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Impact of fruit feeding on overwintering survival of the multicolored Asian lady beetle, and the ability of this insect and paper wasps to injure wine grape berries

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Abstract

The establishment of the multicolored Asian lady beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in North America has resulted in negative impacts on fruit production. We investigated the overwintering survival of *H. axyridis* after feeding on four diets: injured wine grape berries, 25% sucrose solution, water, and a control containing no food or water. After being exposed to these diets for 6 days, live individuals were transferred to clean plastic Petri dishes, and held at 5 ± 1 °C in growth chambers throughout the winter. Survival was recorded every month. Adult lady beetles collected during the overwintering flight in mid-October had higher survival rates than beetles collected from soybean fields in mid-August. These results suggest that an adaptation period prior to diapause increases the chances of lady beetle survival over the winter. In addition, injured wine grape berries, sugar, and water decreased beetle mortality during the overwintering months. Our results also showed that under similar conditions, females have higher survival during the winter than males. The importance of sugar and water on winter survival may drive *H. axyridis* adults to vineyards for feeding on wine grapes. Finally, we tested if adults of *H. axyridis* and the European paper wasp, *Polistes dominulus* Christ (Hymenoptera: Vespidae), were able to break the grape skin. *Harmonia axyridis* adults and paper wasps were not able to cause the primary injury to berries of Frontenac grapes under laboratory conditions. These results suggest that control of paper wasps in vineyards may not affect *H. axyridis* aggregations, and that *H. axyridis* feeding on wine grapes depends on previous injury to grape berries.

Introduction

The multicolored Asian lady beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is a voracious predator feeding on a wide range of soft-bodied insects, such as aphids, psyllids, and scales, as well as eggs and larvae of Lepidoptera and Coleoptera (Koch, 2003). Therefore, this lady beetle has been commonly used as a biological control agent. Aside from the benefits offered through pest suppression, *H. axyridis* is perhaps most well known for its adverse impacts. *Harmonia axyridis* feeds on non-target prey, invades homes and other man-made structures in autumn, and feeds on fruits (Koch & Galvan, 2008).

In particular, *H. axyridis* has become a significant pest of fall ripening fruit, including in wine grapes, in the Great Lakes region in North America. When disturbed or crushed, adult lady beetles release a yellow fluid (reflex bleeding or hemolymph) that causes an unpleasant odor and taste in the resulting wine (Pickering et al., 2004; Galvan et al., 2007a). Sensory thresholds of *H. axyridis* in wine range from 0.1 to 0.2 adult lady beetle per cluster (Pickering et al., 2006; Galvan et al., 2007b). Such low thresholds demonstrate the potential threat of *H. axyridis* to the wine industry. Economic consequences of this pest include complete losses of the contaminated wine, and/or increased production costs from additional time and labor needed to control *H. axyridis* (Galvan et al., 2006a). In addition to the economic problems caused in the wine grape production region around the Great Lakes, the relatively recent arrival of *H. axyridis* in more well-known wine grape areas such as Western Europe, South Africa, and California (USA)

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(Tedders & Schaefer, 1994; Brown et al., 2008) could transform the regional pest status of this insect into a global one.

The behavior of *H. axyridis* switches from carnivory to phytophagy in a manner that is not completely understood. Utilization of food of plant origin (i.e., pollen, nectar, and extrafloral nectaries) is not unusual in carnivorous lady beetles (Hodek & Honěk, 1996; Ricci & Ponti, 2002) or in other predators such as wasps, lacewings, and syrphids (Cortesero et al., 2000). Such feeding increases the chance of survival when prey is scarce, raises food reserve levels for overwintering, and may improve lady beetle fitness even when prey is available (Smith, 1960; Hagen, 1962; Hemptinne & Desprets, 1986; Harmon et al., 2000). However, frugivory (i.e., fruit feeding) in predatory lady beetles is rare (Hodek & Honěk, 1996), and predacious lady beetles have never been considered an agricultural problem of economic importance until now.

A recent study confirmed the preference of *H. axyridis* for previously damaged vs. undamaged grapes (Koch et al., 2004a). This finding indicates the possibility that field observations of beetles feeding in relatively large wounds (>2 mm in diameter) on fruits were most likely taking advantage of previously injured berries. In the same study, the authors also confirmed a highly significant preference for sugar water vs. water alone (Koch et al., 2004a). These preliminary results, along with field observations, suggest that some *H. axyridis* move from senescing soybean and corn fields to nearby vineyards, as prey (aphid) populations in field crops decline, in order to build sugar and fat reserves in preparation for overwintering.

During the movement of *H. axyridis* to vineyards (i.e., 2–3 weeks before harvest) (Galvan et al., 2006c), grape berries are nearing maturity and may be injured by other fruit feeders, including wasps, and birds or by physiological splitting (Galvan et al., 2006b). Splitting is caused by a sudden increase in absorption and/or adsorption of water, atmospheric humidity, or temperature, and its control at least partly depends on the cultural management and water stress of the vines (Opara et al., 1997). Depending on the proportion of clusters with damage, *H. axyridis* populations can easily infest up to 65% of all clusters for some varieties (Galvan et al., 2006b).

Social vespids are known to feed on grapes either by causing primary injury or feeding on previously damaged berries (Watkins et al., 1979; Matsuura & Yamane, 1990; Hickel & Shuck, 1995). The European paper wasp, *Polistes dominulus* Christ (Hymenoptera: Vespidae), is an exotic species that was first reported in the USA in 1981 in Massachusetts (Hathaway, 1981), and has spread westward (Pickett & Wenzel, 2000). It has been found feeding on ripening fruit (Hodgson & Roe, 2007), including wine grapes (TL Galvan, unpubl.).

However, the ability of lady beetles or wasps to injure grape berries remains unclear. Laboratory studies have shown contradictory results with *H. axyridis* adults either able or not able to break the skin of grape berries (Koch et al., 2004a; Kovach, 2004). In addition, there is no current consensus regarding the extent to which wasps can cause the initial break in the fruit skin (Flaherty et al., 1992; Hickel & Shuck, 1995). In this study, we investigated (i) the impact of feeding on Frontenac wine grapes on overwintering survival under laboratory conditions (i.e., if consuming grapes, sugar, or water increases overwintering survival), and (ii) the ability of *H. axyridis* and *P. dominulus* to injure wine grape berries. Frontenac was chosen, because it is one of the most important wine grape varieties in the USA that is affected by the *H. axyridis* fruit feeding behavior (Galvan et al., 2007b), and has become one of the most important varieties for colder climates worldwide (Plocher & Parke, 2001).

Materials and methods

Impact of feeding on wine grapes on overwintering survival

In this part of the study, we conducted three experiments. For the first experiment, *H. axyridis* adults were collected on 9 and 10 October 2004 (overwintering population 2004), during the overwintering flight, which is the event that leads to typical mass aggregations to spend the winter (Obata, 1986). For the second experiment, *H. axyridis* adults were collected from soybean on 12 and 13 August 2005 (summer population 2005). For the third experiment, *H. axyridis* adults were collected during the overwintering flight on 7 and 8 October 2005 (overwintering population 2005). Adults of *H. axyridis* from the overwintering populations in 2004 and 2005 were collected on the outside walls of Hodson Hall, University of Minnesota, St Paul, MN, USA. Adults of *H. axyridis* from the summer populations were collected from soybean fields at the University of Minnesota Outreach, Research and Education (UMORE) Park, Rosemount, MN, USA. *Harmonia axyridis* adults were identified using a diagnostic guide (Schellhorn, 2003) and voucher specimens were deposited in the University of Minnesota Insect Museum (Department of Entomology).

In each of the three experiments, 45 males and 45 females (three replications of 15 beetles per sex) were used for each treatment. Adults were sexed using external morphology characteristics (i.e., dark labrum and prosternum pigmentation for females, and light labrum and prosternum pigmentation for males). These characteristics for sexual determination were validated later by McCornack et al. (2007). After being sexed, 15 males or 15 females were placed into 190×80 mm plastic containers. Because each treatment was replicated three times, six plastic containers (i.e., three for each sex) were used for each treatment. The beetles were then provided with one of four diets in the bottom of a 100 × 15 mm Petri dish placed in the center of the 190 × 80 mm plastic container. The diets included (i) 12 mechanically injured Frontenac grape berries (wounds of 3–4 mm diameter), (ii) cotton ball saturated with a 25% (wt/vol) sucrose solution, (iii) cotton ball saturated with 14 ml water, and (iv) an untreated control containing no food or water. Sugar content of wine grapes used in the experiments averaged 23 ± 0.55% with *H. axyridis* collected in October 2004 and 2005, and 18.4 ± 0.33% in August 2005. Sugar content in August was lower, because grapes were harvested earlier than usual in Minnesota, that is, between the last week of August and the second week of September. Petri dishes with adults and diet were held at 25 ± 1 °C and L16:D8 h in Percival growth chambers (Percival Scientific, Boone, IA, USA). After 6 days, survival was recorded, and live individuals were transferred to clean plastic Petri dishes (150 × 15 mm), and held at 5 ± 1 °C with a photoperiod of L16:D8 h in Percival growth chambers through the winter. Survival was evaluated on 14 October, 18 November, and 21 December 2004, and on 28 January, 23 February, and 4 April 2005 for the 2004 overwintering population experiment; it was recorded on 19 and 23 August, 4 October, 15 November, and 27 December 2005, and on 4 February 2006 for the 2005 summer population experiment; for the 2005 overwintering population experiment, it was evaluated on 11 and 17 October, and 29 November 2005, and on 3 January, 4 February, and 14 March 2006. On each date, beetles were warmed to 24 ± 1 °C for 1 h before evaluation. Survival of *H. axyridis* adults was defined as the ability to crawl when stimulated with a fine camel hair brush.

Data for survival were arcsine $\sqrt{x}$ transformed, because some observations of proportion surviving were less than 0.2 or greater than 0.8 (Southwood & Henderson, 2000). Transformed proportions were analyzed across sample periods using repeated measures analysis of variance (ANOVA) with a first order autoregressive covariance structure (Proc MIXED; SAS Institute, 2006). The ANOVA model included main effects for time, treatment (i.e., diet), and the interaction of the main effects. This model was chosen, because it had an Akaike information criterion (AIC) equal to 79, which was smaller than that of other models, including the model with the three-way interaction (time*treatment*sex) that was used to test the sex effect, but had an AIC of 160 (smaller AIC is better; Lindsey, 1997). If the main effect for treatment (across sample periods) was significant (P<0.05), then differences among levels were tested using Bonferroni-adjusted contrasts of the least squares means for each pairwise combination of levels. Results of this analysis, presented throughout the text, refer to differences among treatments across sample periods.

The ability of *Harmonia axyridis* and *Polistes dominulus* to injure wine grape berries

Adults of *H. axyridis* were collected at the UMORE Park, in August 2005. They were identified using a diagnostic guide (Schellhorn, 2003) and voucher specimens were deposited in the University of Minnesota Insect Museum. Adult paper wasps were collected on August 2005 from a nest in a parking lot in front of Borlaug Hall, University of Minnesota, St Paul, MN, USA. The paper wasps were identified as *P. dominulus* using a diagnostic guide (DiTerlizzi, 2006), and confirmed by John Luhman (University of Minnesota Insect Museum).

Treatments used in this experiment included Frontenac grape berries with intact skin and attached stems exposed to *P. dominulus*, *H. axyridis* adults, or no insects. For each treatment, 3–4 grape berries of Frontenac with intact skin were set over a 55-mm filter paper disk in a clean 150 × 80 mm Petri dish. For the treatments with insects, one *P. dominulus* or *H. axyridis* was used per Petri dish. Insects were starved for 24 h before release. The control contained only the intact berries with filter paper. The treatment with *P. dominulus* was replicated 21 times, and the other two treatments were replicated 10 times. After 24 h, all *P. dominulus* and *H. axyridis* adults were alive, and were removed from the Petri dishes. Each berry was carefully inspected for feeding damage. Filter papers were also checked for any staining from grape juice from potential wounds in grape berries.

Results

Impact of feeding on wine grapes on overwintering survival

For the overwintering population of 2004, survival of *H. axyridis* males on all diets (83.2 ± 6.6 to 92.5 ± 1.2%) was significantly higher than in the control (39.4 ± 10.7%) (Figure 1A; Table 1). Survival of *H. axyridis* males fed on a solution of 25% sucrose was the highest, and it was followed by *H. axyridis* males fed on water, and on injured grapes (Figure 1A; Table 1). Survival of *H. axyridis* females fed on injured grapes (92.1 ± 1.5%) was significantly higher than in the control (75.5 ± 3.2%) (Figure 1B; Table 1). Percentage survival of *H. axyridis* females was significantly higher than of males ($F_{1,96}$ = 14.47, P = 0.0003).

For the summer population in 2005, survival of *H. axyridis* males (14.6 ± 5.8%) and females (17.3 ± 4.0%) fed on 25% sucrose was significantly higher than in the other treatments (Figure 2; Table 2). Survival of *H. axyridis* males and females did not differ ($F_{1,96}$ = 2.66, P = 0.1061).

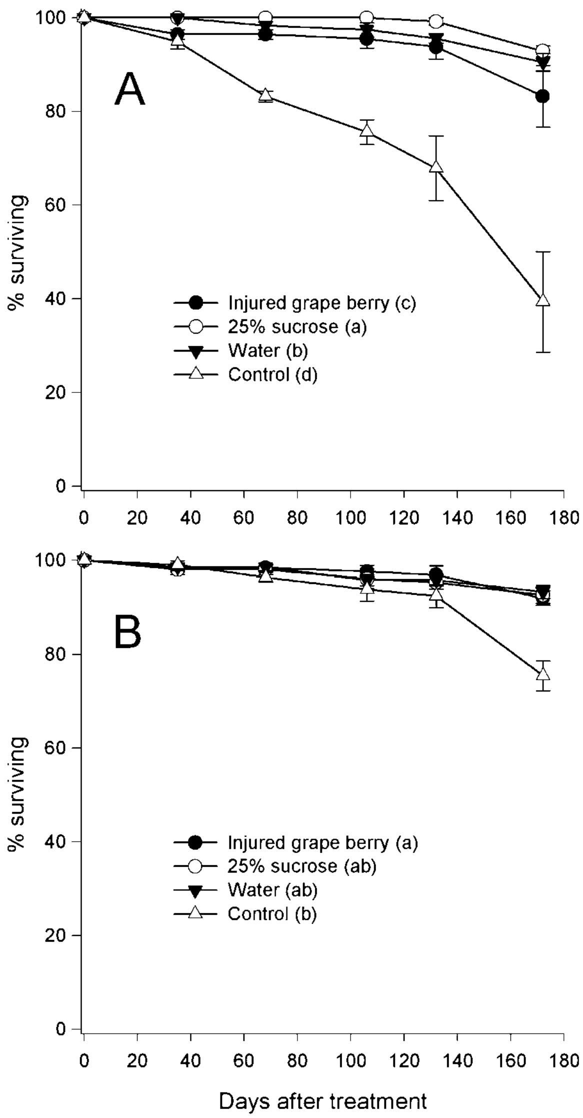

Figure 1 Survival of (A) male and (B) female *Harmonia axyridis*, collected during the autumn flight in the 2nd week of October 2004 (overwintering population), and exposed to four treatments. Treatments in the legend followed by the same letter in parentheses do not differ significantly [P>0.05; repeated measures ANOVA and Bonferroni adjusted contrasts].

Table 1 Repeated measures ANOVA for survival of male and female *Harmonia axyridis*, collected during the autumn flight in the 2nd week of October 2004 (overwintering population), and exposed to four treatments (injured wine grape berries, 25% sucrose solution, water, and the control containing no food or water)

Source	d.f.	F	P
	Males		
Time	5,48	51.30	<0.0001
Treatment	3,48	85.37	<0.0001
Time*treatment	15,48	6.03	<0.0001
	Females		
Time	5,48	24.26	<0.0001
Treatment	3,48	4.13	0.0110
Time*treatment	15,48	1.38	0.1948

Table 2 Repeated measures ANOVA for survival of male and female *Harmonia axyridis*, collected from soybean fields in the 2nd week of August 2005 (summer population), and exposed to four treatments (injured wine grape berries, 25% sucrose solution, water, and the control containing no food or water)

Source	d.f.	F	P
	Males		
Time	5,48	375.85	<0.0001
Treatment	3,48	127.08	<0.0001
Time*treatment	15,48	9.27	<0.0001
	Females		
Time	5,48	602.90	<0.0001
Treatment	3,48	297.12	<0.0001
Time*treatment	15,48	19.85	<0.0001

Table 3 Repeated measures ANOVA for survival of male and female *Harmonia axyridis*, collected during the autumn flight in the 2nd week of October 2005 (overwintering population), and exposed to four treatments (injured wine grape berries, 25% sucrose solution, water, and the control containing no food or water)

Source	d.f.	F	P
	Males		
Time	5,48	1.72	0.1491
Treatment	3,48	1.15	0.3400
Time*treatment	15,48	0.41	0.9706
	Females		
Time	5,48	4.11	0.0035
Treatment	3,48	1.74	0.1723
Time*treatment	15,48	0.50	0.9282

For the overwintering population in 2005, survival among treatments did not differ for *H. axyridis* males (97.8 ± 2.2 to 100 ± 0%) or females (90.5 ± 7.8 to 98.8 ± 1.2%) (Figure 3; Table 3). Survival of *H. axyridis* males and females did not differ ($F_{1,96}$ = 8.04, P = 0.0056).

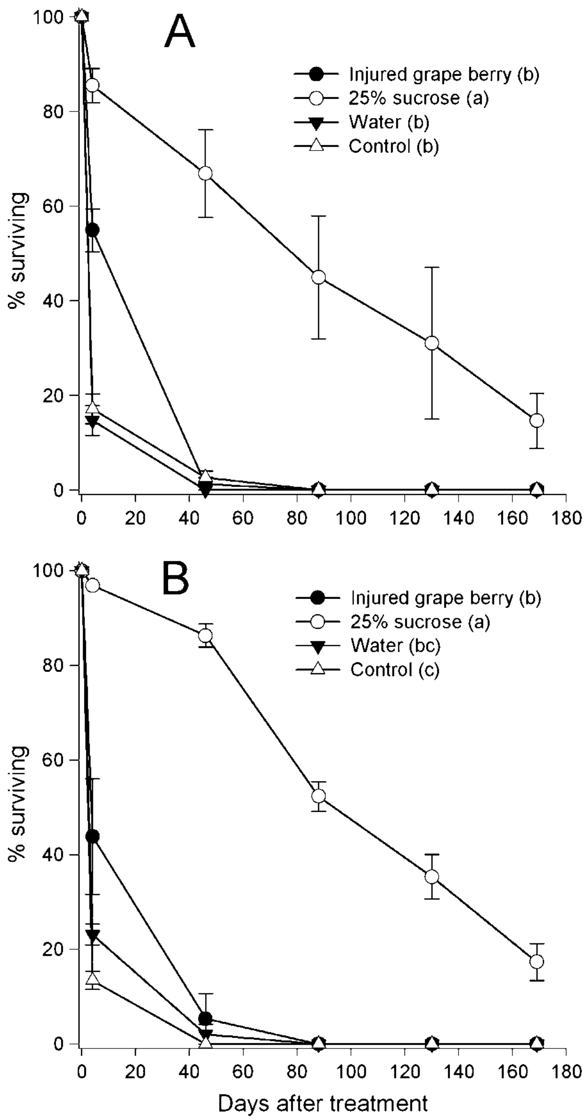

Figure 2 Survival of (A) male and (B) female *Harmonia axyridis*, collected from soybean fields in the 2nd week of August 2005 (summer population), and exposed to four treatments. Treatments in the legend followed by the same letter in parentheses do not differ significantly [P>0.05; repeated measures ANOVA and Bonferroni-adjusted contrasts].

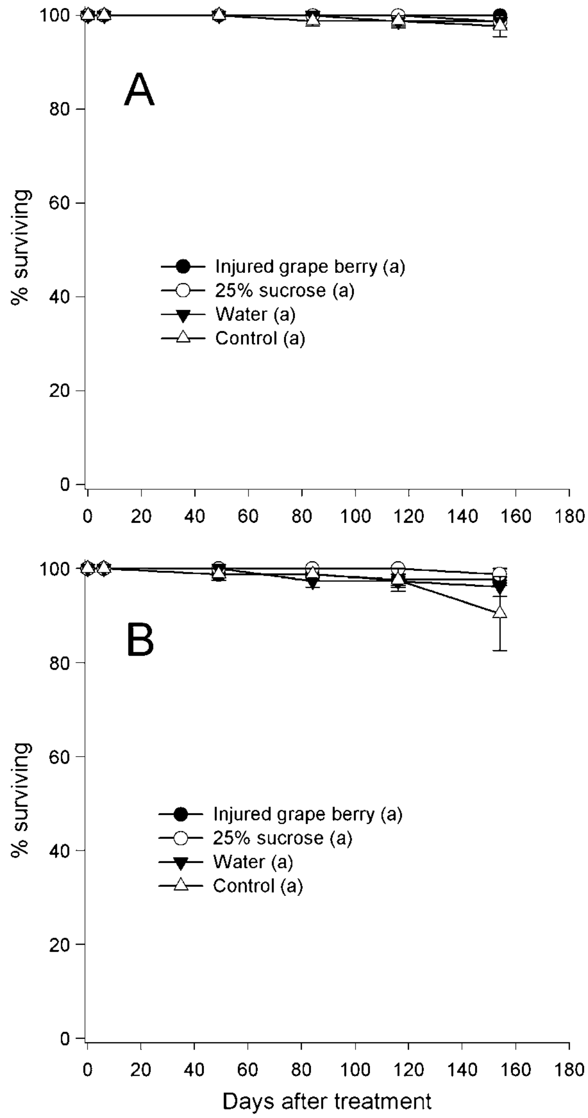

Figure 3 Survival of (A) male and (B) female *Harmonia axyridis*, collected during the autumn flight in the 2nd week of October 2005 (overwintering population), and exposed to four treatments. Treatments in the legend followed by the same letter in parentheses do not differ significantly [P>0.05; repeated measures ANOVA and Bonferroni-adjusted contrasts].

The ability of *Harmonia axyridis* and *Polistes dominulus* to injure wine grape berries

Grape berries in all treatments did not show evidence of injury from the insects. These results showed that neither *P. dominulus* nor *H. axyridis* adults could directly break the skin of Frontenac grape berries under laboratory conditions.

Discussion

The overwintering flight of *H. axyridis* is a well-documented event in Asia and North America (Sakurai et al., 1993; Nalepa et al., 2000), and it may be triggered by changes in temperature, photoperiod, food resources, or reproductive capacity (Hodek, 1986; Danks, 1991). During the overwintering flight, *H. axyridis* search for aggregation sites where they typically form mass aggregations to spend the winter (Obata, 1986). At this stage, *H. axyridis* is becoming acclimated for winter by decreasing its supercooling point and lower lethal temperature, and increasing the levels of myo-inositol, a cryoprotective agent (Watanabe, 2002; Koch et al., 2004b). At the end of the summer, a few months prior to the overwintering flight, lady beetles have begun to prepare for winter by entering prediapause, where beetles accumulate fat content and glycogen reserves in response to a decline in food resources (Hagen, 1962; Hodek & Čerkasov, 1963; Hodek, 1986). The combination of these environmental and physiological changes, which is called an 'adaptation syndrome' (de Wilde, 1970), in the months preceding winter, determines the success of lady beetle survival during diapause (Hagen, 1962; Hodek & Čerkasov, 1963).

This adaptation syndrome may explain the differences in survival under variable overwintering conditions between the overwintering and summer populations of *H. axyridis* observed in our study (Tables 1–3; Figures 1–3). Overwintering populations collected in 2004 and 2005 had higher survival rates than summer populations, independent of diet. Beetles in the overwintering population most likely experienced the environmental and physiological changes that provided the best conditions for them to survive during winter. However, individuals from the summer population were placed abruptly into overwintering conditions, without going through the diapause adaptation period. Barron & Wilson (1998) also observed a lower survival rate of adults of the seven-spot lady beetle, *Coccinella septempunctata* L., collected before the overwintering aggregation than of those collected in aggregation sites. The authors attributed the survival differences between the two populations to the lower accumulation of reserves by the lady beetles collected before the overwintering aggregation.

In our study, females were more tolerant to overwintering conditions than males. One reason for this may be the greater accumulation of fat and glycogen content by females than by males (Hodek & Čerkasov, 1963). Fat and glycogen are precursors of sugar and polyols, such as glycerol, trehalose, and inositol, which act as cryoprotectants of cell membranes, decreasing the mortality of insects due to chilling injury (Lee et al., 2002; Watanabe, 2002). In addition, sugars are an energy source for lady beetles (Pemberton & Vandenberg, 1993), helping them to locate aggregation sites and survive through the winter (Dixon, 2000). The importance of sugars during overwintering was documented in our study: lady beetles that fed on 25% sucrose had higher survival rates than those that fed on other diets in the overwintering population of 2004 (Figure 1) and in the summer population of 2005 (Figure 2).

The search for sugar-containing food sources, prior to moving to aggregation sites, may be the primary reason for the autumn fruit-feeding behavior of *H. axyridis*. Because wine grapes, such as Frontenac, have a high sugar content (20–25%) (Plocher & Parke, 2001) in the weeks prior to harvest, vineyards are an excellent location to increase sugar reserves. In our study, beetles from the overwintering population in 2004 that fed on injured grape berries showed higher survival than those in the control (Figure 1). The fruit-feeding behavior of *H. axyridis* is one example of the exceptional adaptation capacity of this lady beetle under environmental constraints. *Harmonia axyridis* have shown great variability in diet, geographical distribution, and coloration in its native (i.e., Asian) and adventive (e.g., North American and Western European) ranges (Majerus & Roy, 2005).

The role of water on lady beetle survival during overwintering is unknown. For *H. axyridis*, survival of beetles fed on water was greater than that of beetles not fed at all in the overwintering population of 2004 (Figure 1), but it was less than that of beetles fed water and sugar in the summer population of 2005 (Figure 2). However, in the overwintering population of 2005, survival did not differ among diets (Figure 3). Better pre-diapause conditions, such as greater accumulation of fat and sugar, might explain the higher survival of unfed beetles in 2005.

We observed that *H. axyridis* adults are not able to directly break grape berry skins. This finding corroborates a previous laboratory study in which *H. axyridis* adults were not able to cause primary injury to table grape berries (Koch et al., 2004a), as well as a field study that showed a strong correlation between injured wine grape berries and *H. axyridis* infestations (Galvan et al., 2006b). Even though Kovach (2004) concluded from his laboratory experiments that adults of *H. axyridis* are able to feed on intact grape berries, our laboratory and field (Galvan et al., 2006b) data suggest that the presence of *H. axyridis* in the vineyard does not necessarily indicate feeding on intact grapes.

In addition, we also observed that the wasp *P. dominulus* was not able to directly injure grape berries under laboratory conditions. Watkins et al. (1979) and Flaherty et al. (1992) stated that wasps do not drill or bite grapes. However, there are reports of wasps cutting grape and apple skins in Asia, USA, and Brazil (Chang, 1968; Viswanath et al., 1970; Heckman, 1979; Hickel & Shuck, 1995). These contradictions on the ability of wasps, and even lady beetles, to injure intact grape berries could be explained by the differences among grape varieties in their susceptibility to splitting (Matsuura & Yamane, 1990). According to Matsuura & Yamane (1990), wasps feed on grapes previously injured by fruit-piercing insects, such as moth larvae, and on not previously injured overripe berries of grape varieties with soft skin, such as Delaware and Cabernet Sauvignon. However, wasps could not injure the hard skin of splitting-resistant varieties, such as Koshu in Japan (Matsuura & Yamane, 1990).

Our study showed that an in-field adaptation period prior to diapause, as well as sugar and water, may increase the survival of lady beetles during winter. We also showed that under similar conditions, females have higher survival over the winter than males. The importance of sugar and water on winter survival may be a significant factor governing the movement of *H. axyridis* adults to vineyards and feeding on wine grapes. Finally, we observed that *H. axyridis* and *P. dominulus* adults were not able to cause the primary injury to grape berry skins of Frontenac, indicating that the control of paper wasps in vineyards may not affect *H. axyridis* feeding. Furthermore, it seems that *H. axyridis* feeding on wine grapes depends on previous injury to grape berries, including injury caused by birds or physiological splitting (e.g., Galvan et al., 2006b). Future research should be conducted to identify and quantify the sugars obtained by lady beetles during fruit feeding and assess those that increase their overwintering survival. The determination of sugar content as well as fat body content in lady beetles collected in August from agricultural fields, and in lady beetles collected in October during the overwintering flight would show if, and how much, sugar and fat body content is accumulated before the winter. In addition, future research should examine whether fruit-feeding behavior is an evolutionary adaptation of *H. axyridis* populations within the Great Lakes region in North America.

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