

RESEARCH

Open Access



Far-reaching benefits of the consumption of conspecific eggs by neonate larvae of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae): a case study on an artificial diet

Ya-Nan Hao^{1,2}, Ming-Ling Li^{1,2}, Yu-Ping Gou^{1,2} and Yuan-Xing Sun^{1,2*}

Abstract

Background The consumption of conspecific eggs by neonate larvae is a common behavior in aphidophagous coccinellids. However, it is still unknown what far-reaching benefits can be brought to the artificial diet-reared cannibals and whether the age of eggs and/or ovipositing parents can affect the cannibals' fitness. Here, the multicolored Asian ladybird beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) was used as a research model because it exhibits much stronger cannibalism behavior than other beetles. Nine types of eggs, varying according to parental age at oviposition and egg age per se, were respectively provided as foods for *H. axyridis* neonate larvae until they developed to 2nd instar. After that, the larvae were fed on an artificial diet and whether egg consumption by neonate larvae had far-reaching benefits was evaluated. Those larvae that directly fed on artificial diet since hatching were served as control.

Results Compared with the control beetles, the cannibal beetles (with few exceptions) had significantly higher 2nd instar-adult survivals (61.1–75.7% vs. 34.3%) and greatly shortened 2nd instar-adult duration (22.7–24.6 days vs. 27.8 days). At adult emergence, the female cannibal beetles (with few exceptions) had significantly higher fresh weights than the control beetles (14.5–16.3 mg vs. 11.7 mg). Among the nine types of cannibals, non-significant difference was detected in almost all the measured developmental parameters.

Conclusion Consumption of conspecific eggs by neonate larvae of *H. axyridis* had far-reaching benefits for their subsequent development on artificial diet, and neither the egg age nor parental age at oviposition affects the cannibals' fitness. These findings provided new insights into the combined application of conspecific eggs and artificial diets in the mass rearing of coccinellids.

Keywords *Harmonia axyridis*, Egg cannibalism, Parental age at oviposition, Egg age, Artificial diet

Background

The consumption of eggs by conspecific individuals is a common phenomenon in many insect species (Wu et al. 2021). Insect eggs are defenseless and abundant in digestible proteins and lipids that make them ideal prey (Bayoumy and Michaud 2015). For aphidophagous ladybird beetles, females usually lay eggs not close to an aphid colony, and the predation ability of newly hatched larvae is relatively weak (Hemptinne et al. 2000). The neonate

*Correspondence:

Yuan-Xing Sun
sunyx1988@126.com

¹ College of Plant Protection, Gansu Agricultural University,
Lanzhou 730070, Gansu, China

² BioControl Engineering Laboratory of Crop Diseases and Pests of Gansu
Province, Lanzhou 730070, Gansu, China

larvae therefore commonly consume conspecific eggs that are not hatched synchronously as their first meal (Osawa 1989). Many studies have shown that egg consumption can bring extensive influences on the cannibalistic ladybirds, for instance, affecting developmental rate, immature survival, adult body size, and even reproductive capabilities (Bayoumy and Michaud 2015). For example, after cannibalizing conspecific eggs at neonate larva stage, *Coccinella transversalis* Fabricius (Omkar and Gupta 2007) and *Hippodamia convergens* Guerin-Meneville (Bayoumy and Michaud 2015) obtained accelerated larval developmental rates and larger adult body size; a faster developmental rate was also observed in the cannibalistic larvae of *Menochilus sexmaculatus* (Fabricius) (Singh et al. 2020). The far-reaching benefits of egg consumption by neonate larvae were mostly evaluated on high-quality natural or alternative prey and not concerned the background of egg victims. It is still unknown what far-reaching benefits can be brought to the artificial diet-reared cannibals and whether the egg age and/or parental age at oviposition can affect the cannibals' fitness.

Studies have shown that the nutrients in eggs might vary greatly according to parental ages at oviposition and/or egg ages per se. For example, it has been reported that proteins in *Eupelmus vuilletti* (CRW) eggs (Giron and Casas 2003) and lipids in *Musca domestica* L. eggs (McIntyre and Gooding 2000) decreased with the increase of parental age at oviposition; while in *Adalia bipunctata* (L.) eggs, the lipid and glycogen strongly declined with the increase of egg age (Sloggett and Lorenz 2008).

The multicolored Asian ladybird beetle *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), a predator of various aphid species, is an important biocontrol agent (Brown et al. 2008), but also a successful invader throughout the world (Camacho-Cervantes et al. 2017). It has been reported that *H. axyridis* exhibits much stronger cannibalistic behavior than many other aphidophagous ladybird species (Reznik et al. 2017). Studies have shown that *H. axyridis* has an age-specific fecundity consistent with the curves of Bieri model (Lanzoni et al. 2004), i.e. the daily oviposition first increased with age and reaches to the highest on day 12–20, and then decreased (e.g. about 20 eggs on day 40 and less than 10 eggs on day 80) (Lanzoni et al. 2004). Here, it was doubted whether maternal investments of *H. axyridis* in eggs varied according to parental ages at oviposition, and whether consumption of different types of eggs would bring different benefits to the cannibals.

In this study, *H. axyridis* neonate larvae were provided with different types of conspecific eggs and then, a series of developmental parameters were measured to explore the far-reaching benefits on the cannibals feeding on

artificial diets. The results of this study may provide new insights into the combined application of conspecific eggs and artificial diets in the mass rearing of coccinellids.

Methods

Insects and plant materials

Six pairs of *H. axyridis* f. *succinea* adults (reddish background with dark spots on elytra) were collected from an alfalfa field in May 2017 in Lanzhou, Gansu province (36° 03' 00" N, 103° 07' 03" E). They were continuously reared on the green peach aphid, *Myzus persicae* (Sulz.), infesting on chili pepper seedlings, *Capsicum frutescens* L., in a nylon cage (50 × 50 × 50 cm) in the laboratory at Gansu Agricultural University, China. These laboratory colony of *H. axyridis* were maintained for more than 2 years by almost six pairs in each generation. In order to reduce the risk of inbreeding depression, the larvae used for maintaining laboratory colonies were collected randomly from the offspring of six pairs of parents. All insects were reared in bioclimatic chambers at 25 ± 1 °C with 65% RH and 14 L: 10 D photoperiod.

Preparation of egg prey

Step 1, newly produced egg clusters were collected from the laboratory colony of *H. axyridis* and they were incubated in 3 cm Petri dishes. An immersed cotton ball was supplied to ensure humidity. Three days later, 20 randomly selected newly hatched *H. axyridis* larvae were reared in 3 cm Petri dishes with one in each dish. They were fed on daily refreshed *M. persicae* infesting on a pepper leaf, until pupation. Adult emergence was monitored every 12 h. The newly emerged adults were respectively collected and every 2 pairs were reared in one Petri dish (9 cm in diameter) for producing eggs with varying parental ages at the same period. Sufficient *M. persicae* infesting on pepper leaves were provided as food each day. Step 2, their eggs were collected when they developed to certain ages, i.e. 20–25 days old (namely young adults and abbreviated as Yng), 40–45 days old (namely middle-aged adults and abbreviated as Mid), and 80–85 days old (namely old adults and abbreviated as Old). Basing on the curves of Bieri model that fits the age-specific fecundity, egg production of *H. axyridis* decreased to a low level at the age of 80 (Lanzoni et al. 2004). To produce sufficient eggs, four pairs of adults were reared for Yng and Mid groups, respectively, and eight pairs were used for Old group. During egg collection, the oviposition was monitored twice a day at an interval of 12 h. The eggs of each group were carefully collected by a fine brush and mixed together. Step 3, the eggs in each group were divided into three subgroups with different in vitro developmental ages, i.e. age 1 (fresh), age

2 (incubated for 1 day), age 3 (incubated for 2 days). Above egg ages were decided basing on the characteristics that the average egg duration of *H. axyridis* was 2.8 days (Lanzoni et al. 2004). During incubation, the eggs were placed in a 9 cm plastic Petri dish with an immersed cotton ball to ensure humidity, and they were maintained at 25 ± 1 °C with 65% RH and 14 L: 10 D photoperiod (Fig. 1). These procedures were conducted from February to June, 2020.

Based on the above design, nine types of eggs varying according to parental ages at oviposition and egg ages per se were obtained, and they were named following the combination of the two factors, i.e. Yng-1, Yng-2, Yng-3, Mid-1, Mid-2, Mid-3, Old-1, Old-2, and Old-3. These eggs were separately provided as food for *H. axyridis* neonate larvae that resulted in nine cannibal treatments (Fig. 1).

Preparation of cannibals' neonate larvae

Another ten newly hatched larvae were reared on *M. persicae* until pupation, and two pairs of newly emerged adults were selected and reared on *M. persicae* infesting on pepper leaves in a 9 cm Petri dish. Eggs of 20–25 days old adults were collected and incubated in a new 9 cm Petri dish following the methods described above. The newly hatched larvae were subsequently

provided with eggs or directly with artificial diet in following experiments (Fig. 1).

Egg consumption by neonate larvae

Neonate larvae (before dispersal and not consuming any eggs) were kept individually in a 3 cm plastic Petri dish with an immersed cotton ball to ensure humidity and provide water. Two eggs from each of the nine types were provided as a daily dietary for one neonate larvae because our preliminary experiment found that each first instar larva can consume 2–3 eggs per day. The larvae were fed on eggs for 2 days until they developed to 2nd instar and were then reared on artificial diets. Those neonate larvae fed directly on the artificial diets were used as control (Fig. 1). In total, 35–37 larvae were reared for each of the nine egg consumption treatments and the control treatment.

Performance of cannibal beetles on artificial diet

The artificial diet used in this study was prepared according to the methods described by Sun et al. (2018) with the following components: fine pork liver powder (10.0 g), yeast extract (1.0 g), sucrose (2.0 g), honey (1.0 g), linseed oil + olive oil (1.9 ml, 1: 1.4 ratio by volume), potassium sorbate solution (1.0 ml, 17 mg/ml in distilled water), and distilled water (15.0 ml). The 2nd instar cannibalistic larvae or 1st instar control larvae were individually placed in a 3 cm Petri dish, and a diet patch was

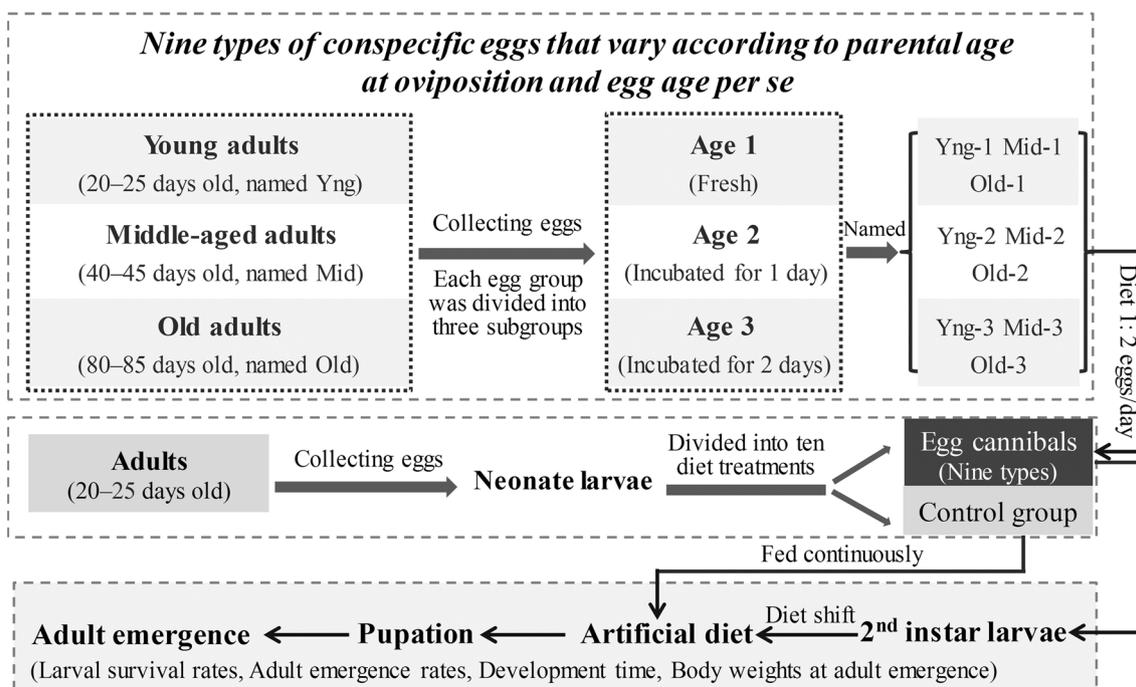


Fig. 1 The flow diagram of experimental design

provided and refreshed every other day. An immersed cotton ball was supplied to provide water. The developmental stages of the larvae were monitored once a day and the survival rates of 2nd–3rd instar, 2nd–4th instar, 2nd instar-pupa, and 2nd instar-adult as well as the emergence rates of pupa-adult were determined. The survival rates were calculated following the equation: number of living individuals at each stage/total number of 2nd instar larvae × 100%; the emergence rate was calculated as number of adults/number of pupae × 100%. Meanwhile, the developmental time of each stage was recorded (days from one stage to the next stage), and the duration of 2nd–4th instar and 2nd instar-adult were also calculated (Fig. 1). After eclosion, the body weights of newly emerged adults (approximately 24 h old) were measured using an AE224C electronic balance (SDPTOP, China).

Data analysis

All statistical analyses were performed with R 4.0.2. First, the differences between each of the nine egg consumption treatments and the control treatment were compared to evaluate what fitness benefits had been obtained by the cannibal beetles. General linear models with binomial distribution (link=“logit”) were performed for the survival rates and the emergence rates of pupa-adult. In these models, the proportion of survived individuals and the two treatments were served as response variables and explanatory variables, respectively. For the

developmental time and body weights of newly emerged adults, a *t* test was used. Second, whether the two factors (parental age at oviposition and egg age per se) and their interactions had significant effects on cannibals’ fitness were further analyzed. General linear models with binomial distribution (link=“logit”) were performed for survivals and adult emergence rates, and the proportion of survived individuals and the two factors with interaction were used as response variables and explanatory variables, respectively. For developmental time and body weights, two-way analysis of variance (ANOVA) was utilized. Before analysis, the data of developmental time were log10 transformed to meet the normal distribution, but untransformed data were presented. For ANOVA, means were separated using Tukey’s HSD test (*p* < 0.05).

Results

Survivals

Compared with the control beetles, the cannibal beetles had significantly higher 2nd–3rd instar survivals ($\chi^2=4.205-4.466$, *df*=1, *p*=0.035–0.040), 2nd instar-adult survivals (except Yng-3, 61.1–75.7% vs. 34.3%) ($\chi^2=5.182-12.864$, *df*=1, *p*=0.0003–0.023) (Fig. 2A), and significantly higher pupa-adult emergence rates (except Yng-3 and Mid-3, 76.5–92.6% vs. 48.0%) ($\chi^2=5.105-13.604$, *df*=1, *p*=0.0002–0.024) (Fig. 2B). During the pre-imaginal development, the cannibal beetles Old-1, Old-2, Old-3, Yng-1 and Yng-3

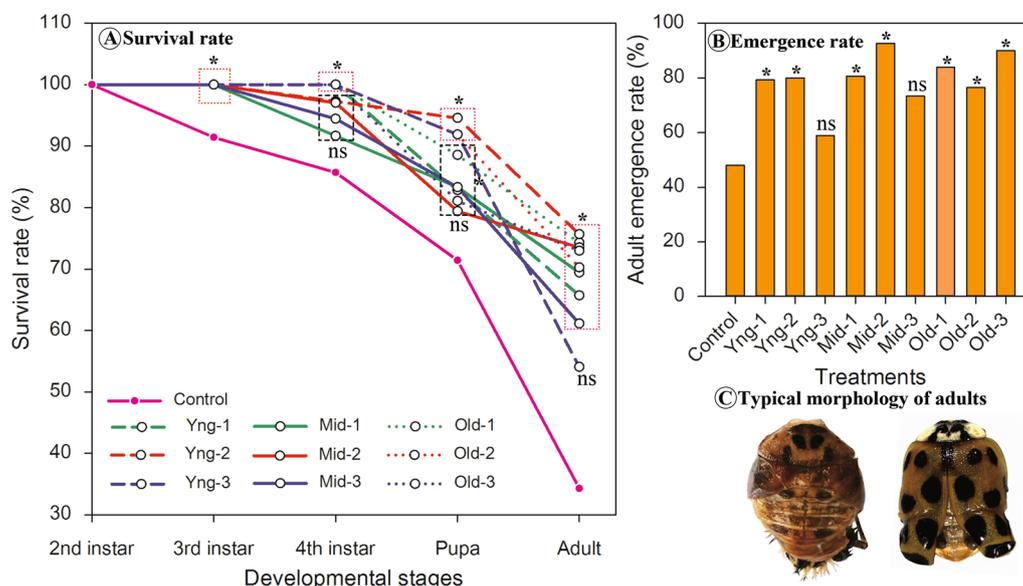


Fig. 2 Performance of *Harmonia axyridis* cannibals when feeding on artificial diets. Stage-specific survivals (A) and the pupa-adult emergence rates (B). Here, the typical morphology of unsuccessfully emerged pupa (left) and the malformed newly emerged adults (right) was highlighted (C). Asterisk indicates a significant difference between the egg cannibal beetles and the control beetles at each stage (*p* < 0.05), while ns means non-significant difference (*p* > 0.05). For stage-specific survivals (A), those treatments in the same box with dotted line had similar variation trends as compared to the control treatment, and they were labelled with shared symbol

had significantly higher 2nd–4th instar survivals than the control beetles ($\chi^2=7.316-7.609$, $df=1$, $p=0.006-0.007$); the cannibal beetles Yng-2, Yng-3 and Old-2 had significantly higher 2nd instar-pupa survivals than the control beetles ($\chi^2=5.299-7.441$, $df=1$, $p=0.006-0.021$) (Fig. 2A). In the experiments, a large proportion of pupae in the control treatment either died or emerged was found as malformed adults, and their typical morphologies were shown in Fig. 2C.

As for the two factors that probably brought different effects on the cannibal beetles, neither parental ages at oviposition nor egg ages per se significantly affected the cannibals' survivals of 2nd–3rd instar, 2nd instar-pupa, 2nd instar-adult or emergence rate of pupa-adult (parental age at oviposition: $\chi^2=0-4.100$, $df=2$, $p=0.129-1.000$; egg age: $\chi^2=0-2.857$, $df=2$, $p=0.240-1.000$), and these two factors had also non-significant interaction effect ($\chi^2=0-7.931$, $df=4$, $p=0.094-1.000$). For the development from 2nd instar to 4th instar, only parental age at oviposition significantly affected the survivals ($\chi^2=9.997$, $df=2$, $p=0.007$), and neither egg ages nor their interaction with parental ages at oviposition caused significant influence (egg ages: $\chi^2=0.270$, $df=2$, $p=0.874$; interaction: $\chi^2=2.900$, $df=4$, $p=0.575$) (Fig. 2).

Developmental time

Compared with the control beetles, all cannibal beetles had significantly shortened developmental time of 2nd–3rd instar (2.1–2.6 days vs. 4.4 days) ($t=9.776-13.807$, $df=1$, $p<0.001$), 2nd–4th instar (6.8–8.0 days vs. 10.2 days) ($t=6.387-10.763$, $df=1$, $p<0.001$) and 2nd instar-adult (22.7–24.6 days vs. 27.8 days) ($t=3.096-5.297$, $df=1$, $p\leq 0.005$); most cannibal beetles also had significantly shortened developmental time of 3rd–4th instar (except Yng-2, Yng-3 and Mid-2; $t=2.256-3.724$, $df=1$, $p=0.0004-0.028$) and 4th instar-pupa (except Yng-3 and Old-2; $t=2.561-5.339$, $df=1$, $p\leq 0.013$). However, all cannibal beetles had similar developmental

time of pupa-adult as compared to the control beetles ($t=-1.975$ to -0.120 , $df=1$, $p=0.059-0.905$) (Table 1).

Neither parental ages at oviposition nor egg ages per se significantly affected the cannibals' developmental time of 4th instar-pupa, or pupa-adult, or from 2nd instar-adult (parental ages at oviposition: $F_{2, 213-271}=0.699-2.707$, $p=0.069-0.489$; egg age: $F_{2, 213-271}=0.132-2.473$, $p=0.086-0.877$). In addition, these two factors had non-significant interaction effect on the developmental time of 4th instar-pupa ($F_{4, 271}=1.714$, $p=0.147$) and 2nd instar-adult ($F_{4, 213}=1.153$, $p=0.332$). In other development stages, the developmental time of 2nd–3rd instar was only significantly affected by egg ages ($F_{2, 315}=6.334$, $p=0.002$), while the developmental time of 3rd–4th instar and 2nd–4th instar was only significantly affected by parental ages at oviposition (3rd–4th instar: $F_{2, 308}=8.956$, $p<0.001$; 2nd–4th instar: $F_{2, 307}=8.882$, $p<0.001$). Specifically, cannibal beetles consuming eggs that had been incubated for 1 day (age 2) generally had shorter developmental time of 2nd–3rd instar than those consuming eggs that had been incubated for 2 days (age 3); cannibal beetles consuming eggs that produced by Old-group parents generally had shorter developmental time of 3rd–4th instar and 2nd–4th instar than those consuming eggs that produced by Yng-group parents (Table 1).

Body weight of newly emerged adults

Compared with the control beetles, the female cannibal beetles (except Yng-3, Mid-2, and Old-1) had significantly higher fresh weights in adulthood ($t=-3.993$ to -2.489 , $df=1$, $p=0.002-0.029$); however, all male cannibal beetles only had slightly higher body weights ($t=-1.495$ to -0.096 , $df=1$, $p=0.162-0.926$). In addition, neither parental ages at oviposition (female: $F_{2, 109}=0.010$, $p=0.990$; male: $F_{2, 92}=0.072$, $p=0.930$) nor egg ages per se (female: $F_{2, 109}=0.136$, $p=0.873$; male: $F_{2, 92}=0.474$, $p=0.624$) significantly affected the cannibals' body weights. Meanwhile, there was non-significant interaction effect between these two factors (female:

Table 1 Developmental time (days ± SE) of *Harmonia axyridis* cannibals when feeding on artificial diets

	Control	Yng-1	Yng-2	Yng-3	Mid-1	Mid-2	Mid-3	Old-1	Old-2	Old-3
2nd–3rd instar	4.4 ± 0.2	2.3 ± 0.1*	2.1 ± 0.1*	2.6 ± 0.1*	2.2 ± 0.1*	2.1 ± 0.1*	2.3 ± 0.1*	2.3 ± 0.1*	2.1 ± 0.1*	2.4 ± 0.1*
3rd–4th instar	5.8 ± 0.2	5.1 ± 0.2*	5.7 ± 0.3 ns	5.5 ± 0.2 ns	4.8 ± 0.2*	5.5 ± 0.2 ns	5.0 ± 0.2*	4.8 ± 0.2*	4.7 ± 0.2*	4.9 ± 0.2*
4th instar-pupa	13.8 ± 0.5	11.3 ± 0.6*	12.0 ± 0.6*	12.9 ± 1.0 ns	10.1 ± 0.5*	11.0 ± 0.4*	11.4 ± 0.5*	11.0 ± 0.5*	12.7 ± 0.9 ns	10.2 ± 0.4*
Pupa-adult	5.3 ± 0.3	5.6 ± 0.2 ns	5.4 ± 0.1 ns	5.3 ± 0.2 ns	5.4 ± 0.2 ns	6.2 ± 0.3 ns	5.3 ± 0.2 ns	5.5 ± 0.1 ns	5.3 ± 0.1 ns	5.8 ± 0.2 ns
2nd–4th instar	10.2 ± 0.3	7.5 ± 0.2*	7.8 ± 0.3*	8.0 ± 0.2*	7.1 ± 0.2*	7.4 ± 0.3*	7.2 ± 0.2*	7.1 ± 0.2*	6.8 ± 0.2*	7.3 ± 0.2*
2nd instar-adult	27.8 ± 0.9	23.9 ± 0.8*	23.9 ± 0.5*	23.4 ± 0.6*	22.7 ± 0.5*	24.6 ± 0.7*	23.2 ± 0.6*	23.3 ± 0.4*	23.0 ± 0.7*	23.0 ± 0.5*

Asterisk in each row indicates a significant difference between the cannibal beetles and the control beetles ($p < 0.05$), while ns means non-significant difference ($p > 0.05$)

Table 2 Body weights (mg ± SE) of newly emerged female and male adults of *Harmonia axyridis* when feeding on artificial diets

	Control	Yng-1	Yng-2	Yng-3	Mid-1	Mid-2	Mid-3	Old-1	Old-2	Old-3
Female	11.7 ± 0.9	16.3 ± 0.7*	14.5 ± 0.6*	14.0 ± 1.5 ns	15.4 ± 0.8*	14.2 ± 0.8 ns	15.5 ± 0.7*	13.8 ± 0.8 ns	16.1 ± 1.0*	15.2 ± 0.7*
Male	12.1 ± 0.9	13.6 ± 0.9 ns	13.3 ± 0.6 ns	13.5 ± 0.8 ns	13.9 ± 0.9 ns	12.2 ± 0.7 ns	13.9 ± 0.9 ns	13.4 ± 0.7 ns	13.3 ± 0.9 ns	13.2 ± 0.7 ns

Asterisk in each row indicates a significant difference between the cannibal beetles and the control beetles ($p < 0.05$), while ns means non-significant difference ($p > 0.05$)

$F_{4, 109} = 2.276$, $p = 0.066$; male: $F_{4, 92} = 0.363$, $p = 0.834$ (Table 2).

Discussion

Egg cannibalism is considered to be an adaptive response under resource-limited conditions (Khodaei and Long 2020). In this study, egg consumption by neonate larvae of *H. axyridis* greatly favored their subsequent development on artificial diets. Compared with the control beetles, almost all cannibal beetles had significantly increased 2nd instar-adult survivals (61.1–75.7% vs. 34.3%) and significantly reduced 2nd instar-adult durations (22.7–24.6 days vs. 27.8 days). In particular, egg consumption had prominent far-reaching benefits in the survivals of the last developmental stage, i.e. the pupa-adult emergence rates of most cannibal beetles (76.5–92.6%) were significantly higher than those of the control beetles (48.0%).

The insect-free artificial diets of many predatory ladybird beetles have been shown to be inferior in nutrition (Sun et al. 2017). Here, when directly feeding on artificial diets (control beetles), a large proportion of pupae (52%) died or emerged as deformed adults. Similarly, low survivals at adulthood were commonly observed in other artificial diet-fed ladybird beetles, e.g. *Coccinella septempunctata* L. (Sarwar and Saqib 2010), *Eriopis connexa* (Germar) (Silva et al. 2009), and *Cleobora mellyi* (Mulsant) (Bain et al. 1984). However, when several conspecific eggs were consumed by the neonate larvae (cannibal beetles), 75% of the pupae successfully emerged as normal adults. The metamorphosis development from pupa to adult is a complex biochemical process (Damos et al. 2011). Here, except for supplying essential nutrients, other components in eggs, such as carotenoids (Winters et al. 2014), alkaloids (e.g. (-)-adalinine) (Paul et al. 2018), etc. might also play vital roles. For example, one previous study has revealed that supplementation of β -carotene in artificial diet can greatly improve the 1st instar-adult survivals of *H. axyridis* (Sun et al. 2018). At adult emergence, the body weights of female cannibal beetles (except Yng-3, Mid-2, and Old-1) were significantly higher than those of the control beetles. Adult body size is an important factor that determines the fitness of insects, including survival, mating success or fecundity (Kemp et al. 2006).

Therefore, the cannibal beetles should have a superior reproductive performance than the control beetles.

The variation in the ages of eggs and ovipositing parents did not cause a great difference in the fitness of cannibals. For the nine groups of cannibal beetles, their pre-imaginal survivals (except for the 2nd–4th instar survivals) and developmental time of 2nd instar-adult, 4th instar-pupa and pupa-adult were not significantly affected by the above two factors. Finally, all cannibal beetles had similar fresh weights in adulthood. From these, it can be deduced that all egg victims had similar contents of nutrients and/or other non-nutritional components. Although the contents of some species may vary according to parental age at oviposition and/or egg age (Sloggett and Lorenz 2008), functional mutual indemnification of different compounds would contribute to the nearly undifferentiated benefits of different egg victims. In *A. bipunctata*, with the increase of egg ages, the lipid and glycogen contents gradually declined, whereas the free carbohydrate contents increased (Sloggett and Lorenz 2008); in eggs of *C. septempunctata*, the total concentration of carotenoids increased with the increase of parental age at oviposition (Winters et al. 2014).

Conclusions

The results demonstrated that providing several conspecific eggs for the neonate larvae might be a suitable approach for rearing *H. axyridis* larvae with artificial diets. More importantly, the background of egg victims (i.e. egg ages and parental ovipositing ages) was not required to be concerned.

Abbreviations

Yng-1	<i>Harmonia axyridis</i> cannibals which fed on fresh eggs produced by young adults (20–25 days old)
Yng-2	<i>Harmonia axyridis</i> cannibals which fed on eggs produced by young adults (20–25 days old) and incubated for 1 day
Yng-3	<i>Harmonia axyridis</i> cannibals which fed on eggs produced by young adults (20–25 days old) and incubated for 2 days
Mid-1	<i>Harmonia axyridis</i> cannibals which fed on fresh eggs produced by middle-aged adults (40–45 days old)
Mid-2	<i>Harmonia axyridis</i> cannibals which fed on eggs produced by middle-aged adults (40–45 days old) and incubated for 1 day
Mid-3	<i>Harmonia axyridis</i> cannibals which fed on eggs produced by middle-aged adults (40–45 days old) and incubated for 2 days

- Old-1 *Harmonia axyridis* cannibals which fed on fresh eggs produced by old adults (80–85 days old)
- Old-2 *Harmonia axyridis* cannibals which fed on eggs produced by old adults (80–85 days old) and incubated for 1 day
- Old-3 *Harmonia axyridis* cannibals which fed on eggs produced by old adults (80–85 days old) and incubated for 2 days

Acknowledgements

We are grateful for the assistance of all staff and students in the Biocontrol Engineering Laboratory of Crop Diseases and Pests of Gansu Province, College of Plant Protection, Gansu Agricultural University, Lanzhou, China.

Author contributions

YXS and YNH planned the research project, wrote, revised, and edited the manuscript; MLL helped to conduct the experiments and wrote the manuscript; YPG made revisions to the manuscript. All authors have read and agreed to the final version of the manuscript.

Funding

This research was financed by the the National Natural Science Foundation of China (31960561), the Youth Natural Science Foundation of Gansu Province (21JR7RA848), the Funds for Fuxi Young Scientific Talents of Gansu Agricultural University (Gaufx-03Y05). These funders supported the trips for collection insects and provided all materials used in preparation rearing units and rearing insects.

Availability of data and materials

The datasets generated and analyzed during the current study are available in the fgshare repository, <https://doi.org/10.6084/m9.figshare.20782048.v1>

Declarations

Ethics approval and consent to participate

The materials used in this study were ethical approval and consent to participate.

Consent for publication

All authors have read and agreed to the submission of the final version of the manuscript.

Competing interests

The authors declare no conflict of interest.

Received: 2 September 2022 Accepted: 21 February 2023

Published online: 26 February 2023

References

- Bain J, Singh P, Ashby M, Van Boven R (1984) Laboratory rearing of the predatory coccinellid *Cleobora mellyi* [Col.: Coccinellidae] for biological control of *Paropsis charybdis* [Col.: Chrysomelidae] in New Zealand. *Entomophaga* 29(2):237–244. <https://doi.org/10.1007/BF02372111>
- Bayoumy MH, Michaud JP (2015) Egg cannibalism and its life history consequences vary with life stage, sex, and reproductive status in *Hippodamia convergens* (Coleoptera: Coccinellidae). *J Econ Entomol* 108(4):1665–1674. <https://doi.org/10.1093/jee/148>
- Brown PMJ, Adriaens T, Bathon H, Cuppen J, Goldarazena A, Hägg T, Kenis M, Klausnitzer BEM, Kovář I, Loomans AJM, Majerus MEN, Nedved O, Pedersen J, Rabitsch W, Roy HE, Ternois V, Zakharov IA, Roy DB (2008) *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. *Biocontrol* 3(1):5–21. <https://doi.org/10.1007/s10526-007-9132-y>
- Camacho-Cervantes M, Ortega-Iturriaga A, Del-Val E (2017) From effective biocontrol agent to successful invader: the harlequin ladybird (*Harmonia axyridis*) as an example of good ideas that could go wrong. *PeerJ* 5:e3296. <https://doi.org/10.7717/peerj.3296>
- Damos P, Papadopoulos N, Rigas A, Savopoulou-Soultani M (2011) Energetic loads and informational entropy during insect metamorphosis: measuring structural variability and self-organization. *J Theor Biol* 286:1–12. <https://doi.org/10.1016/j.jtbi.2011.06.029>
- Giron D, Casas J (2003) Mothers reduce egg provisioning with age. *Ecol Lett* 6(4):273–277. <https://doi.org/10.1046/j.1461-0248.2003.00429.x>
- Hemphill JL, Gaudin M, Dixon AFG, Lognay G (2000) Social feeding in ladybird beetles: adaptive significance and mechanism. *Chemoecology* 10(3):149–152. <https://doi.org/10.1007/PL00001817>
- Kemp DJ, Alcock J, Allen GR (2006) Sequential size assessment and multi-component decision rules mediate aerial wasp contests. *Anim Behav* 71(2):279–287. <https://doi.org/10.1016/j.anbehav.2005.03.038>
- Khodaei L, Long TAF (2020) Kin recognition and egg cannibalism by *Drosophila melanogaster* larvae. *J Insect Behav* 33(1):20–29. <https://doi.org/10.1007/s10905-020-09742-0>
- Lanzoni A, Accinelli G, Bazzocchi G, 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(4):298–306. <https://doi.org/10.1111/j.1439-0418.2004.00847.298-306>
- McIntyre G, Gooding R (2000) Egg size, contents, and quality: maternal-age and -size effects on house fly eggs. *Can J Zool* 78:1544–1551. <https://doi.org/10.1139/z00-086>
- Omkar PA, Gupta A (2007) Sibling cannibalism in aphidophagous ladybirds: its impact on sex-dependent development and body weight. *J Appl Entomol* 131(2):81–84. <https://doi.org/10.1111/j.1439-0418.2006.01133.x>
- Osawa N (1989) Sibling and non-sibling cannibalism by larvae of a lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in the field. *Res Popul Ecol* 31(1):153–160. <https://doi.org/10.1007/BF02515813>
- Paul SC, Stevens M, Burton J, Pell JK, Birkett MA, Blount JD (2018) Invasive egg predators and food availability interactively affect maternal investment in egg chemical defense. *Front Ecol Evol* 6:4. <https://doi.org/10.3389/fevo.2018.00004>
- Reznik SY, Belyakova NA, Ovchinnikov AN, Ovchinnikova AA (2017) The influence of density-dependent factors on larval development in native and invasive populations of *Harmonia axyridis* (Pall.) (Coleoptera, Coccinellidae). *Entomol Rev* 97(7):847–852. <https://doi.org/10.1134/S0013873817070016>
- Sarwar M, Saqib SM (2010) Rearing of predatory seven spotted ladybird beetle *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) on natural and artificial diets under laboratory conditions. *Pak J Zool* 42(1):47–51
- Silva RB, Zanuncio JC, Serrão JE, Lima ER, Figueiredo MLC, Cruz I (2009) Suitability of different artificial diets for development and survival of stages of the predaceous ladybird beetle *Eriopis connexa*. *Phytoparasitica* 37:115–123. <https://doi.org/10.1007/s12600-008-0015-2>
- Singh S, Mishra G, Omkar, (2020) Ladybird, *Menocheilus sexmaculatus* (Fabricius) can survive on oophagy but with altered fitness than aphidophagy. *Curr Sci* 118(10):1602–1608. <https://doi.org/10.18520/cs/v118/10/1602-1608>
- Sloggett JJ, Lorenz MW (2008) Egg composition and reproductive investment in aphidophagous ladybird beetles (Coccinellidae: Coccinellini): egg development and interspecific variation. *Physiol Entomol* 33(3):200–208. <https://doi.org/10.1111/j.1365-3032.2008.00622.x>
- Sun YX, Hao YN, Riddick EW, Liu TX (2017) Factitious prey and artificial diets for predatory lady beetles: current situation, obstacles, and approaches for improvement: a review. *Biocontrol Sci Techn* 27(5):601–619. <https://doi.org/10.1080/09583157.2017.1324112>
- Sun YX, Hao YN, Liu TX (2018) A β -carotene-amended artificial diet increases larval survival and be applicable in mass rearing of *Harmonia axyridis*. *Biol Control* 123:105–110. <https://doi.org/10.1016/j.biocontrol.2018.04.010>
- Winters AE, Stevens M, Mitchell C, Blomberg SP, Blount JD (2014) Maternal effects and warning signal honesty in eggs and offspring of an aposematic ladybird beetle. *Funct Ecol* 28(5):1187–1196. <https://doi.org/10.1111/1365-2435.12266>
- Wu SL, Zeng WA, Deng W, Li M, Hu W, Cai HL, Li YZ, Xie PF, Tan L, Zhou ZC (2021) Egg cannibalism varies with sex, reproductive status, and egg and nymph ages in *Arma custos* (Hemiptera: Asopinae). *Front Ecol Evol* 9:705318. <https://doi.org/10.3389/fevo.2021.705318>

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.