The aggregation behavior of Harmonia axyridis in its native range in northeast China

S. Wang, J.P. Michaud, X.L. Tan, F. Zhang, and X.J. Guo



**Published Version Information**

**Citation**: Wang, S., Michaud, J.P., Tan, X.L., Zhang, F., & Guo, X.J. (2011). The aggregation behavior of Harmonia axyridis in its native range in northeast China. BioControl, 56(2), 193-206.



**Digital Object Identifier (DOI)**: doi : 10.1007/s10526-010-9325-7

**Publisher's Link**: http://www.springerlink.com/content/1386-6141/56/1/

# The Aggregation Behavior of *Harmonia axyridis* in its Native Range in Northeast China

**Abstract** *Harmonia axyridis* has become notorious as an urban pest in many of the regions where it has been introduced, despite its numerous contributions to the biological control of insects injurous to agriculture and horticulture. Aggregative behavior prior to overwintering leads to invasions of human habitations as beetles seek refuge from freezing temperatures. Here we describe the aggregation behavior of native *H. axyridis* populations of northeast China that breed in agricultural fields (mostly corn and rice) and shrub/forest habitats and then migrate through rural villages in autumn. More than 140,000 beetles were collected during direct observations in 16 villages in five townships in Jilin Province. Beetles aggregated on dwellings shortly after agricultural harvests, favoring white walls with southern exposures, the largest aggregations occurring in villages in mountainous townships at higher elevations. The sex ratio was consistently female-biased and succinic phenotypes were more than twice as abundant as melanic phenotypes in all locations. A special trap compared the relative attractiveness of different surface colors (white > yellow = black > green > red = natural wood) and potential baits (corn pollen = honey > caramel = cocoa > milk = blank control). All aggregations disappeared abruptly just prior to the first frost, whereupon beetles were discovered sheltering in montane caves with southern aspects at higher elevations. Villagers reported substantial expenditures on pesticides in efforts to eliminate beetles from their homes every autumn. Invasion of human habitations appears to be an intrinsic tendency of native *H. axyridis* populations in China, which is the result of behavioral adaptations for cold-avoidance.

**Keywords:** aggregation, attraction, bait, Coleoptera, Coccinellidae, overwintering

## Introduction

The Asian multicolored lady beetle (aka Harlequin ladybird), *Harmonia axyridis* (Coleoptera: Coccinellidae), has been successfully utilized as a biological control agent in various agricultural contexts since the early 20$^{th}$ century (Gordan 1985; Colunga-Garcia and Gage 1998; Iperti and Bertand 2001). Unfortunately, this euryphagous predator has also become an aggressive invasive species in regions where it has been introduced, either intentionally or inadvertently, and has impacted native ecosystems and non-target insects (Williamson 1996; Koch 2003; Kajita et al. 2006; Majerus et al. 2006; Soares et al. 2008). A high degree of phenotypic plasticity and strong intraguild predation abilities are among the attributes that have contributed to invasive *H. axyridis* populations dominating assemblages of native coccinellid species (Brown and Miller 1998; Hesler et al. 2001; Alyokin and Sewell 2004; Hodek and Michaud 2008; Brown et al. 2008a,b; Lombaert et al. 2008). A paucity of natural enemies and effective intra-guild competitors, a high degree of environmental adaptability, and behavioral strategies for mitigating the impact of severe winter conditions are among other factors that appear to facilitate its range expansion in novel habitats (McClure 1987; Bazzocchi et al. 2004; Pell et al. 2008; Labrie et al. 2008).

In their native range, overwintering *H. axyridis* typically migrate up mountain slopes to moderate elevations and aggregate in natural shelters such as caves, usually selecting those with good exposure to the sun (Tanagishi 1976; Sakurai et al. 1993). Sometimes, many thousands of beetles will swarm together in refugia that mitigate their exposure to freezing conditions. The size, location and differential survival of these aggregations largely determine the local abundance of *H. axyridis* populations that return to nearby agricultural habitats the following spring. This general behavior is replicated in regions where *H. axyridis* is an invasive alien species and often results in swarms that invade human residences, sometimes in exceedingly large numbers (Kidd et al. 1995; Nalepa et al. 1996), resulting in the beetle's reputation as an urban pest. Home invasions by *H. axyridis* cause a range of nuisance problems: stained furniture, soiled surfaces (Nalepa et al. 2004) superficial bites (Kovach 2004) and even allergic reactions (Yarbrough et al. 1999; Goetz 2007). Research in the USA suggests that migration begins in late autumn when temperatures approach 5 ºC (Huelsman et al. 2004) and cummulative exposure to low temperature has been used to predict aggregative flight in Japan (Zenyogi 2008). High colour contrasts on the surface of buildings tends to attract migrating beetles (Nalepa et al. 2005). With the advent of invasive populations in Europe and elsewhere the species is alien, considerable research attention has been directed toward studying the biology and behavior of *H. axyridis* in these novel habitats (Keins et al. 2008; Pell et al. 2008; Soares et al. 2008). Apart from some work in Japan (Osawa 2001), little is known about the overwintering behavior of indigenous *H. axyridis* populations in Asia compared to what is known of invasive populations in alien regions.

The aim of the present investigation was to characterize the migration and aggregation behavior of *H. axyridis* overwintering populations in a mountainous region of northeast China. Jilin Province is an important agricultural region comprised of a sweeping plateau of cultivated fields in the west that slopes upward toward forested mountains in the east. Previous studies have examined the phenotypic composition of overwintered *H. axyridis* aggregations in this and other regions of China. For example, Yuan et al. (1994), catalogued 164 different succinic phenotypes and 12 melanic forms in a survey of the central and western parts of Jilin province. Other surveys have found that succinic phenotypes tend to outnumber melanics in northern Chinese provinces (Jing et al. 2001; Jiang et al. 2007). Our study focused on rural areas surrounding Jilin City in the center of Jilin province in the transition zone between the agricultural belt and more mountainous regions subject to natural conservation. Preliminary observations indicated high densities of *H. axyridis* in major field crops of the region (rice, corn and soybean) and the potential for impacts of overwintering beetles in nearby towns and villages. We began our study of *H. axyridis* migration and aggregation in mid-September to coincide with the completion of harvest, on the assumption that the abrupt drop in food availability for beetles would trigger their departure from agricultural habitats. We considered sex ratio, phenotype ratio (succinic: melanic), temporal variation in arrival of colour morphs, the character of surrounding landscape, and additional geographic factors. The local density of human inhabitants was estimated as metric of village size to test for any relationship with beetle aggregations. A special trap was employed to evaluate the relative attractiveness of various visual, tactile, and olfactory stimuli. Finally, the impacts of invading *H. axyridis* aggregations on local residents were estimated by use of interviews and distribution of a questionnaire.

## Materials and Methods

### Study sites

Surveys of *H. axyridis* overwintering populations were conducted during the period from 11 September to 10 October, 2009 in Jiaohe and Yongji counties in Jilin province, China. Sixteen villages were selected for sampling, 10 in Jiaohe County and five in Yongji County (Fig. 1). The villages were separated by an arbitrary minimum distance of 1.0 km to ensure they represented independent observation points. The landscape surrounding villages ranged from mostly agricultural (categorized by the predominant crop as either corn fields or rice paddies) to mostly natural (categorized by the predominant woody vegetation as either scrubland or forest). The towns of Lafa and Qingling occur within nationally protected nature conservancies where there is little agriculture, but considerable disturbance from tourism.

Global position data were collected for each site using a handheld GPS receiver. The habitats surrounding each village to a radius of 5.0 km were digitized using ARC GIS 8.3 (Ormsby et al., 2004). Four primary landscape types were resolved from digital images: cultivated fields dominated by either corn or rice, and natural vegetation dominated by either trees or shrubs. The altitude of each village was measured at the spatial coordinate for its central point. The geographic characteristics of the sampled villages are reported in Table 1. For purposes of analysis, we divided villages into three categories according to their elevation: low (200 – 270m ASL), medium (271 – 340m), and high (> 340m). Villages were divided into two categories according to population density: small (< 100 inhabitants) or large (> 100).

### Direct sampling of adults

In each village, white houses with an open southern exposure were selected for sampling

*H. axyridis* on their outer walls between the hours of 14:00 and 17:00 when these surfaces were under direct insolation. Ten independent observation points were established in each village, each separated by a minimum distance of 100 m. At each sampling site, a white plastic board (1.0 $m^2$) with a roughened surface was stuck to the wall and a raised plastic frame (3.0 cm high) was mounted around the perimeter of the board (Fig. 2). As beetles tended to land toward the center of the board and then accumulate in the corners, we collected them as they passed through the two trapezoidal regions using a small insect net. Boards were mounted on each house at 9:00 h and removed shortly after sunset. Beetles were collected continuously for a 3 h period, from 14:00 to 17:00 h, once at each of ten different observation sites in each of the 16 villages.

Samples of live beetles obtained from direct collection were transferred to plastic boxes (45 × 30 × 30 cm, ca. 1200 beetles per box). Each box was covered with fabric (19.2 holes / $cm^2$) to permit ventilation and provisioned with milk popcorn as a food supplement. All samples were sent by airmail to the Entomology Laboratory of the Institute of Plant and Environment Protection, Beijing Academy of Agriculture and Forestry Sciences were they were examined within 48h of arrival. Three types of data were recorded for all experiments: total number of beetles (caught by netting or in traps), sex ratio, and the ratio of succinic to melanic phenotypes. All phenotypes in which the background colour of the elytra was dark were categorized as melanic; all in which the background colour was some shade of yellow, orange or red were categorized as succinic. Beetles were sexed according to the colour of the clypeus, which is significantly paler in males.

## Trapping

At 15 of the 16 sampling locations, we installed traps made of wood and polyurethane in order to collect *H. axyridis* adults over specified time intervals and to test the attractiveness of trap attributes and potential food resources when placed in the bottom of the trap chamber (Fig. 3). Extensive construction activity prevented trapping in Hou-baliqi village. Two baffle plates were installed in the interior of the chamber to prevent beetles escaping and a layer of soft sponge covered the bottom. Traps were installed on southern-facing external house walls at 9:00 a.m. on each sampling day and beetles were collected between 4:00 and 5:00 p.m. by dropping the hinged floor of the trap and emptying the contents into containers.  Tests of surface colour, surface texture and food baits were performed at each sampling location on each of three successive days in each village.

*Comparison of trap surface colors*

Since the assembly of insects on surfaces can be correlated with the background colour (Marshall 2006), we tested six trap surface colours: yellow, red, black, white, green and natural wood.  Honey was used as an attractant and all surfaces were coated with a layer of varnish.  The six traps of different colours were tested on a single day at each sampling location by mounting each trap on the southern-facing wall of a different house, each separated by a minimum distance of 10 metres.

*Comparison of trap surface textures*

We tested various surface textures for effects on beetle assembly including varnished natural wood (smooth), granular (rough) and corrugated (ridged).  The traps in this experiment were white in colour and used honey as an attractant.  Three traps, each of a different surface texture, were tested on a single day at each sampling location by mounting each trap on the southern-facing wall of a different house, each separated by a minimum distance of 10 metres.

*Comparison of food baits*

To compare the relative attractiveness of different materials to *H. axyridis* adults, we conducted a series of experiment using honey, cocoa, milk, corn pollen and caramel as potentially attractive resources, with water as a control.  Each material was tested once at each observation site in a white trap.  Times of collection and replication were the same as for surface colour trials.  The traps containing different baits were tested on a single day at each sampling location by mounting each trap on the southern-facing wall of a different house, each separated by a minimum distance of 10 metres.

Assessment of urban impact

To estimate the numbers of beetles invading homes, residents of cooperating households were requested to count all beetles within a window frame (1.5 m x 1.5 metres on one afternoon during the period of peak beetle activity, sometime between 1:00 and 3:30 p.m.

Interviews were conducted with inhabitants of the sampled villages to assess the impact of overwintering *H. axyridis* on the urban population. Residents were shown representative specimens of common coccinellid species so as to be able to distinguish species (*Coccinella septempunctata*, *H. axyridis*, *Hippodamia variegata*, *Propylea japonica*). The following questionnaire was distributed:

1) What is the major crop planted on your farm?
2) What was the approximate harvest date of the major crops?
3) What was the date on which *H. axyridis* aggregations appeared?
4) What was the date on which *H. axyridis* aggregations disappeared?
5) Do beetles enter your home and cause nuisance problems?

Statistical analysis

The numbers of adults sampled directly at each observation site were analyzed using a nested ANOVA design to resolve the respective effects of 'township' and 'village'. When more than two groups were compared, means were separated by Fisher's LSD when sample sizes were equal, and by Duncan's Multiple Range Test when they were not. A binomial test was used to test sex and phenotype ratios for asymmetry. A 3-way ANOVA was used to analyze results with landscape type, elevation, and human population density as independent variables. A one-way ANOVA was used to compare trap catches, followed by Fisher's LSD test to separate means of different trap types.

## Results

Direct sampling of adults

A total of 144,528 adult *H. axyridis* were collected during direct observations. The nested ANOVA revealed significant effects of 'township' ($F_{4,15}$ = 50.41; df = 4,15; $P$ < 0.0001) and 'village (township)' ($F_{4,11}$ = 9.90; $P$ < 0.0001) on the numbers of beetles collected during direct sampling, the ratio of succinic: melanic phenotypes ($F_{4,15}$ = 4.52; $P$ = 0.0018 and $F_{4,11}$ = 3.85; $P$ < 0.0001, respectively), the numbers of beetles intrusive in residences ($F_{4,15}$ = 86.34; $P$ < 0.0001 and $F_{4,11}$ = 39.28; $P$ < 0.0001, respectively), but the effects of location on sex ratio were only marginally significant ($F_{4,15}$ = 2.30; $P$ = 0.0617 and $F_{4,11}$ = 1.83; $P$ = 0.0544, respectively).

The mean values of dependent variables and their standard errors are reported for each village in Table 2. On the basis of these data, beetle landing rates averaged 2.5 / $m^2$ / min over all observation periods, although this is certainly an underestimate considering that not all beetles landing on the sampling board were successfully collected. Comparing the mean number of beetles collected per site among townships ($F_{4,15}$ = 30.77; $P$ < 0.0001), the mountainous townships of Qingling and Lafa yielded the highest counts (568.5 ± 193 and 541.4 ± 28.50), followed by Chaluhe (417.3 ± 8.8) which was not different from Xinnong (412.5 ± 9.5) which, in turn, was not different from Jinjia (370.9 ± 11.8), the locality that had the earliest agricultural harvest, beginning in September (Duncan's MRT, $\alpha$ = 0.05).

There were significant effects of 'landscape' and 'elevation' on the numbers of beetles collected, and the 'landscape*elevation' interaction was significant (Table 3). The latter interaction occurred because landscape varied significantly with elevation ($F_{3,156}$ = 94.89; $P$ < 0.0001) and beetle numbers increased significantly with elevation ($F_{2,157}$ = 65.57; $P$ < 0.0001; $r^2$ = 0.293). The number of beetles collected (means ± SE) varied with landscape type as follows: shrubland (643 ± 24) > forest (523 ± 21) > corn (428 ± 10) = rice (395 ± 12). There was no significant effect of 'population density', nor was there any significant interaction between 'population density' and any other independent variable. Shrubland had the highest mean counts of *H. axyridis* but this landscape type was represented by only a single village. Forest landscape, with three villages represented, had the next highest counts, followed by the two agricultural landscapes, corn fields and rice paddies, that were not significantly different from one another (Duncan's MRT, $\alpha = 0.05$).

Landscape also had a strong effect on the number of beetles intrusive in residences, whereas elevation had a small effect, population density had no effect and the landscape*elevation interaction was highly significant, once again because these variables were not entirely independent (Table 4). The number of intrusive beetles was positively correlated with the proportion of succinic phenotypes in outdoor samples ($F_{1,158} = 42.91$; $P < 0.0001$; $r^2 = 0.214$).

Results of binomial tests revealed that the phenotype ratio was significantly biased in favor or succinics in all five townships ($P_{(2\text{-tailed})} < 0.001$ in all cases). Landscape was the only independent variable to have a significant effect on phenotype ratio in a 3-way ANOVA ($F_{3,156} = 11.385$; $P < 0.001$), and this was only because of the effect of the forest village of Erdaogou in Qingling Township which had more than twice the ratio of succinics to melanics compared with any other landscape type. Sex ratios were consistently female-biased in all five townships ($P_{(2\text{-tailed})} < 0.001$ in all cases). Apart from a marginal effect of elevation on sex ratio ($F_{2,157} = 2.96$; $P = 0.055$), no other independent variable had a significant effect (landscape: $F_{3,156} = 0.37$; $P = 0.777$; population density: $F_{1,158} = 0.05$; $P = 0.822$), so a 3-way ANOVA was not performed. The number of beetles tallied as intrusive during observations within residences was correlated with counts of beetles tallied in outdoor aggregations ($F_{1,158} = 131.52$; $P < 0.0001$; $r^2 = 0.451$).

## Trapping

### *Comparison of trap surface colours*

Surface coloration significantly influenced trap catches ($F_{5,84} = 54.47$; $P < 0.0001$) and the ratio of phenotypes caught ($F_{5,84} = 2.45$; $P = 0.041$). Bright white was more attractive to *H. axyridis* than other colours, with yellow and black the next most attractive (Fig. 4). Red and natural wood were the least attractive background colors, with green intermediate. All colours attracted more succinic beetles than melanics ($P_{(2\text{-tailed})} < 0.001$ in all cases), because succinic beetles were more than twice as abundant as melanics at all locations.

*Comparison of trap surface textures*

Surface texture did not affect the total numbers of beetles caught ($F_{2,42} = 1.12$; $P = 0.336$) and succinic beetles outnumbered melanics on all surfaces ($P_{(2\text{-tailed})} < 0.001$ in all cases). Whereas traps with smooth and granulated surfaces caught three times as many succinic beetles as melanics, traps with ridged surfaces caught 4.5 times as many, a significantly greater proportion ($F_{2,42} = 3.33$; $P = 0.045$; Fisher's LSD; $\alpha = 0.05$).

*Comparison of food baits*

The type of food resource offered in traps significantly affected the numbers of beetles caught ($F_{5,84} = 86.52$; $P < 0.001$). Honey and corn pollen were the most attractive baits, followed by caramel and cocoa, whereas milk was no more attractive than the water control (Fig. 5). The ratio of succinic to melanic phenotypes was not affected by the type of bait ($F_{5,84} = 1.65$; $P = 0.157$), although succinics outnumbered melanics in every treatment ($P_{(2\text{-tailed})} < 0.001$ in all cases).

Urban impact of *H. axyridis* aggregations

It should be noted that our observations and survey data were restricted to villages where we found evidence of *H. axyridis* aggregations and do not include other villages where *H. axyridis* was not problematic, for whatever reason. Data on the appearance and disappearance of *H. axyridis* aggregations in rural villages and the summary of responses to survey questions are reported in Table 5. Migration from low-lying agricultural fields occurred about two weeks later than that from scrubland and forest habitats. Anecdotal records kept by local residents over the past five years indicated that beetles usually began aggregating in villages after 1 September and later migrated to higher mountainous regions before the first frost. In our survey, beetles left residences and disappeared *en masse* on 3 October, the day immediately prior to the first frost. At this time, large numbers of *H. axyridis* adults were found at higher elevations in montane habitats to the east.

Typical village residences are constructed of brick with windows and doors framed in wood and *H. axyridis* adults easily penetrated these structures through gaps around the framing. Intrusions by *H. axyridis* occurred throughout daylight hours, with peak periods of entry reported in to occur in the morning and evening. Of a total of 1481 village residents responding to the survey questionnaire, 1456 (98.3%) reported that beetles invaded their homes and caused nuisance problems. Almost every household resorted to insecticide applications of some form in attempts to control or prevent home invasions, often at considerable expense. However, most of the materials applied were formulated for control of household pests or mosquitos and were not considered effective in deterring *H. axyridis* aggregations or preventing their entry into habitations.

## Discussion

Factors influencing beetle abundance in villages appeared to act at landscape scale more than at a local level, as reflected by the fact that 'township' accounted for substantially more variation in number of beetles than did 'village' in the nested ANOVA. This was consistent with effects of landscape type on beetle counts and the numbers of beetles intrusive in residences, since landscape type varied among townships. Human population density, reflecting the relative size of villages, had no discernable effect on any dependent variable. Natural landscapes (shrubland and forest) were associated with higher elevations and greater beetle counts than agricultural landscapes that were dominated by corn fields and rice paddies. Agricultural crops might be expected to generate abundant aphid populations for beetle reproduction, but although *H. axyridis* is known to be active in corn, it is not reported to forage in rice. However, it clearly has an inherent predilection for woody shrubs and trees, as reflected in its biological control contributions in arboreal habitats such as apple orchards (Brown and Miller 1998), pecan orchards (Mizell 2007), citrus groves (Michaud 2002), and stands of coniferous trees

(McClure 1987; Berthiaume et al. 2007).

The onset of *H. axyridis* migration from the countryside into villages typically lagged the harvest date of the primary local crops by only a few days (Table 5). The size of local aggregations was correlated with the numbers of beetles observed to be intrusive in houses, even though these likely varied somewhat with ease of entry into particular houses. Nalepa et al. (2000) dismissed any significant role of pheromones in preserving *H. axyridis* annual fidelity to particular overwintering sites, but rather implicated accumulations of feaces, residues, and contact chemical cues from conspecifics. Despite successfully entering residences in substantial numbers, the beetles did not remain inside them for more than a week or two before continuing their migration to 'natural' overwintering sites at higher elevations (shallow caves, crevices and rocky depressions on montane slopes with southern aspects). Populations of *H. axyridis* that are invasive in temperate regions of Europe and North America often attempt to remain indoors for the entire winter (Labrie et al. 2008; Berkvens et al. 2010); however, this is typical of regions where there are no mountains to draw beetles to higher elevations. Similarly, in less mountainous regions of China such as Shandong Province, beetle aggregations may remain problematic in residences throughout the winter (Wang Su, unpublished).

Female-biased sex ratios have been reported for Japanese populations of *H. axyridis* (Osawa 2001) and various post-zygotic factors have been implicated, including differential overwintering mortality (Osawa 2001) and infection with male-killing bacteria (Majerus et al. 1998). Even a small discrepancy in the developmental time of male and female eggs could result in differential mortality as a consequence of sibling egg cannibalism (Osawa 2002; Michaud and Grant 2004). The preponderance of succinic morphs over melanics was not unexpected given previous reports (Jing et al. 2001; Jiang et al. 2007) However, autumn sampling at similar latitudes around Beijing indicated that melanics tended to increase in frequency in the fall due to assortative mating until they occured at frequencies similar to succinics (Wang et al. 2009).

The most adverse impact of invasive *H. axyridis* populations has been their procilivity to enter buildings, especially human habitations, and this has driven research into attractants, repellents and various tactics aimed at trapping, killing or excluding them (Kenis et al. 2008). The orientation of *H. axyridis* to buildings, especially those in prominent locations such as hill tops (Obata 1986), is consistent with visual orientation to prominent landmarks, or ‘macrosites’, in the initial stages of aggregation (Nalepa et al. 2005). Cursory inspection revealed that aggregations of *H. axyridis* tended to form on white, exterior walls with southern exposure, hence our selection of these locations for the trapping experiments. Although different surface textures (smooth, granulated or ridged) had no apparent effect on alightment behavior, tests with various trap colours yielded differences in trap catches via apparent effects on landing frequency. Our results were very similar to those of Obata (1986) and confirmed that a white surface attracted more beetles than any other colour. Nalepa et al. (2005) conducted experiments to demonstrate the importance of visual contrast in close range orientation, rather the colour white *per se*, and challenged the results of Obata (1986) on the basis that backgound contrast was not controlled in those colour trials. However, our results are not entirely consistent with this view; since all our tests were conducted on a white background, the dark coloured traps would have presented higher contrast than white traps, but they collected fewer beetles. If linear contrasts, in specific, are important, as Nalepa et al. (2005) propose (presumably dark lines on a pale background conform to the shape of cracks and crevices that may provide shelter), then the rectangular trap may not have provided the right shape or scale of contrast to increase attraction to dark colours on a white background. The fact that both yellow and black traps attracted similar numbers of beetles, second only to white, suggests that beetles may respond to different colours for different reasons. For example, very light colours such as white and yellow may be intrinsically attractive because of their high reflectivity, whereas black and patterns of linear contrast may be attractive because they are indicative of potential shelter.

Trials in which traps were baited with potential food resources confirmed a positive response to honey and corn pollen, materials well-recognized as important supplementary foods for many aphidophagous coccinellids (Hodek, 1996). Since the baits were concealed within the traps, an olfactory response to these materials can be inferred, presumably both pre- and post-alightment. From a practical perspective, the efficiency of any traps installed to collect and remove *H. axyridis* aggregations could be significantly improved by baiting with either of these materials, an approach now commonly refered to as ‘attract and kill’ when combined with insecticides.

The invasion of dwellings by *H. axyridis* is a strongly seasonal behavior and appears to be driven by cold avoidance in the fall. Although *H. axyridis* acclimates to falling temperatures with freeze-avoidant physiological mechanisms typical of many insects, including reduced water content, accumulation of polyols, and altered enzymatic activities, a considerable acclimation period is required for beetles to achieve their lowest supercooling points and substantial cold-induced mortality may occur even though they do not freeze (Watanabe 2002; Zhao et al. 2008; 2010). Berkvens et al. (2010) demonstrated that the supercooling points of beetles overwintering indoors in Belgium were considerably elevated compared to those overwintering outdoors and suggested that this could lead to significant mortality if indoor beetles became active prematurely. Similarly, Schaefer (2004) observed substantial overwintering mortality in aggregations forming annually in an unheated concrete observation tower that lacked insulation. The tendency to enter buildings is likely an adaptation to avoid cold-induced mortality during quiescence. Thus, *H. axyridis* remains a successful alien invader in northern latitudes such as Quebec, Canada, despite an inability to overwinter successfully outdoors (Labrie et al. 2008).

Our results demonstrate that aggregation and invasion of buildings are intrinsic propensities of this species within its native range, rather than emergent traits of invasive alien populations. While these findings underscore the importance of obtaining a complete behavioral profile of biological control agents prior to their intoduction to exotic locations, even modern standards for assessing candidate predator species for introduction would not necessarily reveal such adverse behavior, since most criteria are based on diet breadth and predatory behavior observed under laboratory conditions. The undeniable biological control contributions of *H. axyridis* to agriculture are now largely offset by the nuisance impact of this species in urban environments, diminishing general public perception of lady beetles as beneficent agents and generating adverse publicity for biological control efforts. However, the appropriate placement of suitably designed and baited traps may prove to be a viable tactic for collecting aggregations of beetles in locations where they are consistently problematic.

**Acknowledgments**

## References

Alyokin, A. and G. Sewell, 2004. Changes in a lady beetle community following the establishment of three alien species. Biol. Invasions 6: 463-471.

Bazzocchi, G.G., A. Lanzoni, G. Accinelli and G. Burgio, 2004. Overwintering, phenology and fecundity of *Harmonia axyridis* in comparison with native coccinellid species in Italy. BioControl 49: 245-260.

Berkvens, N., J.S. Bale, D. Berkvens, L. Tirry and P. de Clercq, 2010. Cold tolerance of the harlequin ladybird *Harmonia axyridis* in Europe. J. Ins. Phsyiol. 56: 438-444.

Berthiaume, R., C. Hebert and C. Cloutier, 2007. Comparative use of *Mindarus abietinus* (Homoptera: Aphididae) by two coccinellids (Coleoptera: Coccinellidae), the native *Anatis mali* and the exotic *Harmonia axyridis*, in a Christmas tree plantation. Environ. Entomol. 36: 319-328.

Brown, M.W. and S.S. Miller, 1998. Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. Entomol. News 109: 136-142.

Brown, P.M.J., T. Adriaens, H. Bathon, J. Cuppen, A. Goldarazena, T. Hagg, M. Kenis, B.E.M. Klausnitzer, I. Kovar, A.J. Loomans, M.E.N. Majerus, O. Nedved, J. Pedersen, W. Rabitsch, H.E. Roy, V. Ternois, I. Zakharov and D.B. Roy, 2008a. *Harmonia axyridis* in Europe: Spread and distribution of a non-native coccinellid. BioControl 53: 5-22.

Brown, P.M.J., H.E. Roy, P. Rothery, D.B. Roy, R.L. Ware and M.E.N. Majerus, 2008b. *Harmonia axyridis* in Great Britain: analysis of the spread and distribution of a non-native coccinellid. BioControl 53: 55-68.

Colunga-Garcia, M. and S.H. Gage, 1998. Arrival, establishment, and habit use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. Environ. Entomol. 27: 1574-1580.

Goetz, D.W., 2007. *Harmonia axyridis* ladybug hypersensitivity in clinical allergy practice. Allergy Asthma Proc. 28: 50-57.

Gordan, R.D., 1985. The Coccinellidae (Coleoptera) of America north of Mexico. J. New

York Entomol. Soc. 93: 1-912.

Hesler, L.S., R.W. Keickhefer and D.A. Beck, 2001. First record of *Harmonia axyridis* (Coleoptera: Coccinellidae) in South Dakota and notes on its activity there and in Minnesota. Entomol. News 112: 264-270.

Hodek, I., 1996. Food relationships. In: Hodek I, Honek A (eds), Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht, Netherlands, pp 143-238.

Hodek, I. and J.P. Michaud, 2008. Why is *Coccinella septempunctata* so successful? Eur. J. Entomol. 105: 1-12.

Huelsman, M,F,, J. Kovach, J. Jasinski, C. Young and N. Eisley, 2002. Multicolored Asian ladybird beetle (*Harmonia axyridis*) as a nuisance pest in households in Ohio. In: S.C. Jones, J. Zhai & W.H. Robinson (eds.), Proceedings of 4th International Conference on Urban Pests. pp 234-250.

Iperti, G, and E. Bertand, 2001. Hibernation of *Harmonia axyridis* (Coleoptera: Coccinellidae) in south-eastern France. Acta Soc. Zool. Bohem. 65: 207-210.

Jiang, W.H., X.H. Pan, J.X. Liu, and L.B. Liu, 2007. Studies on the type of spot in the wings of *Harmonia axyridis* (Pallas) in Baoding. Hebei Journal of Forestry and Orchard Research 22: 198-202.

Jing, Y., Y.J. Zhang and D.Y. Ma, 2001. Studies of the types of spots in the wings of *Harmonia axyridis* (Pallas) in Shanxi province. Journal of Shanxi Agricultural University 3: 230-232.

Kajita, Y., F. Takano, H. Yasuda and E.W. Evans, 2006. Interactions between introduced and native predatory ladybirds (Coleoptera: Coccinellidae): factors influencing the success of species introductions. Ecol. Entomol. 31: 58-67.

Kenis, M., H.E. Roy, R. Zindel and M.E.N. Majerus, 2008. Current and potential management strategies against *Harmonia axyridis*. BioControl 53: 235-252.

Kidd, K.A., C.A. Nalepa, E.R. Day and M.G. Waldvogel, 1995. Distribution of *Harmonia axyridis* (Pallas) (Coleoptera:Coccinellidae) in North Carolina and Virginia. Proc. Entomol. Soc. Wash. 97: 729-731.

Koch, R.L., 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. J. Ins. Sci. 3.32. Available online: http://www.insectscience.org/3.32/.

Kovach, J., 2004. Impact of multicolored Asian lady beetles as a pest of fruit and people. Am. Entomol. 50: 159-161.

Labrie, G., D. Coderre and E. Lucas, 2008. Overwintering strategy of multicolored Asian lady beetle (Coleoptera : Coccinellidae): Cold-free space as a factor of invasive success. Ann. Entomol. Soc. Am. 101: 860-866.

Lombaert, E., T. Malausa, R. Devred and A. Estoup, 2008. Phenotypic variation in invasive and biocontrol populations of the harlequin ladybird, *Harmonia axyridis*. BioControl 53: 89-102.

Majerus, M.E.N., V. Strawson and H. Roy, 2006. The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain. Ecol. Entomol. 31: 207-215.

Majerus, T.M.O., M.E.N. Majerus, B. Knowles, J. Wheeler, D. Bertrand, V.N. Kuznetzov, H. Ueno and G.D.D. Hurst, 1998. Extreme variation in the prevalence of inherited male-killing microorganisms between three populations of *Harmonia axyridis* (Coleoptera: Coccinellidae). Heredity 81: 683-691.

Marshall, S.A., 2006. Insects: Their Natural History and Diversity. Firefly Books Ltd., Buffalo, New York.

McClure, M.S., 1987. Potential of the Asian predator, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), to control *Matsucoccus resinosae* Bean and Godwin (Homptera: Margarodidae) in the United States. Environ. Entomol. 16: 224-230.

Michaud, J.P., 2002. Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. Environ. Entomol. 31: 827-835.

Michaud, J.P. and Grant, A.K., 2004. Adaptive significance of sibling egg cannibalism in Coccinellidae: Comparative evidence from three species.  Ann. Entomol. Soc. Am. 97: 710-719.

Mizell, R.F., 2007. Impact of *Harmonia axyridis* (Coleoptera: Coccinellidae) on native arthropod predators in pecan and crape myrtle. Fla. Entomol. 90: 524-536.

Nalepa, C.A., K.A. Kidd and K.R. Ahlstrom, 1996. Biology of *Harmonia axyridis* (Coleoptera: Coccinellidae) in winter aggregations. Ann. Entomol. Soc. Am. 681-685.

Nalepa, C.A., K.A. Kidd and D.I. Hopkins, 2000. The multicolored Asian lady beetle (Coleoptera: Coccinellidae): orientation to aggregation sites. J. Entomol. Sci. 55: 150-157.

Nalepa, C.A., G.G. Kennedy and C. Brownie, 2004. Orientation of multicolored Asian lady beetles to buildings. Am. Entomol. 50: 165-166.

Nalepa, C.A., G.G. Kennedy and C. Brownie, 2005. Role of visual contrast in the alighting behavior of *Harmonia axyridis* (Coleoptera: Coccinellidae) at overwintering sites. Environ. Entomol. 34: 425-431.

Obata, S., 1986. Determination of hibernation site in the ladybird beetle, *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae). Kontyu 54: 218-223.

Ormsby, T., E.J. Napoleon, R. Burke, C. Groeesl and L. Bowden, 2004. Getting to Know ArcGIC Desktop. ESRI Press, Redlands, California, USA. 380p.

Osawa, N., 2001. The effect of hibernation on the seasonal variations in adult body size and sex ratio of the polymorphic ladybird beetle *Harmonia axyridis*: the role of thermal melanism. Acta Soc. Zool. Bohem. 65: 269-278.

Osawa, N., 2002. Sex-dependent effects of sibling cannibalism on life history traits of the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). Biol. J. Linn. Soc. 76: 349-360.

Pell, J.K., J. Baverstock, H.E. Roy, R.L. Ware and M.E.N. Majerus, 2008. Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives. BioControl 53: 147-168.

Sakurai, H., Y. Kumada and J. Takeda, 1993. Seasonal prevalence and hibernating-diapause behavior in the lady beetle *Harmonia axyridis*. Res. Bull. Fac. Agric Gifu Univ. 58: 51-55.

Schaefer, P.W., 2004. Winter aggregation of *Harmonia axyridis* (Coleoptera: Coccinellidae) in a concrete observation tower. Entomol. News 114: 23-28.

Soares, A.O., I. Borges, P.A.V. Borges, G. Labrie and E. Lucas, 2008. *Harmonia axyridis*: What will stop invader? BioControl 53: 127-145.

Tanagishi, K., 1976. Hibernation of the lady beetle, *Harmonia axyridis*. Insectarium 13: 294-298.

Wang, S., J.P. Michaud, R.Z. Zhang, F. Zhang and S.A. Liu, 2009. Seasonal cycles of assortative mating and reproductive behaviour in polymorphic populations of *Harmonia axyridis* in China. Ecol. Entomol. 34: 483-494.

Watanabe, M., 2002. Cold tolerance and myo-inositol accumulation in overwintering adults of a lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). Eur. J. Entomol. 99: 5-9.

Williamson, M., 1996. Biological Invasions. Chapman & Hall. London, UK.

Yarbrough, J.A., J.L. Amstrong, M.Z. Blumberg, A.E. Phillips, F. McGahee and W.K. Dolen, 1999. Allergic rhinoconjunctivity caused by *Harmonia axyridis* (Asian lady beetle, Japanese beetle, or lady bug). J. All. Clinic Immunol. 104: 704-709.

Yuan, R.C., F.M. Zhang, G.Z. Wen, M. Yu, X.Q. Wang and F.C. Ma, 1994. Investigation and research about the polymorphism of *Harmonia axyridis* in Changbai mountain of Jilin. Agric. Sci. 4: 45-54.

Zenyogi, S., 2008. Prediction of the time of flight for aggregation of *Harmonia axyridis* (Coleoptera Coccinellidae) in late autumn based on the concept of accumulation of exposure to low temperature. Jap. J. Entomol. 11: 159-167.

Zhao, J., L.Y. Yu, M. Li, F.Q. Zheng, F. Zhang and Y.Y. Xu, 2008. Seasonal variation in cold tolerance of the multicolored ladybeetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) adults. Acta Entomol. Sin. 51: 1271-1278.

Zhao, J., Z.Z. Chen, J.J. Qu, F. Zhang, X.C. Yin and Y.Y. Xu, 2010. Responses of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) adults to cold acclimation and the related changes of activities of several enzymes in their bodies. Acta Entomol. Sin. 53: 147-153.

**Table 1.** Geographic and demographic information for sampled villages. Population was recorded as the number of year-round residents in a village, obtained from the most recent local government records.

| County | Township | Village | Latitude | Longitude | Elevation (m ASL) | Population | Predominant Vegetation |
|---|---|---|---|---|---|---|---|
| Jiaohe | Xinnong | Xiashitouhezi | 43°39'N | 127°17'E | 264 | 130 | Corn fields |
| | | Banlawoji | 43°38'N | 127°16'E | 262 | 145 | Corn fields |
| | | Niu-a | 43°40'N | 127°17'E | 265 | 266 | Corn fields |
| | | Paoziye | 43°38'N | 127°16'E | 254 | 242 | Corn fields |
| | | Qijianfang | 43°37'N | 127°16'E | 275 | 185 | Corn fields |
| | Lafa | Minzhu-tun | 43°49'N | 127°23'E | 440 | 145 | Forest |
| | | Liangzi-tun | 43°47'N | 127°24'E | 309 | 113 | Forest |
| | Qingling | Xiadian | 43°43'N | 126°52'E | 353 | 262 | Scrubland |
| | | Erdaogou | 43°42'N | 126°52'E | 417 | 254 | Forest |
| | | Bei-liushugou | 43°45'N | 127° 02'E | 339 | 203 | Corn fields |
| Yongji | Jinjia | Dayanggo | 43°35'N | 125°57'E | 249 | 144 | Rice paddies |
| | | Hanjiago | 43°36'N | 125°59'E | 293 | 272 | Rice paddies |
| | | Huangqibao | 43°39'N | 125°59'E | 235 | 133 | Rice paddies |
| | Chaluhe | Xiwopeng | 43°43'N | 125°55'E | 200 | 260 | Rice paddies |
| | | Qian-baliqi | 43°42'N | 125°55'E | 203 | 140 | Corn fields |
| | | Hou-baliqi | 43°41'N | 125°57'E | 206 | 225 | Corn fields |

582

**Table 2.** Mean numbers (± SE) of *H. axyridis* adults collected in three hours of sampling from the outer walls of each of 10 houses in each of sixteen villages located in five different townships in Jilin Province, China, their phenotype ratios, sex ratios and the numbers observed within residences during a single mid-afternoon window observation (No. intrusive).

| Township | Village | No. beetles | Succinic: melanic | Female: male | No. intrusive |
|---|---|---|---|---|---|
| Xinnong | Xiashitouhezi | 402.9 ± 12.6 | 3.2 ± 0.7 | 2.3 ± 0.1 | 47.5 ± 3.0 |
| | Banlawoji | 364.3 ± 10.9 | 2.7 ± 0.6 | 2.0 ± 0.1 | 40.1 ± 2.2 |
| | Niu-a | 352.4 ± 15.3 | 3.1 ± 0.5 | 1.9 ± 0.1 | 38.2 ± 1.9 |
| | Paoziye | 447.2 ± 11.8 | 3.0 ± 0.8 | 1.5 ± 0.1 | 46.4 ± 2.2 |
| | Qijianfang | 495.7 ± 15.8 | 3.2 ± 0.4 | 1.5 ± 0.1 | 50.3 ± 2.1 |
| Lafa | Minzhu-tun | 617.7 ± 22.4 | 2.7 ± 0.5 | 1.9 ± 0.2 | 53.0 ± 2.7 |
| | Liangzi-tun | 465.1 ± 40.3 | 1.9 ± 0.3 | 1.9 ± 0.2 | 40.9 ± 4.1 |
| Qingling | Xiadian | 643.3 ± 24.2 | 6.5 ± 0.6 | 2.0 ± 0.1 | 131.2 ± 8.1 |
| | Erdaogou | 487.3 ± 28.3 | 2.5 ± 0.3 | 2.2 ± 0.1 | 47.1 ± 3.3 |
| | Bei-liushugou | 574.9 ± 29.5 | 2.9 ± 0.3 | 2.1 ± 0.1 | 64.5 ± 3.3 |
| Jinjia | Dayanggo | 401.3 ± 16.0 | 2.6 ± 0.2 | 2.1 ± 0.3 | 42.6 ± 1.6 |
| | Hanjiago | 308.4 ± 17.2 | 2.6 ± 0.6 | 1.7 ± 0.3 | 35.5 ± 2.1 |
| | Huangqibao | 402.9 ± 11.9 | 2.3 ± 0.4 | 2.1 ± 0.3 | 44.5 ± 1.6 |
| Chaluhe | Xiwopeng | 467.6 ± 22.2 | 3.5 ± 0.5 | 2.3 ± 0.1 | 51.2 ± 2.5 |
| | Qian-baliqi | 382.0 ± 14.8 | 2.8 ± 0.4 | 2.2 ± 0.1 | 39.3 ± 1.6 |
| | Hou-baliqi | 402.3 ± 16.9 | 2.4 ± 0.3 | 2.1 ± 0.1 | 40.8 ± 0.8 |
| Grand means | | 451.0 ± 8.8 | 3.0 ± 0.1 | 2.0 ± 0.05 | 50.8 ± 1.9 |

**Table 3.** Three-way ANOVA results for effects of landscape, elevation and human population density on the number of beetles obtained through direct collection in sixteen villages in Jilin Province, China.

| Source of variation | df | Mean square | *F* | *P* |
|---|---|---|---|---|
| Landscape | 3 | 88769.636 | 19.456 | < 0.001 |
| Elevation | 2 | 61170.441 | 13.407 | < 0.001 |
| Population density | 1 | 2.853 | 0.001 | 0.980 |
| Landscape × elevation | 1 | 333600.053 | 73.116 | < 0.001 |
| Landscape × population density | 1 | 10604.328 | 2.324 | 0.129 |
| Elevation × population density | 1 | 14245.004 | 3.122 | 0.079 |
| Landscape × elevation × population density | 0 | - | - | - |
| Error | 149 | 4562.642 | | |
| Total | 160 | | | |

**Table 4.** Three-way ANOVA results for effects of landscape, elevation and human population density on the number of beetles intrusive in residences in sixteen villages in Jilin Province, China.

| Source of variation | df | Mean square | *F* | *P* |
|---|---|---|---|---|
| Landscape | 3 | 12402.02 | 123.87 | < 0.0001 |
| Elevation | 2 | 335.54 | 3.35 | 0.038 |
| Population density | 1 | 339.00 | 3.38 | 0.068 |
| Landscape × elevation | 1 | 4423.68 | 44.12 | < 0.001 |
| Landscape × population density | 1 | 306.57 | 3.06 | 0.082 |
| Elevation × population density | 1 | 810.34 | 8.08 | 0.005 |
| Landscape × elevation × population density | 0 | - | - | - |
| Error | 149 | 100.27 | | |
| Total | 160 | | | |

Table 5. Summary of responses to survey questions by residents of rural villages in Jilin Province, China.

| Township | Village | N* | Major crops | Harvest dates | Date of *H. axyridis* urban appearance | Date of *H. axyridis* disappearance | Are beetles a nuisance in your home? (% "yes" answers) |
|---|---|---|---|---|---|---|---|
| | Xiashitouhezi | 92 | corn & rice (80)<br>vegetables (12) | corn: 12 – 18 September<br>rice: 13 – 27 September | 17 – 27 September | 1 – 5 October | 98.9 ± 1.09 |
| | Blanlawoji | 84 | corn & rice (82)<br>ornamentals (2) | corn: 13 – 18 September<br>rice: 13 – 26 September | 15 – 23 September | 1 – 5 October | 95.2 ± 2.33 |
| Xinnong | Niu-A | 98 | corn & rice (76)<br>vegetables (22) | corn: 13 – 17 September<br>rice: 13 – 26 September | 17 – 26 September | 2 – 5 October | 100.0 |
| | Paoziye | 100 | corn & rice (90)<br>vegetables (10) | corn: 14 – 17 September<br>rice: 13 – 26 September | 15 – 28 September | 1 – 6 October | 100.0 |
| | Qijianfang | 94 | corn & rice (83)<br>vegetables (11) | corn: 12 – 17 September<br>rice: 13 – 27 September | 16 – 24 September | 1 – 5 October | 98.9 ± 1.08 |
| Lafa | Minzhu-tun | 88 | corn & rice (13)<br>medicinal herbs (75) | herbs: 4 – 21 September | 17 – 27 September | 1 – 2 October | 97.7 ± 1.60 |
| | Liangzi-tun | 95 | corn & rice (11)<br>ginger (84) | herbs: 3 – 24 September | 19 – 26 September | 1 October | 100.0 |
| | Xiadian | 95 | corn & rice (10)<br>vegetables (85) | vegetables: 15 – 18 September | 17 – 27 September | 1 October | 95.8 ± 2.06 |
| Qingling | Erdaogou | 98 | corn & rice (15)<br>medicinal herbs (83) | herbs: 10 – 18 September | 13 – 14 September | 1 – 2 October | 100.0 |
| | Beiliushugou | 80 | corn & rice (7)<br>medicinal herbs (73) | herbs: 11 – 15 September | 15 – 19 September | 1 – 2 October | 100.0 |
| | Dayanggou | 88 | corn & rice (78)<br>vegetables (10) | corn: 10 – 16 September<br>rice: 14 – 27 September | 14 – 25 September | 1 – 4 October | 92.0 ± 2.89 |
| Jinjia | Hanjiagou | 95 | corn & rice (76)<br>ornamentals (19) | corn: 9 – 14 September<br>rice: 16 – 27 September | 12 – 23 September | 1 – 4 October | 97.9 ± 1.47 |
| | Huangqibao | 104 | corn & rice (85)<br>ornamentals (19) | corn: 10 – 15 September<br>rice: 14 – 27 September | 12 – 23 September | 2 – 5 October | 98.1 ± 1.34 |
| | Xiwopeng | 89 | corn & rice (69)<br>ornamentals (30) | corn: 13 – 16 September<br>rice: 17 – 27 September | 12 – 23 September | 2 – 5 October | 100.0 |
| Chaluhe | Qian-baliqi | 87 | corn & rice (79)<br>vegetables (8) | corn: 11 – 16 September<br>rice: 14 – 27 September | 13 – 23 September | 1 – 3 October | 97.7 ± 1.61 |
| | Hou-baliqi | 94 | corn & rice (86)<br>vegetables (8) | corn: 14 – 18 September<br>rice: 13 – 27 September | 12 – 23 September | 1 – 4 October | 100.0 |

* = no. respondents.

**Figure 1.** Map of Jilin Province, PRC, showing location of villages where *H. axyridis* aggregations were observed and sampled.

QuickTime™ and a
decompressor
are needed to see this picture.

**Figure 2.** Diagram of sampling board (1.0 $m^2$) used for direct collection of aggregating *H. axyridis* adults. The triangular black regions in opposite corners were 40 x 40 x 57 cm (800 $cm^2$), and the two gray trapezoidal regions directly adjacent to them were each 736 $cm^2$ in area. Beetles were collected with a small hand-held insect net as they passed through the trapezoidal regions.

QuickTime™ and a
decompressor
are needed to see this picture.

**Figure 3.** Diagram showing dimensions and design of the traps used to catch aggregating *H. axyridis* adults. Traps were constructed of wood with a hinged floor to facilitate removal of beetles. The exterior roof and wall surfaces were painted different colors or modified with different surface textures to test for effects on trap catches (see text for details). The relative attractiveness of various food baits was tested in white traps.

QuickTime™ and a
decompressor
are needed to see this picture.

**Figure 4.** Mean (+SE) numbers of *H. axyridis* adults caught in traps of different colors. Means bearing the same letters were not significantly different (Fisher's LSD, $\alpha = 0.05$).

QuickTime™ and a
decompressor
are needed to see this picture.

**Figure 5.** Mean (+SE) numbers of *H. axyridis* adults caught in traps baited with different food resources. Means bearing the same letters were not significantly different (Fisher's LSD, $\alpha = 0.05$).

QuickTime™ and a
decompressor
are needed to see this picture.