salminen et al., 2012), and many other insects (Tauber et al., 1986; Saunders et al., 2002; Dmitriew, 2011). As for Coccinellidae, the initial weight of *Coccinella septempunctata brucki* Mulsant, *Propylea japonica* (Thunberg) and *Scymnus* (*Neopullus*) *hoffmanni* Weise, in contrast to that recorded for *H. axyridis* in this study, was lower when reared under long day conditions, at least within the range of "natural" photoperiods (Kawauchi, 1985). It is noteworthy that the duration of development of these species increases and the time to reproductive maturation decreases with day length (Kawauchi, 1985), as recorded here for *H. axyridis*. Generally, diapause-inducing short photoperiods often cause an adaptively beneficial increase in the weights of insects (Kawauchi, 1985; Tauber et al., 1986; Saunders et al., 2002; Kutcherov et al., 2011; Hao et al., 2013; Chen et al., 2014; Clemmensen & Hahn, 2015). However, in *H. axyridis* the increase in the rate of development under these conditions prevents this: fast development results in small adults, as in the cotton bollworm, *Helicoverpa armigera* (Hubner) (Chen et al., 2014), *D. montana* (Salminen et al., 2012) and some other species of insects (Abrams et al., 1996; Nylin & Gotthard, 1998; Kingsolver & Huey, 2008; Dmitriew, 2011). Short-day acceleration of preimaginal development combined with its inhibition of reproductive maturation is recorded for several species of Coccinellidae (Hodek, 2012; Nedved & Honěk, 2012) including *H. axyridis* (Ongagna & Iperti, 1994; Iperti & Bertrand, 2001; Berkvens et al., 2008; Dmitriew, 2011; Reznik & Vaghina, 2011; Belyakova & Reznik, 2013). Note that in certain species of insects development is longest when reared under short days or at the critical photoperiod, as, for example, the linden bug *Pyrrhocoris apterus* (L.) (Saunders, 1983; Musolin & Saulich, 1997; Saunders et al., 2002). The relatively strong short-day (autumnal) acceleration of development in *H. axyridis* is possibly connected with the late induction of diapause in this species (Hodek, 2012; Nedvěd & Honěk, 2012).

Returning to the main aim of this study, we conclude that the hypothesis is confirmed: larvae reared under "autumnal" short-day conditions tended to develop faster and invest resources in structural growth rather than in increasing their weight and thus the daily rate of increase in size under a 12 h long photoperiod was greater than that under a 18 h long photoperiod, whereas the rate of gain in weight showed the opposite tendency. This resulted in a marked decrease in the weight/size ratio of the emerging adults. However, their low initial nutritional status was at least partly improved by feeding in early adult life: the relative increase in adult weight of "short-day individuals" was greater than that of the beetles that developed under long day conditions and therefore the effect of photoperiod during preimaginal development on the final nutritional status was very weak.

The growth optimization model predicts that a time constraint (in particular, the approach of winter) should result in an increase in growth rate (Dmitriev, 2011). Our experiments only partly support this prediction: under a short photoperiod there was an increase in the rate of structural growth but not in weight. Allocation models predict that a time constraint may favour the allocation to fat reserves rather than structural growth (Dmitriev, 2011), which is not supported by the results of this study. However, *H. axyridis* is not a unique exception in this regard. A similar effect is reported, for example, for the damselfly *Enallagma cyathigerum* (Charpentier): when larvae develop under "summer-autumnal photoperiods", the growth rate based on size is greater and that based on weight the same as when larvae develop under "spring-summer photoperiods" (Strobbe & Stoks, 2004). Different environmental effects on mass and size of emerging adults was recently reported for *H. axyridis* but in that study the thermal, not photoperiodic, responses were investigated (Knapp & Nedvěd, 2013). Compensatory growth was also previously recorded in *H. axyridis*, but only in terms of an increase in larval growth after a period of food restriction. In particular, even full compensation of adult body size does not prevent some delayed negative consequences of larval starvation (Dmitriew & Rowe, 2007). The long-term consequences of the short-day acceleration of development need to be resolved by a continuation of this study.

ACKNOWLEDGEMENTS. We thank T.Yu. Moskaleva and L.S. Ramenskaya for their excellent technical assistance. We greatly appreciate the useful comments on our manuscript of three anonymous reviewers. This work was partly supported by the Russian Foundation for Basic Research (grant # 15-29-02526), State project # 52 "Morphological and ecophysiological adaptations of insects as a component of biodiversity" (state registration # 01201351183), the Program of the Department of Biological Sciences of the Russian Academy of Sciences "Rational Use of Biological Resources of Russia: Fundamental Bases of Management", and the Program of the Presidium of the Russian Academy of Sciences "Biodiversity of Natural Systems".

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Received March 17, 2015; revised and accepted June 22, 2015