



Harmonia axyridis Does Not Have Obvious Fitness Gain and Preference to the Red Morph of *Acyrtosiphon pisum*: A Case Study on a Laboratory Strain

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Prey selection was assumed to be a vital strategy to maximize the fitness of predators. Visual cues are important for predators to locate a prey, and several species of lady beetles have been reported to prefer the red morph pea aphid *Acyrtosiphon pisum* rather than the green morph in empty containers with different colors. However, the preference of a predator on the red and green color morphs of *A. pisum* on green plant leaves and the relationship between the fitness of the predator that feeds on the two color morphs have not been revealed. In this study, two colonies of the multicolored Asian lady beetle, *Harmonia axyridis*, a generalist predator, fed on a red morph and a green morph of *A. pisum* (indicated as RA-Har and GA-Har, respectively) were used to determine their prey preferences on the two morphs of *A. pisum* on leaf discs. The fourth instars and newly emerged adults of *H. axyridis* that fed on the two aphid morphs did not show any significant prey preference, except that GA-Har males consumed significantly more green morph than red morph. The fitness of RA-Har and GA-Har, including larval development and body weights of the fourth instars and the newly emerged female adults were not significantly different, and so were the predation capability and fecundity. However, RA-Har had significantly greater larval hatch rate than GA-Har, and tended to produce more eggs on cage walls or plant pots than on broad bean leaves in the cage assays. Our results provide evidences that *H. axyridis* did not prefer either morph of *A. pisum*, and also had no significant differences of the fitness. We hope that results from this study will stimulate more studies to reveal the mechanism of colored prey preference of predators.

Keywords: fitness, prey preference, signal, *Harmonia axyridis*, *Acyrtosiphon pisum*, red morph

INTRODUCTION

The optimal foraging theory assumes that prey selection is to maximize the fitness of predators (Stephens and Krebs, 1986). Base on this theory, the predators will make a decision with the optimal balance of caloric and nutritive value and associated foraging costs when several preys are simultaneously presented (Stephens and Krebs, 1986). In addition, visual cues of prey are

important signals for the predators (Bahlai et al., 2008). Coccinellid adults generally have three types of visual receptors (UV, blue, and green) that allow them to respond to wavelengths from 310 to 600 nm (Agee et al., 1990; Lin, 1993). For example, the seven-spotted lady beetle, *Coccinella septempunctata* had high phototactic response rates to ultraviolet (UV) (340 nm) (Zhou et al., 2013). Practically, visual cues have been proved to play important roles in host-finding of many coccinellids (Nakamura, 1984; Hattingh and Samways, 1995; Adedipe and Park, 2010). Several coccinellid species have been shown to prefer aphids that display colors contrast with different environmental backgrounds (Harmon et al., 1998; Mondor and Warren, 2000).

Most research on color morph preference was conducted on the pea aphid, *Acyrtosiphon pisum*, which displays noteworthy color-polymorphism of red and green. The color morphs of *A. pisum* have been proved to be genetically determined, with red being dominant over green (Markkula, 1963; Caillaud and Losey, 2010). Under field conditions, the two morphs of *A. pisum* generally coexisted at a relative stable ratio within a population (Lowe and Taylor, 1964; Balog and Schmitz, 2013). The red morph preference of *C. septempunctata* has been proved to be an important factor to maintain the color-polymorphism of *A. pisum* (Losey et al., 1997; Balog and Schmitz, 2013). However, the color morph preference of predators showed to be variable on different colored backgrounds. For example, in green containers, predation by *C. septempunctata* adults was higher on red morph than on green morph; whereas, in red containers, higher predation was found on green morph, and no difference was detected in white containers (Losey et al., 1997; Harmon et al., 1998). Moreover, preferences of the two morphs of *A. pisum* vastly varied among different coccinellid species. For example, under similar condition as that conducted for *C. septempunctata*, both the adults of *Hippodamia convergens* and *Coleomegilla maculata* had similar predation rates on the two morphs of *A. pisum* (Harmon et al., 1998). However, almost all studies regarded to color morph preference were conducted in empty containers. Actually, to locate a prey on plants, the conditions were much more complicated (e.g., olfactory and gustatory cues could also provide important signals for the coccinellids) (Obata, 1986; Bahlai et al., 2008; Gencer et al., 2009). Thus, the cases of color morph preferences by coccinellids under conditions similar to those on plants needed to be explored.

The multicolored Asian lady beetle, *Harmonia axyridis*, is a generalist predator and mainly an aphidophagous predator, but also feeds on many other soft bodied insects (Koch, 2003; Provost et al., 2006). This lady beetle has been widely introduced into many parts of the world as an important biological control agent (Koch, 2003). For *A. pisum*, *H. axyridis* has been shown to prefer the red morph to the green morph regardless of background coloration in an empty container (Harmon et al., 1998). But whether *H. axyridis* exhibits any preference of the two color morphs of *A. pisum* on green plant leaves has not been explored. In this study, we conducted the prey preference experiments on green leaf discs. In addition, we determined the fitness of *H. axyridis* preying on the two morphs of *A. pisum* because the information may help to understand the color morph preference mechanism of the predator.

MATERIALS AND METHODS

Insects

Harmonia axyridis were obtained from a continuous rearing colony in our laboratory ($24 \pm 1^\circ\text{C}$, 65% RH and 14:10 h L:D). They were reared with the green peach aphid, *Myzus persicae*, infesting on pepper seedlings (*Capsicum annum* fasciculatum, var. "Changfeng"). One pair of newly emerged adults were collected from the laboratory colony and maintained in a plastic Petri dish (9 cm in diameter and 1.5 cm in depth) with sufficient *M. persicae*, and their offspring were used in all subsequent experiments.

The green and red morphs of *A. pisum* were collected from Lanzhou, Gansu, China, and were separately reared on broad bean seedlings (*Vicia faba* L., var. "Jinnong") in different cages ($60 \times 60 \times 45$ cm) in an insectary ($24 \pm 1^\circ\text{C}$, 65% RH and 14:10 h L:D). Eggs laid by the stock pair of *H. axyridis* were collected and incubated in plastic Petri dishes (9 cm in diameter and 1.5 cm in depth). Thirty to forty newly hatched *H. axyridis* larvae in each day were equally separated and raised with one of the two morphs of *A. pisum* in separate cages (these two colonies of *H. axyridis* were named as RA-Har and GA-Har, respectively). Larval development of *H. axyridis* was monitored daily. The pupae (almost 3 days old) were picked out with a fine brush and maintained in plastic Petri dishes (9 cm in diameter and 1.5 cm in depth) until adult emergence. Fifteen pupae were placed in one Petri dish and the detached pupae were re-attached on the bottom surface of Petri dish with double-faced adhesive tapes to maintain the natural dorsal-ventral position of the pupae. To avoid sticking the newly emerged adults, the upper-surface of tapes was gently wiped with a piece of filter paper to decrease the stickiness. The fourth instars and newly emerged adults of RA-Har and GA-Har were used in subsequent experiments. All experiments were conducted in bioclimatic chambers ($24 \pm 1^\circ\text{C}$, 65% RH and 14:10 h L:D).

Color Morph Preference Experiment

Color morph preference of the fourth instars, newly emerged adults (48 h post-emergence) of RA-Har and GA-Har were determined on leaf discs (9 cm in diameter and 1.5 cm in depth) with 20 replicates conducted at five different times, and each replicate had four individuals. The leaf discs were maintained fresh using a thin layer of agar (10 ml, 1% concentration) at the bottom. A hole (1 cm in diameter) on the center of the Petri dish lid was covered with gauze (100 mesh) for ventilation. The leaf disc was cut to fit the bottom of the Petri dish. Twenty adult *A. pisum* were selected from the stock colonies, and were weighted individually using an electronic microbalance (Sartorius MSA 3.6P-000-DM, Gottingen, Germany). The average weight of one red and green morph was about 3.399 ± 0.089 mg and 4.687 ± 0.079 mg, respectively. The aphids were then introduced onto each leaf disc (10 for each morph) and kept in 4°C for 1 h to minimize nymph production and slow down their activity. After a 20-min recovery of the aphids, a fourth instar larva or an adult was introduced onto each leaf disc and was allowed to feed on the aphids for 6 h. Number of aphids of each morph consumed by the predator was recorded.

Fitness Evaluation

Development

Eggs laid by the stock pair of *H. axyridis* were collected and incubated in plastic Petri dishes (3 cm in diameter and 1.5 cm in depth). Newly hatched larvae were individually reared in the plastic Petri dishes with sufficient red or green morph of *A. pisum* (approximately 60 mg for first and second instar larvae, and 200 mg for third and fourth instar larvae) until pupation. Larval development was recorded daily. The fourth instars and newly emerged adults (<24 h) were individually weighted using an electronic balance (Mettler Toledo AL204, Shah Alam Selangor, Malaysia). For each colony, 20 replicates (four individuals by five different times) were measured.

Predation Capacity

The predation capacity of fourth instars and newly emerged adults (48 h post-emergence) of RA-Har and GA-Har was measured on leaf discs as described previously. Ten adult aphids of each morph were selected from the stock colonies and introduced onto a leaf disc. The aphids were kept in 4°C for 1 h to minimize nymph production and slow down the activity. After a 20-min recovery of the aphids, one lady beetle was introduced onto each leaf disc for 6 h, and number of aphids consumed was recorded. A total of 20 lady beetles were used for each colony.

Reproduction

Reproduction of RA-Har and GA-Har was compared using cage experiments in an air-conditioned insectary (24 ± 1°C, 65% RH and 14:10 h L:D). Newly emerged adults (48 h post-emergence) were sexed, and four pairs were introduced into each cage (30 cm in diameter and 45 cm in height). Four broad bean plants (about 30 cm in height) that were infested with *A. pisum* were introduced into each cage (red morph was supplied for RA-Har, and green morph for GA-Har). The infested plants were replaced every 4 days, and egg production of *H. axyridis* was carefully checked daily (female started to lay eggs 6–7 days after emergence). The eggs were gently removed from the attached substance with a water-dampened fine brush (had been confirmed to be no negative effect to the eggs), and then were transferred to plastic Petri dishes (9 cm in diameter and 1.5 cm in depth) with an immersed cotton ball for maintaining moisture. The eggs deposited on broad bean leaves vs. cage walls or plant pots were separately counted and incubated in different Petri dishes. Newly hatched larvae were removed with a fine brush to avoid egg cannibalism. Oviposition of *H. axyridis* was monitored for 10 days, and number of eggs laid was examined daily. The development of eggs was monitored, and the larval hatch rates were calculated following the equation: number of larvae/ total number of eggs × 100%. Five replicates (in total of 20 pairs) were conducted for RA-Har and GA-Har, respectively.

Data Analysis

Mean numbers of red and green morphs consumed by *H. axyridis* in the color morph preference experiment were compared with a paired two-tailed, Student *t*-test ($p < 0.05$). The fitness parameters between GA-Har and RA-Har were compared using the independent sample *t*-test ($p < 0.05$). The data were analyzed

after testing for homogeneity of variances using the Levene test. SPSS (version 20; SPSS Inc., Chicago, IL, USA) was used for all statistical analysis.

RESULTS

Color Morph Preference

When the predators were exposed to both red and green morphs of *A. pisum*, the fourth instars and newly emerged adults (female and male) of RA-Har did not exhibit any preference as shown by the similar numbers of the two morphs of *A. pisum* consumed ($df = 19$, fourth instars: $t = 1.44$, $p = 0.17$; female: $t = -0.99$, $p = 0.34$; male: $t = 0.78$, $p = 0.45$; **Figure 1A**). For GA-Har, the numbers of red and green morphs consumed by the fourth instars and the newly emerged female adults were also not significantly different ($df = 19$, fourth instars: $t = 0.73$, $p = 0.47$; female: $t = 0.12$, $p = 0.91$), while the males showed preference for green over red morph of *A. pisum* ($df = 19$, $t = -2.65$, $p = 0.02$; **Figure 1B**).

Fitness Evaluation

Development

The development times of *H. axyridis* feeding on red or green morph of *A. pisum* were not significantly different at each larval stage, and consequently, the whole pre-imaginal development times of RA-Har and GA-Har were almost the same (**Table 1**). The weights of the fourth instars and the newly emerged female adults of RA-Har also did not significantly differ from those of GA-Har ($df = 38$, fourth instars: $t = 0.30$, $p = 0.77$; female: $t = 0.59$, $p = 0.56$). However, the males of RA-Har were significantly heavier (28.3 mg) than those of GA-Har (26.5 mg) ($df = 38$, $t = 3.04$, $p < 0.01$; **Table 1**).

Predation Capacity

H. axyridis did not show significant differences in consumption between the two color morphs of *A. pisum* ($df = 38$, fourth instars: $t = -1.81$, $p = 0.08$; female: $t = 0.93$, $p = 0.36$; male: $t = 0.31$, $p = 0.76$). Specifically, nearly one aphid was consumed by a fourth instar larva in 1 h, and to be almost 0.9 and 0.7, respectively, for a newly emerged female and male adult (**Figure 2**).

Reproduction

Each RA-Har female oviposited an average of 46 eggs in each day during a period of 10 days, and each GA-Har female oviposited an average of 37 eggs daily during the same period, and there were no significant differences between RA-Har and GA-Har ($df = 8$, $t = 2.10$, $p = 0.07$; **Figure 3A**). However, RA-Har females produced significantly fewer eggs on broad bean leaves than on the cage walls and plant pots (36.8% vs. 63.3%) ($df = 4$, $t = -2.98$, $p = 0.04$), whereas GA-Har oviposited a similar proportion of eggs on broad bean leaves (50.6%) and the cage walls and plant pots (49.4%) ($df = 4$, $t = 0.09$, $p = 0.93$). Of the eggs produced by RA-Har, 59.3% were hatched, which was significantly more than those by GA-Har (48.2%) ($df = 8$, $t = 2.33$, $p = 0.048$; **Figure 3B**).

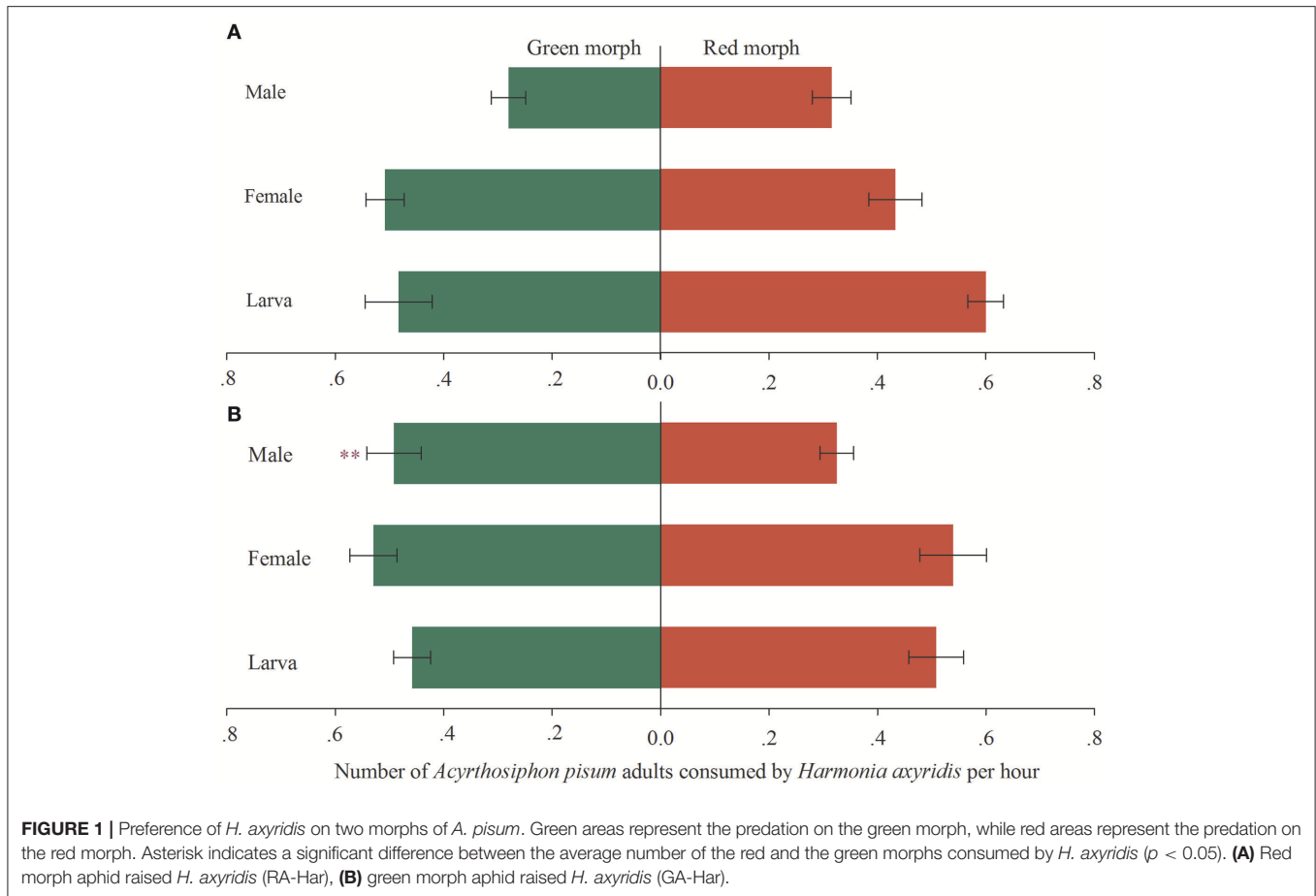


TABLE 1 | Pre-imaginal development time and the weights of fourth instars and newly emerged adults of *H. axyridis*.

<i>H. axyridis</i>	Developmental time (days \pm SE)						Weight (mg \pm SE)		
	1st	2nd	3rd	4th	Pupa	Total	4th larva	Female	Male
RA-Har	2.2 \pm 0.1	1.2 \pm 0.1	1.9 \pm 0.1	3.9 \pm 0.2	5.1 \pm 0.1	14.2 \pm 0.1	32.50 \pm 0.99	31.00 \pm 0.69	28.30 \pm 0.62a
GA-Har	2.1 \pm 0.1	1.2 \pm 0.1	1.8 \pm 0.1	3.9 \pm 0.2	5.1 \pm 0.2	14.1 \pm 0.1	32.00 \pm 1.38	30.50 \pm 0.50	26.50 \pm 1.31b
<i>t</i>	0.467	-0.406	0.312	0	-0.238	0.467	0.283	0.588	3.036
<i>p</i>	0.643	0.487	0.757	1	0.813	0.643	0.770	0.560	0.004

df-value of each treatment was 38. Where no letters exist, no significant differences were recorded. Different letters indicate a significant difference between RA-Har and GA-Har ($p < 0.05$).

DISCUSSION

The fourth instars and newly emerged adults of *H. axyridis*, regardless of which morph of *A. pisum* they fed on, did not exhibit significant color morph preference on either red or green morph. This was different from the results that were found in empty container in previous studies. For example, Harmon et al. (1998) reported that the adults of *H. axyridis* preferred to choose red morph of *A. pisum* in green container. This difference could be caused by the different substrates of an empty container and a leaf disc. As we know, herbivore-induced leaf volatiles and honeydew excreted by aphids when feeding plants usually provide important signals to foraging

predators for location of their prey (Havelka and Syrovatka, 1991; Dicke et al., 1993; Zhu and Park, 2005). However, it seems that these chemical signals were not be used by *H. axyridis* inside a Petri dish due to the short distance, high prey density and weak airflow (Liu and Sengonca, 1994; Pinto et al., 2007). Several other reasons might be considered. Firstly, coccinellid adults generally have several specific types of visual receptors (e.g., UV, blue, and green), and they might only be sensitive to a limited range of light spectrum or wavelengths (Agee et al., 1990; Lin, 1993). The reflect wavelengths of the green broad bean leaves should be different from those of the green container, and the color contrast of the red morph *A. pisum* on the green leaf disc might be undetectable by *H. axyridis*.

Secondly, the red morph of *A. pisum*, especially the adults, exhibited more intense defensive reactions as compared to the green morph (Lowe and Taylor, 1964; Braendle and Weisser, 2001), which are expected to partially compensate its visual attractiveness (Farhoudi et al., 2014). In contrast to the adults, coccinellid larvae do not use their vision to locate prey (Banks, 1954; Storch, 1976; Stubbs, 1980; Hattingh and Samways, 1995). Thus, the fourth instars of *H. axyridis* could not distinguish the difference between the red and green morphs of the aphid. Like other aphid species, the two morphs of *A. pisum* could cause plant foliage becoming yellowish after feeding (Seagraves, 2009; Ramezani et al., 2013), and *H. axyridis* exhibited obvious preference to yellowish plants on which aphids likely occur (Seagraves, 2009; Adedipe and Park, 2010). All these characteristics make *H. axyridis* an effective biological control agent of *A. pisum*.

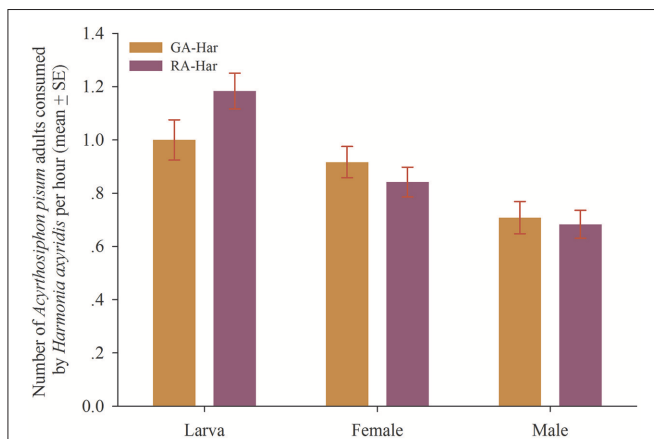


FIGURE 2 | Predation capacity of *H. axyridis* on the red and the green morphs of *A. pisum*. The two lady beetle colonies were named as RA-Har and GA-Har, respectively.

We found that *H. axyridis* feeding on the red and green morphs of *A. pisum* did not have significant differences in developmental time and egg production. Ahsaei et al. (2013) found that the two morphs of *A. pisum* had similar content of total energy reserves. Thus, the two morphs of *A. pisum* seemed to be equal in satisfying the nutritional requirements of development and egg production of *H. axyridis*. However, the larval hatch rate of RA-Har was significantly greater than that of GA-Har, and this difference could be caused by the fact that RA-Har males were heavier or larger than GA-Har males. In insects, adult body size is an important indicator of quality, and large males generally have advantages in mating success over small males (Himuro et al., 2006). It has been reported that the red morph of *A. pisum* had higher percentage of water-soluble carbohydrates and lipids than the green morph which stored a higher percentage of protein than the red morph (Ahsaei et al., 2013). The different compositions of energy reserves of the two morphs of *A. pisum* might result in the differences of body weights of male *H. axyridis*. In fact, the enzyme equipment and nutritional budgets of aphids (Klingauf, 1988; Srivastava, 1988; Dixon, 1998) as well as the nutritive requirements of predators (Eubanks and Denno, 2000) could affect the fitness of predators on an aphid species. For example, *H. axyridis* larvae could not complete their development when fed exclusively on *Megoura viciae*, but successfully developed into adult on *Aphis gossypii*. However, when the first instar *H. axyridis* first fed on *A. gossypii* and then on *M. viciae* in subsequent larval stages, the larvae completed their development, and their adults consumed a greater weight of *M. viciae* than *A. gossypii* (Tsaganou et al., 2004).

We also found that RA-Har females tended to lay their eggs on plant pots and cage walls rather than on broad bean leaves. As we know, coccinellid females prefer to lay eggs on sites where distributed sufficient aphids to ensure the survival of their offspring (Dixon, 1959; Wratten, 1973; Seagraves, 2009). However, when coexist with predators, the red morph of *A. pisum*

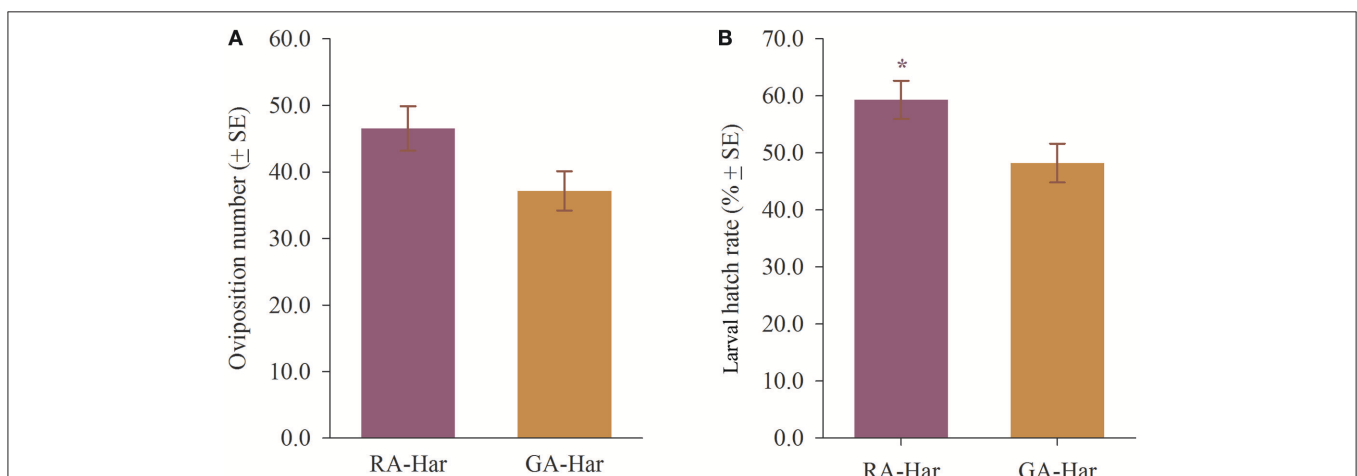


FIGURE 3 | Reproduction of *H. axyridis* on red and green morphs of *A. pisum*. The two lady beetle colonies were named as RA-Har and GA-Har, respectively. (A) Average number of eggs laid by a female, (B) larval hatch rate. Asterisk indicates a significant difference between RA-Har and GA-Har ($p < 0.05$).

drop more frequently than the green morph (Braendle and Weisser, 2001), which might prompt RA-Har females to lay eggs dispersedly. This phenomenon can be regarded as an evolved strategy to improve offspring survival. In addition, *H. axyridis* females could balance the direct distance from a cluster to the nearest aphid colony to decrease the intensity of non-sibling cannibalism (Osawa, 2003). Oviposition-site choice is a major maternal effect which might be affected by many factors (Refsnider and Janzen, 2010). The mechanism of different oviposition-site choice of *H. axyridis* feeding on the two morphs of *A. pisum* remains unclear and needs more studies.

Our study provide sufficient evidences that *H. axyridis* exhibited no-preference on the red morph of *A. pisum* on green leaf disc, which might be due to that feeding on the red morph aphids did not result in greater fitness for *H. axyridis* than those fed on the green morph aphids. These results might encourage more studies to reveal the biological significance of the predators when they exhibit obvious preference for a specific prey.

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Y-XS and T-XL designed research; Y-XS performed research; Y-XS and T-XL wrote the paper.

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